ASPECTS OF THE ENERGY AND WATER METABOLISM IN THE ROCK HYRAX *PROCAVIA CAPENSIS* AND THE ELEPHANT SHREW *ELEPHANTULUS EDWARDI*

by

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ABSTRACT

Aspects of the energy and water metabolism in the rock hyrax *Procavia capensis* and the elephant shrew *Elephantulus edwardi*

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In three digestion trials the energy intake and assimilation of the hyrax *Procavia capensis* was evaluated. Energy intake was low but the efficiency of energy assimilation was within the range found for other herbivores. Thus the metabolizable energy intake (312,3 $kJ.kg^{-0,75}.day^{-1}$) was low but commensurate with the low basal metabolic rate of the hyrax (0,27 $ml O_2.g^{-1}.h^{-1}$). The increment in energy cost of free existence over the basal metabolic rate was 1,83 which suggests a low energy expenditure for free-living hyraces. The digestibility of the different food components was affected by the crude fibre content of the food, but the hyrax was able to digest crude fibre effectively by virtue of the fermentation systems in three major areas of the alimentary tract. Fermentation in the cardiac portion of the stomach resembled silage fermentation with the predominance of acetic and lactic acids. The expanded regions of the large intestine contained volatile fatty acids in similar proportions and concentrations to those found in the typical herbivore rumen or caecum. The high glucose levels in the plasma and the high proportions of unsaturated fatty acids in the depot

fat, however, precluded the hyrax from the group of ruminant-like mammals.

The unusual occurrence of a calcium carbonate precipitate in the urine of the hyrax prompted an investigation of the pathways of excretion of calcium, phosphorus and magnesium using two balance trials. The renal pathway played a major role in calcium excretion suggesting an efficient absorptive mechanism for this element in the gastro-intestinal tract. Phosphorus was excreted mainly through the gastro-intestinal tract but the major route for magnesium excretion was uncertain. Excretion of all three elements was diet-dependent.

The water metabolism of hyraces exposed to natural climatic conditions was investigated using tritiated water. The water turnover rate was lower than predicted for its size (85,1 $mlH_2O.kg^{-0,8}.day^{-1}$) and declined still further when the animals were dehydrated. The water requirements of the hyrax can be met by the water contained in the food in a wet season, but in a dry season the animals would have to select vegetation with a high moisture content or reduce the water turnover rate and tolerate a reduction in mass. The low water turnover rate of the hyrax is associated with the low basal metabolic rate, the avoidance of extreme temperatures and efficient renal function. The latter also allowed for the conservation of essential ions within the body and contributed to the maintenance of a stable plasma osmolality on dehydration.

Both the extensive use of behavioural thermoregulation and the inactive

lifestyle of the hyrax contributed to the low energy expenditure of the hyrax. Physiological regulation, however, could maintain the body temperature constant at 37,2°C even at low ambient temperatures in the laboratory. In the field, though, the hyrax increased its body temperature to a higher level during the day through the exploitation of solar radiation while basking. Shuttling between the sun and shade then kept the body temperature fairly stable at this higher level. In the absence of solar radiation at night, the body temperature dropped by *ca.* 2°C even when the animals were huddled together in a crevice. Because of the increased air temperature in a crevice occupied by several animals, the oxygen consumption and thermal conductance of huddled animals was lower than in single animals. Cold-adapted hyraces showed no significant response to nor-adrenaline administration and therefore non-shivering thermogenesis does not appear to be an important mechanism of heat production in the cold.

In contrast, in the elephant shrew *Elephantulus edwardi*, the increased heat production during non-shivering thermogenesis accounted for all of the metabolic heat produced at low ambient temperatures. This small insectivorous mammal was able to maintain a stable body temperature of 37,6°C over a wide range of ambient temperatures. At the thermoneutral zone between *ca.* 33 to 36°C its resting metabolic rate was 1,09 $ml O_2.g^{-1}.h^{-1}$, which was lower than predicted for its mass. Thermal conductance below thermoneutrality was as predicted from its mass and evaporative water loss at these temperatures was stable (2,02 mg $H_2O.g^{-1}.h^{-1}$). At high ambient temperatures, evaporative

water loss increased but not enough to dissipate all the metabolic heat produced. The low water turnover rate of the elephant shrew (between 6,4 and 7,5 ml $H_2O.day^{-1}$) would allow the animal to survive on an insectivorous diet without additional drinking water. When dehydrated the elephant shrew was able to increase the osmolality of the urine to 3118 $mosm.kg^{-1}$ with an increased concentration of urea and electrolytes.

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SECTION 1

GENERAL INTRODUCTION

This study is concerned with two unusual African mammals, the rock hyrax *Procavia capensis* Pallas 1766 and the elephant shrew *Elephantulus edwardi* Smith 1839. Both belong to families (Procaviidae and Macroscelididae respectively) which are endemic to Africa (Bigalke, 1972) and the order of the hyraces, Hyracoidea is considered by Keast (1972) to be one of the two endemic orders of Africa. The paucity of mammalian fossils prior to the Upper Eocene (Cooke, 1972) prevents a clear picture of the early evolution of these two families, though ancestral fossil forms of both have been found in the early Oligocene deposits of the Egyptian Fayum area. Thus they are indeed old elements of the contemporary African fauna. It is perhaps because of their ancient lineages, the sparse fossil record of the early African mammals and their unusual morphology - aspects which are discussed further in this section, that the affinities of the two groups to extant mammals were uncertain until fairly recently. However, even today the taxonomy of the elephant shrews is a controversial issue.

The hyrax, commonly called the dassie or rock rabbit in South Africa, is a medium sized, herbivorous mammal often seen in rocky areas, basking in groups in the sun. They are extremely successful animals in South Africa, to the extent of being considered vermin since they compete directly with sheep for food (Hanse, 1962; Kolbe, 1967). The elephant shrews, sometimes called the jumping shrews (Fitzsimons, 1920) are small insectivorous mammals with an elongated snout, as the name implies, and with large eyes and ears and a long tail. Unlike the hyrax, they are more active, solitary animals, rarely seen in the rocky areas they inhabit.

in the remainder of this section where the evolution, taxonomy and general life history aspects have been discussed in greater detail, the hyrax and the elephant shrew have been separated for ease of explanation and reading.

1.1 THE HYRAX *PROCAVIA CAPENSIS*

1.1.1 Evolution

Scholars in natural history and zoology have been intrigued by the hyrax since the eighteenth century. Since then, the systematic position of this animal among the mammals has been controversial, owing to its anomalous assemblage of morphological features. In 1766, Pallas gave the hyrax the generic name *Cavia* thus linking it to the guinea-pig and the rodents. Indeed, the rabbit-like size and shape of the hyrax, its short legs, rudimentary tail, small rounded ears and prominent incissors do bear some outward similarity to the guinea-pig. Storr (1780), however, renamed the genus *Procavia* recognising the generic error of Pallas, but the systematic position of the hyrax within the Rodentia was questioned only after Cuvier (1884) had examined the skeletal structure. He placed it together with the hippopotamus and rhinoceros under the Pachydermata, and therefore of ungulate origin, a classification based on the similarities in tooth structure. Subsequently it was placed with the Perissodactyla, but as additional, conflicting information became available on the placentation and embryology of the hyrax, Milne-Edwards and Huxley

(from George, 1874) placed the animal in an order of its own, the Hyracoidea. The new order was allied to the Proboscidea and the Sirenia under the superorder Subungulata or Paenungulata (Simpson, 1945), a systematic position which is retained today. This classification is based on similarities in skeletal and anatomical structures, between the elephants, manatees, dugongs and the hyraces. Common to the three orders of the Subungulata are the presence of four or more pedal digits which are in close conjunction, except for the distal phalanges. These terminate with poorly developed hoofs which appear rather like nails. Other skeletal features in common are elements in the skull, the enlarged, separated incisors and the molarised character of the premolars which have cross-lophs for grinding (Romer, 1966). All three groups are true testicond mammals and the placental and foetal membranes show structural similarities (Wislocki, 1928; Wislocki and van der Westhuysen, 1940). Weitz (1953) has also shown a serological relationship between the hyrax (*Heterohyrax brucei prittwitzi*) and the Indian elephant (*Elephas elephas*), while Buettner-Janusch *et al.* (1964) have noted similarities in the plasma proteins and haemoglobins of the African elephant and the hyrax, further supporting their taxonomic relationship.

Incongruous as it may seem to link mammals of such disparate sizes and habitats, the relationship is supported by the fossil records of the three orders, which date back to the Upper Eocene and early Oligocene, some 35 million years ago. In Africa, the earliest Tertiary mammals were apparently dominated by the subungulate orders of the Hyracoidea, Proboscidea and Embrithopoda (large mammals

outwardly resembling the rhinoceros, but now extinct), with Sirenians present but not as numerous (Cooke, 1972). By the Oligocene, the hyracoids had already radiated or adapted into different ecological niches, three African fossil families being recognised and comprised of six genera and 24 species (Matsumoto, 1926). The diversity of size and form of the early hyracoids was far greater than those of today, ranging from the large *Titonohyrax* larger than a domestic pig, to *Saghatherium*, the size of extant *Procavia* (Cooke, 1972). Subsequently however, their abundance declined, possibly due to increasing competition from the artiodactyls, rodents and lagomophs or from increasing numbers of predators (Cooke, 1972). Nevertheless, even until the fairly recent Pleistocene epoch (beginning three million years ago) the hyracoids retained their diverse sizes and therefore must have successfully withstood the impact of successive groups of competitors. Kitching (1966) has described three coexisting hyracoid species from the Pleistocene deposits in the dolomite caves at Makapansgat, South Africa. These range in size from that of the present day *Procavia* species to *Gigantohyrax maguirei*, three times larger. Some later selection pressure must have favoured the success of the smaller hyracoids since only these are present today. Possibly this took the form of predation by large carnivores or the hunting activities of primitive man, which the small forms could avoid by retreating into rock crevices, inaccessible to both the larger hyraces and the predators or hunters. Although there is some size differentiation among the genera of the Hyracoidea today, it is by no means as marked as in the Pleistocene and only one family, the Procaviidae, is still retained, incorporating all the living genera.

1.1.2 Taxonomy and distribution

The revision of the taxonomy of the Procaviidae by Bothma (1971) clarified some of the confusion which existed previously (Ellerman & Morrison-Scott, 1951; Roberts, 1951; Ellerman *et al.*, 1953; Bothma, 1964). This unenviable task could not have been easy, given the large variation in appearance within a single species in any one area. The three genera *Procavia*, *Heterohyrax* and *Dendrohyrax* recognised prior to Bothma's (1971) revision, have been retained by him with a total of eleven species (*Procavia* - five, *Heterohyrax* - three, *Dendrohyrax* - three) each with several subspecies.

Of the three genera, *Procavia* has the widest distribution occurring throughout southern Africa and extending through most of Africa up to Syria and Israel (Fig. 1.1). Generally this genus appears to prefer drier regions, particularly evident if one compares its distribution shown in Fig. 1.1 with that of the "drought corridor" (Fig. 1.2) - an area with a monthly rainfall of less than 10 mm for three consecutive months (Balinsky, 1962). Although Ellerman and Morrison-Scott (1951) have made the interesting suggestion that there is only one species of *Procavia* which varies clinally from the Cape (34°S) to the Lebanon (34°N), I have accepted Bothma's (1971) classification of the genus here. Thus *Procavia capensis*, the species under study, occurs throughout southern Africa, from South Africa to Zimbabwe, north-eastern Botswana and Namibia (South West Africa) excluding the Kaoko-veld (Bothma, 1971). Within these areas are desert, semi-desert, steppe, savannah, riparian, montane forest and Cape Macchia (Fynbos)

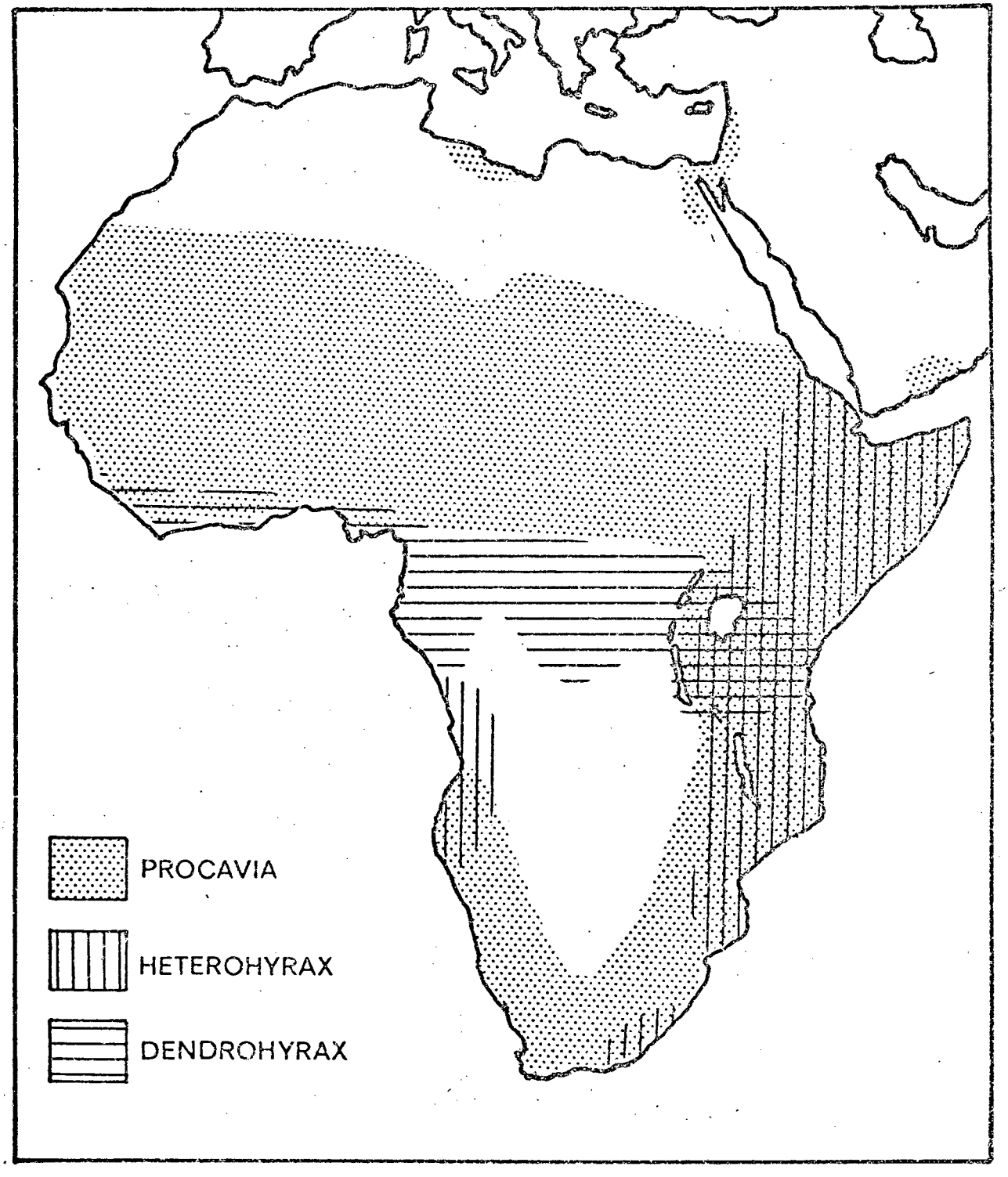

Fig. 1.1 Recorded distribution of the three genera of the Hyracoidea. (From Sale, 1960)

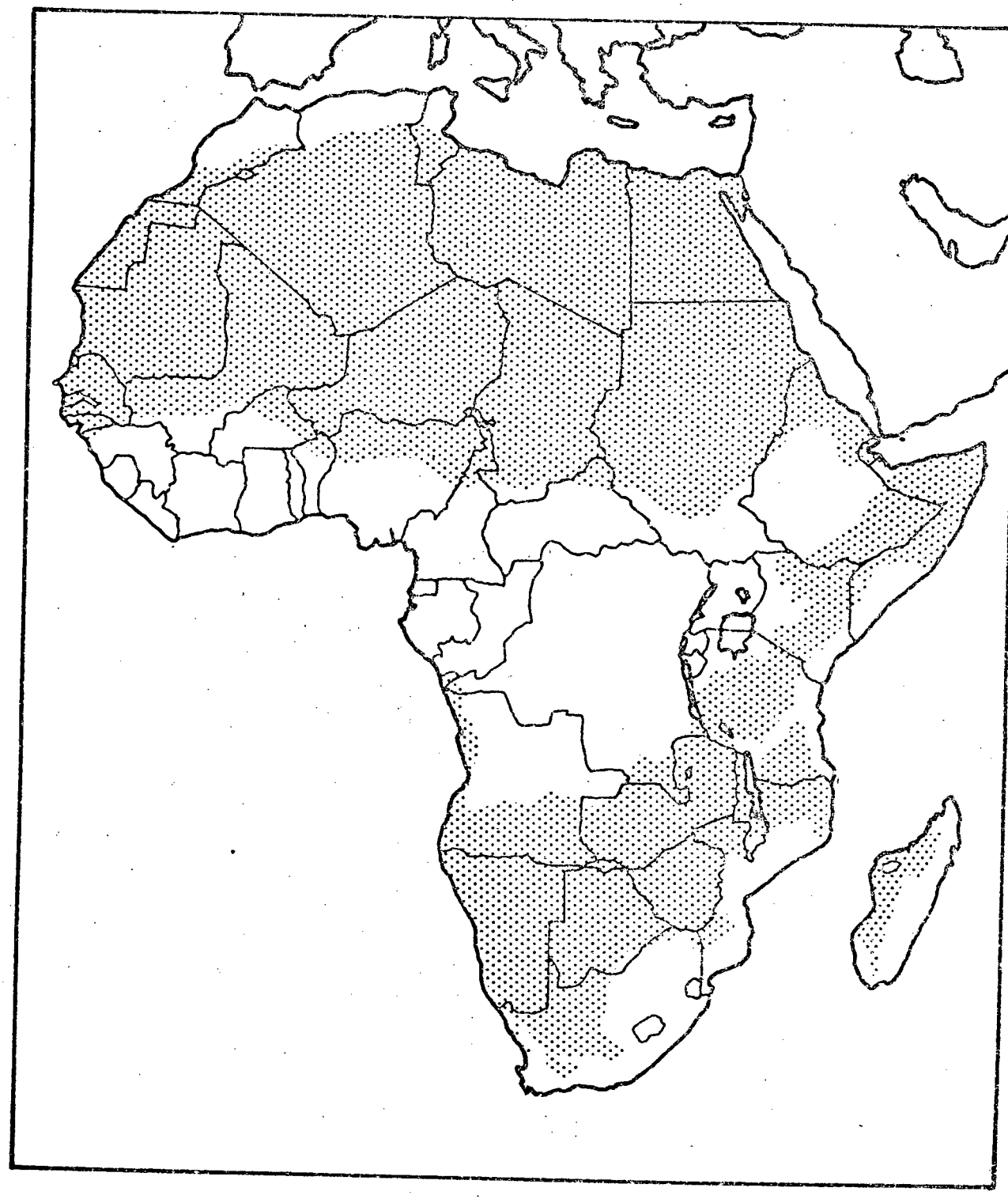

Fig. 1.2 Map of Africa showing the areas (stippled) in which the rainfall is less than 10 mm per month in at least three consecutive months. (From Balinsky, 1962)

vegetation, with climatic conditions as varied as the vegetation types.

Heterohyrax has a more restricted distribution along the eastern part of Africa (Fig. 1.1), though one species is also found in southern Algeria and the central Sahara. The most southerly extent of this genus is in the more humid parts of the northeastern Transvaal of South Africa and the most northerly, the Red Sea coastal mountains of Egypt (Bothma, 1971). *Heterohyrax* may prefer moister habitats than *Procavia*, which would partly explain their restricted distribution. *Procavia* and *Heterohyrax* however, do occur sympatrically in some areas of their distribution, even to the extent of sharing the same rock crevices, basking sites and using the same urinary and defecating places.(Turner & Watson, 1965; Hoeck, 1975). *Dendrohyrax*, with its tree-dwelling habitat, is restricted to forest regions particularly around the equator, though it does extend south to the evergreen forests of the eastern Cape Province of South Africa (Fig. 1.1)

1.1.3 Habitat, habits and morphological adaptations

The earliest written reference to the habitat of the hyrax comes from the Old Testament where the animal is called the "coney". In Proverbs 30: 26 and again in Psalms 104: 18 the rocks and cliffs are referred to as the "houses" or "refuge for the conies". Both *Procavia* and *Heterohyrax* do indeed occupy a rock-dwelling niche in the numerous koppies (rock outcrops) throughout Africa or in the kloofs or ravines in the mountainous areas where rock outcrops or boulder scree are present. They are gregarious diurnial herbivores, utilising

the rock crevices as retreats. Although both genera are referred to as rock hyraces, *Heterohyrax* is also called the bush hyrax (Roche, 1962; Hoeck, 1975) because of its tendency to browse as opposed to the grazing habit of *Procavia* (Turner & Watson, 1965). This distinction is unwarranted however, since *Procavia* also browses, at least seasonally in East Africa when grasses are unavailable (Sale, 1965a; Hoeck, 1975) and both grazes and browses when grasses are available in the Cape (personal observations). *Dendrohyrax*, the tree hyrax, differs markedly from the rock hyraces, being a solitary, nocturnal and arboreal form which shelters in hollow tree trunks within the forest habitat (Roberts, 1951; Sale, 1960). Little information on the habits and habitat of the tree hyrax is available, however, and since this study is concerned with *Procavia capensis* the rest of this discussion has been centred on the rock hyraces.

The koppie and rock crevice habitat together provide an equable environment for the hyraces in many ways. While the koppie is a specialised habitat in itself, acting as a natural water catchment system which promotes the growth of vegetation (Turner & Watson, 1965), the rock crevices provide a microclimate where temperatures and humidity fluctuations are less extreme than in the outside environment (Sale, 1966a; Turner & Watson, 1965). Where the shelters are in mountainous regions, Norton (1980) found that in the Cape, *Procavia* showed a marked preference for dry rocky slopes. Whether the slopes were selected because of the lower moisture levels was not established. Moisture levels may have been coincidental to site selection based on other criteria, such as hours of illumination, prevailing wind direction

or even the availability of palatable food. Sale (1966a) has shown that the hyraces tend to select crevices or holes which are either protected from or do not face the prevailing wind. Site selection undoubtedly depends on a variety of factors, some of which have been elucidated by Sale (1966a). As he states, "it is difficult to define a 'typical' hyrax habitat in terms of environmental necessities" possibly because of the apparent flexibility with which the animals can adapt to a new site, the major criteria for selection being "protection from the elements and predators" (Sale, 1966a). Hyraces have been known to use abandoned burrows of other mammals and even road culverts and stone walls as retreats, but this seems to be an unusual occurrence (Thomas, 1946; Roberts, 1951; Sale, 1966a). Under more natural circumstances particular rock crevices are not used permanently and a hyrax colony frequently moves to a new series of rocks and crevices, albeit within the general area of those used previously. Sale (1965a) suggests that these small migratory movements are made for the purpose of finding new vegetation since they take place less frequently during the rainy season when vegetation is abundant.

The presence of Pleistocene fossil *Procavia* in the Makapansgat areas (Kitching, 1966) suggests that hyraces have inhabited a rocky terrain for some 3 million years. Moreover, specific morphological adaptations of these animals appear to have evolved in association with a rock crevice habitat. In particular are tactile vibrissae which are generally distributed over the body surface giving the animal complete tactile coverage, and a gland on the dorsal surface of the back,

surrounded by erectile hairs. The function of the former in a crevice-dwelling animal is obvious, and Sale (1970b) has suggested that the secretion of the dorsal gland may serve as an olfactory identification for individual animals, huddling on top of each other, within the dark rock crevices. An additional adaptation to the rocky habitat are the thick rubbery soles of the plantigrade feet which undoubtedly contribute to the agility of the rock hyrax in gaining purchase on steep rock faces.

1.1.4 Activity and feeding behaviour

The Xhosa people of South Africa have an idiom and explanatory fable which, aside from the moral message, conveys a general impression of the degree of activity shown by the dassie or hyrax. It goes as follows:

> The great day arrived when all the animals in the land were to receive their tails. Eagerly, they set off early so as to reach the selected place in time. Only the dassie was not excited. He yawned lazily and sank back on his rock, basking in the warmth of the sun. He watched the other animals passing by, but rather than join them, asked the jackal to accept a tail on his behalf. The jackal smiled slyly and agreed. At the appointed time and place, each of the animals received their tails with delight. Amongst them was a short, fluffy tail for the rabbit, a long fat tail for the lizard and a beautiful bushy tail for the jackal. When the dassie was called, the jackal dutifully accepted the tail but rather than carry it all the way back, he ate it.

Thus "Imbila yaswela umsila ngokuyalezela"

- The dassie has no tail because he sent for it.

(Traditional folk-lore)

Field observations confirm the generally inactive life of the hyrax with much of the day spent basking in the sun on an exposed rock, resting in the shade of the bushes and rock crevices or shuttling between the sun and shade (Sale, 1965a; 1970a; Turner & Watson, 1965). Sale (1970a) has shown that only approximately 5 per cent of the day is spent in an active state, but this increases during the mating season. Juveniles are generally more active than the adults, however.

The daily pattern of activity appears to be remarkably constant and is shared by all species of rock hyraces thus far studied, with only minor variations (Sale, 1965a; 1970a; Turner & Watson, 1965; Hoeck, 1975). They emerge from the deep crevices with first light and begin basking, in close contact with each other on exposed rock faces which catch the rays of the sun. Slowly the group disperses as the sun rises, individual animals taking up solitary positions scattered over the rocks. One to three hours after sunrise the whole colony gradually descends to the vegetation and begins feeding in small groups (Hoeck, 1975; personal observations), usually within 50 m of the rock crevices (Sale, 1965a). This group feeding activity lasts from 20 minutes (Sale, 1965a) to two hours (Hoeck, 1975) and often while the colony is feeding, one or two adults act as sentinels on a high rock, presumably watching for predators. At the end of the

feeding period, the animals either return to basking or rest in the shade of the bushes and rocks. Thereafter, they alternate between basking and resting in the shade until approximately midday when air temperatures are maximum. Intense solar radiation is thus avoided and only in the cooler hours of the afternoon basking is resumed. A second group feeding period takes place roughly three hours before sunset and appears to be the more pronounced and longer of the two. Generally the hyraces return to the deep crevices soon after sunset and remain there until morning. On moonlit nights, however, some may emerge to feed sporadically (Coe, 1962; Turner & Watson, 1965; Fourie, 1978). Apart from the group feeding periods, individuals may feed casually at any time of the day, nipping off a few leaves or shoots and returning to their former positions (Sale, 1965a). Rain and strong winds disrupt the described activity pattern, inhibiting basking and group feeding. Hyraces have been known to stay within the crevices for three days under adverse climatic conditions (Coe, 1962; Hoeck, 1975).

1.1.5 Unusual aspects of digestion and the digestive tract

Although the short feeding periods of the hyrax limit the amount of food that can be eaten, this is offset to some extent by the intensity and rapidity of prehension, facilitated by the long cutting edge of the molar and premolar tooth row (Sale, 1966b). The use of this lateral tooth row for biting leaves off bushes is an unusual characteristic of the hyrax (Sale, 1966b). It has been shown, however, that despite the rapidity of feeding, the East African hyraces *Provacia*

johnstoni mackinderi and *Procavia habessinica* consume a small amount of food, relative to their size (Sale, 1966b; Hume *et al.*, 1980). From one feeding period to the next, food can be stored in the proximal cardiac region of the stomach, an expansible sac lined with keratinized epithelium (Elias, 1946). Here anaerobic fermentation of the ingesta takes place (Clemens, 1977; von Engelhardt *et al.*, 1979). It has been suggested that the hyrax may be considered a ruminant-like mammal (Moir, 1968) since it does have an unusual digestive tract which incorporates, in addition to the large, partitioned stomach, two caecae (Owen, 1832; Grassé, 1956) the most distal one bearing two horn-like appendices. Allusions to rumination by the hyrax in the Old Testament (Leviticus 11: 5) and by Hendrichs (1963) have not been verified and probably refer to the grinding of the molar teeth when captive animals are disturbed. Apart from the fermentation system in the gut, another ruminant-like character of the hyrax is the ability to recycle urea (Hume *et al.*, 1980). Urea recycling, however, does occur in other non-ruminants such as the horse (Prior *et al.*, 1974) and rabbit (Regoeczi *et al.*, 1965), and more information on the digestive physiology is necessary before associating the hyrax with ruminant-like mammals.

1.1.6 Social organisation and reproduction

The size of the hyrax colony varies from 6 to 100 individuals depending on the availability of suitable shelters (Sale, 1966a; Glover & Sale, 1968; Hoeck, 1975). The basic unit of the colony is a family group of 6 to 19 animals comprised of one territorial male, several adult

females and their young (Coe, 1962; Sale, 1965b; Hoeck, 1975). The social organisation of large colonies is not well known and may differ with geographical location in keeping with the differences in mating and parturition seasons from high to low latitudes (Millar, 1971; Millar & Glover, 1973). In the southernmost areas of South Africa (34°S) the mating season is restricted to February but occurs later in the year with decreasing latitude. The Syrian hyrax *Procavia syriacus*, however, mates in August-September, six months out of phase with the Cape hyrax which would be expected from the similar latitude north of the equator (Mendelssohn, 1965). Millar and Glover (1973) have shown that the rate of decrease in photoperiod acts as an environmental cue inducing the enlargement and activation of the testes, thus regulating the timing of the mating season. The single mating season at high latitudes does not apply to hyraces near the equator and in Kenya, Glover and Sale (1968) have noted sexually active and quiescent males throughout the year. Since the changes in photoperiod are relatively small near the equator, Millar and Glover (1973) have suggested that other environmental cues such as temperature or rainfall may be more important factors triggering sexual activity.

The gestation period of all species, however, is 7,5 to 8 months, unusually long for an animal of this size (van der Horst, 1941; Murray, 1942; Roche, 1960; 1962; Mendelssohn, 1965; Sale, 1965c; Millar, 1971) and the precocious young are born in litters of one to six, but three to four is the more usual number. They are weaned at about three months of age but within two weeks of birth begin taking in some vegetation (Mendelssohn, 1965; Sale, 1965b; Millar, 1971).

In *P. capensis* and *P. syriacus* sexual maturity is reached after 16 to 17 months (Mendelssohn, 1965; Millar, 1971) but other species may vary in this respect (O'Donoghue, 1963; Sale, 1969).

The social structure of the Syrian hyrax described by Mendelssohn (1965) probably also applies to *P. capensis*. During the mating season, *P. syriacus* females form polygynous herds associated with a single male and the young of the previous mating season. This group probably constitutes the family unit observed by the authors mentioned above. Other adult males form bachelor herds during this season, but in winter when the testes are quiescent and the females are gravid, there is greater intermingling of the two sexes and gregarious behaviour is more pronounced. After parturition the young form nursery groups either with several adult females (probably the mothers), or with only one or two females (Hahn, 1959; personal observations). Glover and Sale (1968) have suggested essentially the same social structure for *P. habessinica* in Kenya, though they describe three classes of males:- males with harems of females; lone males which have separated from the gravid females of the harems but rejoin them after the nursery period; males which form bachelor herds. These three classes probably exist concurrently, given that there is no specific mating season.

The dorsal gland and the surrounding erectile hairs or dorsal spot should be mentioned here, since they appear to have a sexual and social function. The maximal activity of the gland has been noted in sexually active adult male and female hyraces and is thus probably as

important in courtship behaviour, as is the full erection of the surrounding hairs (Sale, 1970b). The gland is only rudimentary in juvenile animals, and Sale (1965b) has suggested that the secretion by adult females may serve to establish an olfactory bond between the new-born young and the mother.

Partial erection of the dorsal gland hairs, however, is a signal of alarm and threat which can be directed towards other animals or serve as a warning to the group (Sale, 1970b). This occurs more frequently during group feeding or when first emerging from the crevices. It should be noted that the functions of the dorsal spot described above are for *P. johnstoni* in which the hairs are pale in colour and visually obvious. My own observations of *P. capensis*, which has a black dorsal spot, confirm that the erection of the hairs is most obvious when feeding and when the animals first emerge and that this behaviour appears to be associated with threat or aggression. Whether or not the erection of the dorsal spot specifically acts as a visual stimulus for other hyraces within the colony has not been firmly established.

Since the Ahaggar dassie of southern Algeria, *Heterohyrax antinae*, lacks a dorsal spot (Bothma, 1971) the interpretation of its function in social behaviour must be viewed with caution until further knowledge is gained.

1.1.7 Predation

Rock hyraces are particularly susceptible to predation because of their relatively small size and their habits of basking and feeding in exposed situations. The major potential predators are larger carnivorous mammals and birds of prey which are associated with rocky or mountainous environments. The most common of the former are the lynx (*Felis caracal*) and black-back jackal (*Canis mesomelas*) particularly common in the open koppie terrain of the Karroo regions while in the more mountainous areas, the leopard (*Panthera pardus*) is prevalent. Several other potential mammalian predators have been mentioned by Hanse (1962) of which the African wild cats predominate.

Of the avian predators, several eagles and particularly the Black eagle (*Aquila verreauxi*) and Martial eagle (*Polemaetus bellicosus*) are known to prey extensively on hyraces (Roberts, 1951; McLachlan & Liversidge, 1978). The Cape Eagle owl (*Bubo capensis*) preys on hyraces, possibly when the animals come out of the crevices on moonlit nights, though this owl has been reported to be somewhat diurnal (McLachlan & Liversidge, 1978) and may therefore, also take them during the day.

Since the hyraces are relatively defenceless when attacked by the larger predators, the primary response to the presence of an intruder is to seek refuge in the inaccessible rock crevices. During the periods of exposure such as basking and feeding, however, one or two of the adults occupy an elevated position with a clear view of the

surroundings. These sentinels more often than not, provide adequate warning of a possible predator. Sighting of Black eagles or other raptors, which tend to attack from out of the sun, is thought to be facilitated by the presence of a light-shielding extension of the iris diaphram, the umbraculum, which allows the hyraces to stare into the sun (Millar, 1973). Stoddart (personal communication), however, has observed these eagles hunting in pairs and while one of the pair flies above the hyrax colony, distracting them, the second attacks unexpectedly from ground level.

Smaller predators which may enter the rock crevices are unlikely to overcome an aggressive adult hyrax which can inflict a serious wound with the sharp upper incisors. Hanse (1962) has noted that the Cape cobra (*Naja nivea*), puff adder (*Bitis arietans*) and the python (*Pyton sebae*) prey on hyraces and certainly these snakes can gain entrance to the small crevices.

1.1.8 Energy metabolism and thermoregulation

Research on the energy metabolism and thermoregulation of the hyrax has undoubtedly been prompted by the unusually inactive and heliotropic behaviour of the animals. These characteristics and the low daily intake of food do indeed suggest an economical energy expenditure. If one considers that a large portion of the energy expenditure is directed towards maintaining a stable body temperature in mammals (assuming an inactive state), then behavioural thermoregulation can be regarded as a means of saving energy normally expended in physiological

control of body heat losses and gains. In the case of the hyrax, the social grouping patterns viz. heaping, huddling and solitary resting, categorised respectively by a progressive decrease in physical contact between the animals, seem to be correlated with progressive increases in air temperature (Sale, 1970a). For example, with low air temperatures, the hyraces form a heap or huddle together, groupings which maximise the contact between several individuals. These formations are usually adopted within the crevices at night, or on cold mornings when the animals first emerge from their holes (Sale, 1970a). Solitary resting, however, can be observed while the animals bask in the sun around mid-morning, and as the name implies, involves no physical contact between individuals. These patterns of social behaviour as well as the habit of shuttling between the sun and shade, suggest that temperature regulation may be achieved predominantly by behavioural means - unusual for a mammal.

Several studies have shown that the body temperature of the hyrax is labile and that the metabolic rate is lower than predicted (Taylor & Sale, 1969; Sale, 1970a; Meltzer, 1971; Bartholomew & Rainy, 1971; Louw *et al.*, 1973; McNairn & Fairall, 1979; Rubsamen *et al.*, 1979; Rubsamen & Kettembeil, 1980). Several of these studies are contradictory, however, particularly those on *P. capensis* (Taylor & Sale, 1969; Louw *et al.*, 1973; McNairn & Fairall, 1979). In the comparative study of Taylor & Sale (1969), it is clear that there are marked differences between different species of hyraces from different habitats with respect to the physiological factors mentioned above. In view of the paucity and conflicting information on the energy

metabolism and temperature regulation of *P. capensis* it seemed worthwhile to examine these aspects in the present study. Furthermore, as yet no information is available on the effect of huddling on these parameters in any species of *Procavia*. The only work in this regard has been on *Heterohyrax brucei* by Bartholomew and Rainy (1971). These authors recorded a diurnal change of 2°C in the body temperature of an adult in semi-natural surroundings. The highest body temperature was recorded while it basked and the lowest at night while huddling with others.

In the present study, the energy metabolism of the hyrax *P. capensis* has been approached in two ways - that is examination of aspects of the energy intake and energy expenditure. With respect to the former, the food intake, its assimilation and the fermentative process in the alimentary tract was studied. Energy expenditure has been examined in terms of the effects of air temperature on oxygen consumption and body temperature and how these are affected by the behaviour of the hyrax. Furthermore, the apparent susceptibility of hyraces to winter conditions (Mendelssohn, 1965; Millar, 1972) deserved attention and the thermal responses of the animal to cold adaptation was examined.

1.1.9 Water metabolism

Survival in an arid environment where drinking water is often unavailable, necessitates physiological and behavioural adaptations geared towards water conservation. Over the last decade the water metabolism of the hyrax has been examined fairly extensively in order to assess

its ability to survive in such conditions. These studies, conducted in the laboratory, have examined the water economy (Meltzer, 1976), water turnover rate (Rubsamen *et al.*, 1979; Rubsamen & Kettembeil, 1980) and renal function (Louw *et al.*, 1973; Maloiy & Sale, 1976) of different species of *Procavia* under different temperature and water regimes. It appears that, even when drinking water is available, a characteristic of the species *P. capensis*, *P. habessinica* and *P. syriacus* is a low water intake. This has been measured either in water balance experiments (Louw *et al.*, 1973; Maloiy & Sale, 1976; Meltzer, 1976; - for *P. capensis* and *P. syriacus*) or as the water turnover rate using tritiated water (Rubsamen *et al.*, 1979; Rubsamen & Kettembeil, 1980; - for *P. habessinica*). Although measurement of water turnover rate is not a direct measurement of the fluid intake of an animal, it does give an indication of the degree to which the animal is able to tolerate arid conditions. In this respect, Rubsamen *et al.*, (1979) and Rubsamen and Kettembeil (1980) have shown that *P. habessinica* is well adapted to aridity, having a water turnover rate *ca.* 60 per cent lower than other eutherian mammals, when water and food were freely available. Furthermore, since the water turnover rate of this species is influenced by ambient temperature, and is reduced together with the oxygen consumption when water is restricted, these authors have suggested that the low rate may be a secondary effect of the low metabolic rate in the hyrax.

The ability to tolerate a reduction in the water intake is due, in part, to the renal efficiency of the hyrax and also the ability to reduce water losses by reducing the urine volume, faecal water content

and evaporative water loss (Louw *et al.*, 1973; Maloiy & Sale, 1976; Rubsamen *et al.*, 1979). Although renal function studies show that the kidneys of the hyrax *P. capensis* work at near maximum efficiency even when the animals are normally hydrated (Louw *et al.*, 1973), dehydration does cause an increase in the urine osmolality so that values of over 3000 m osmol/kg have been recorded in this species and in *P. habessinica*. Furthermore, when dehydrated the hyrax can tolerate a reduction in mass of up to 20 per cent (Louw *et al.*, 1973; Meltzer, 1976).

The general conclusion reached by all of the above-mentioned authors is that the hyrax is not independent of exogenous water, but that the water provided in the plants eaten, even in dry seasons (Meltzer, 1976) is probably enough to fulfil the water requirements of the animals. None of these studies, however, have been done on free-living animals where climatic factors and the effects of activity and social living are manifest. Therefore, in the present study, I have examined some aspects of the water metabolism of *P. capensis* under such conditions.

An interesting and unusual feature of the hyrax urine is the calcium carbonate content which gives the urine a milky appearance (Louw *et al.*, 1973). In the communal urinating and defecating sites, aggregations of the solid calcium carbonate collect, sometimes forming stalagmites, while the fluid portion collects below, and over the years, together with some faecal matter, forms a brown tar-like accretion. The latter, commonly called "klipsweet" in South Africa or hyraceum

elsewhere, has been used medicinally at least in the rural areas of South Africa.

The origin of the calcium in the urine is probably dietary since the precipitate disappears when food intake stops (Louw *et al.*, 1973) but nothing further is known of the calcium excretion in the hyrax. Since a high calcium load and a precipitate can be deleterious to normal kidney functioning, the excretion of calcium and the elements associated with it in nutritional terms, viz. magnesium and phosphorus was of interest and therefore examined in this thesis.

1.2 THE ELEPHANT SHREW *ELEPHANTULUS EDWARDI*

1.2.1 Taxonomy and evolution

The most recent and extensive taxonomic revision of the extant elephant shrews is that of Corbet and Hanks (1968). These authors have clarified much of the confusion that existed within the family of elephant shrews, Macroscelididae, and recognise two sub-families, Rhynchocyoninae and Macroscelidinae. The former encompasses the largest of the extant elephant shrews within a single genus *Rhynchocyon* comprised of three species. The remaining eleven species are incorporated within the Macroscelidinae, with three genera, *Petrodomus* and *Macroscelides* being monospecific and *Elephantulus* with nine species.

The taxonomic status of the family within the Mammalia is still controversial, however, due to the poor fossil record and the misplacement of several of the early macroscelidid fossils in a variety of other groups. Indeed, only in 1937 was an extinct elephant shrew, from the Pleistocene, correctly identified and placed within the Macroscelididae by Broom. Other fossil macroscelidids had been included with the marsupials, mixodectid insectivores and the hyracoids until Butler and Hopwood (1957) and Patterson (1965) detected and rectified these errors. In Table 1.1, the amended, brief taxonomy of the fossil elephant shrews is shown, according to Patterson (1965), together with their age and place of origin. The groups with which they were formerly associated are also shown.

As can be seen from Table 1.1 the family is an ancient one, dating back to the early Oligocene, and has probably evolved in Africa, since fossils have been found only from this continent (Bigalke, 1972). The variety of fossil forms suggests that the elephant shrews underwent an extensive radiation during the Cenozoic and clearly, from Table 1.1 the two sub-families remaining today must have diverged prior to the Miocene, probably in the early Oligocene (Patterson, 1965). Large, intermediate and small forms coexisted during the Cenozoic, as is the situation at present, and there also appears to have been a diversity in tooth structure ranging from rodent-like hypsodont molars to definite ungulate-like cheek teeth in the Myohyracinae. In general, however, all the extinct sub-families appear to have been predominantly herbivorous or possibly omnivorous (Patterson, 1965) unlike the predominantly insectivorous diet described for the extant species (Rathbun, 1979).

TABLE 1.1 Fossil forms of the family Macroscelididae (adapted from Patterson, 1965)

	Age	Locality	Previous affinity
Sub-family: MACROSCELIDINAE			
Metoldobotes			
M. stromeri Schlosser 1910	Early Oligocene	Fayum, Egypt	Mixodectid insectivore
Palaeothentoides			
P. africanus Stromer 1932	Late Pliocene	Little Namaqualand South Africa	Marsupial
Elephantulus			
E. langi Broom 1938	Pleistocene	Transvaal, South Africa	-
E. antiquus Broom 1948	Early Pleistocene	Transvaal, South Africa	-
Sub-family: RHYNCHOCYONINAE			
Rhynchocyon			
R. clarki Butler & Hopwood 1957	Early Miocene	Kenya	-

- continued

Table 1.1 (continued)

	Age	Locality	Previous affinity
Sub-family: MYLOMYGALINAE			
Mylomygale			
M. Spiersi Broom 1948	Early Pleistocene	Kimberley, South Africa	-
Sub-family: MYOHYRACINAE			
Myohyrax			
M. oswaldi Andrews 1914	Early Miocene	Kenya and South West Africa	Hyracoid
Protypotheroides			
P. beetzi Stromer 1922	Early Miocene	South West Africa	Hyracoid

The position of the Macroscelididae within the Insectivora has long been controversial. Peters (1864) recognising that this family and the tree shrews, Tupaiidae were ill-fitting members of the order, separated them from the rest of the insectivores and two sub-orders of the Insectivora were created by Haeckel (1866), the Menotyphla and the Lipotyphla. The former comprised of the two controversial families and the rest of the insectivores were included in the Lipotyphla. The characteristics of the Menotyphla which differed from the Lipotyphlan families included skull morphology, the possession of a caecum, specialised dentition, enlarged brains and acute vision (Peters, 1864; Vaughan, 1972). Patterson (1965), however, regards these characteristics as poor evidence on which to base any systematic affinity since they are common to many groups of mammals. Subsequently, as the tupaiid-primate relationship became accepted, a similar indirect association with the primates was considered for the Macroscelididae (Evans, 1942). Patterson (1965), while acknowledging the former association, refutes the latter, as well as a tupaiid-macroscelidid association within the Menotyphla, as do several other authors (Carlsson, 1909, 1922; Saban, 1954, 1956; Patterson, 1957). The evidence against the latter association is based on differences in placentation (Meister & Davis, 1956), skull morphology (Saban, 1956), tooth structure (Butler, 1956) and brain structure (Le Gros Clark, 1933). Furthermore, while serological evidence for the tupaiid-primate relationship exists, the same has not been found for the Macroscelididae (Goodman, 1963, 1974). More recently Sauer (1973) and Sauer and Sauer (1971, 1972) have supported the relationship between the elephant shrews and tree shrews, based on behavioural studies. In

contrast, an extensive study of the ecology and behaviour of the Macroscelididae (Rathbun, 1979) supports the monophyletic origin for these animals, originally suggested by Butler (1956) and Patterson (1965). Patterson (1965) also defined the new order for the elephant shrews, the Macroscelidea.

Thus, as can be seen, taxonomic confusion still exists, due largely to the lack of information about the elephant shrews. In this study, I have not taken a definite stand in this controversy since it seems unnecessary to do so in a physiological study. In view of the predominantly insectivorous diet of the animals, however, comparisons with members of the Insectivora have been made as well as with other groups of mammals.

1.2.2 Distribution

The family Macroscelididae are confined to Africa with a range, given by Corbet and Hanks (1968) as "the Mediterranean zone of north west Africa and the whole of Africa south of the Sahara, except for the region northwest of the rivers Congo and Ubangi and west of about 27°E". Within this range, the elephant shrews are found in tropical forests, semi-arid bushlands, rocky scrublands and deserts. Both *Rhynchocyon* and *Petrodomus* inhabit forested areas or dense savanna woodland and therefore are restricted to areas with a closed canopy (Fig. 1.3). *Macroscelides* and *Elephantulus* are found in more arid environments such as dry woodlands, steppe zones and deserts (Corbet &

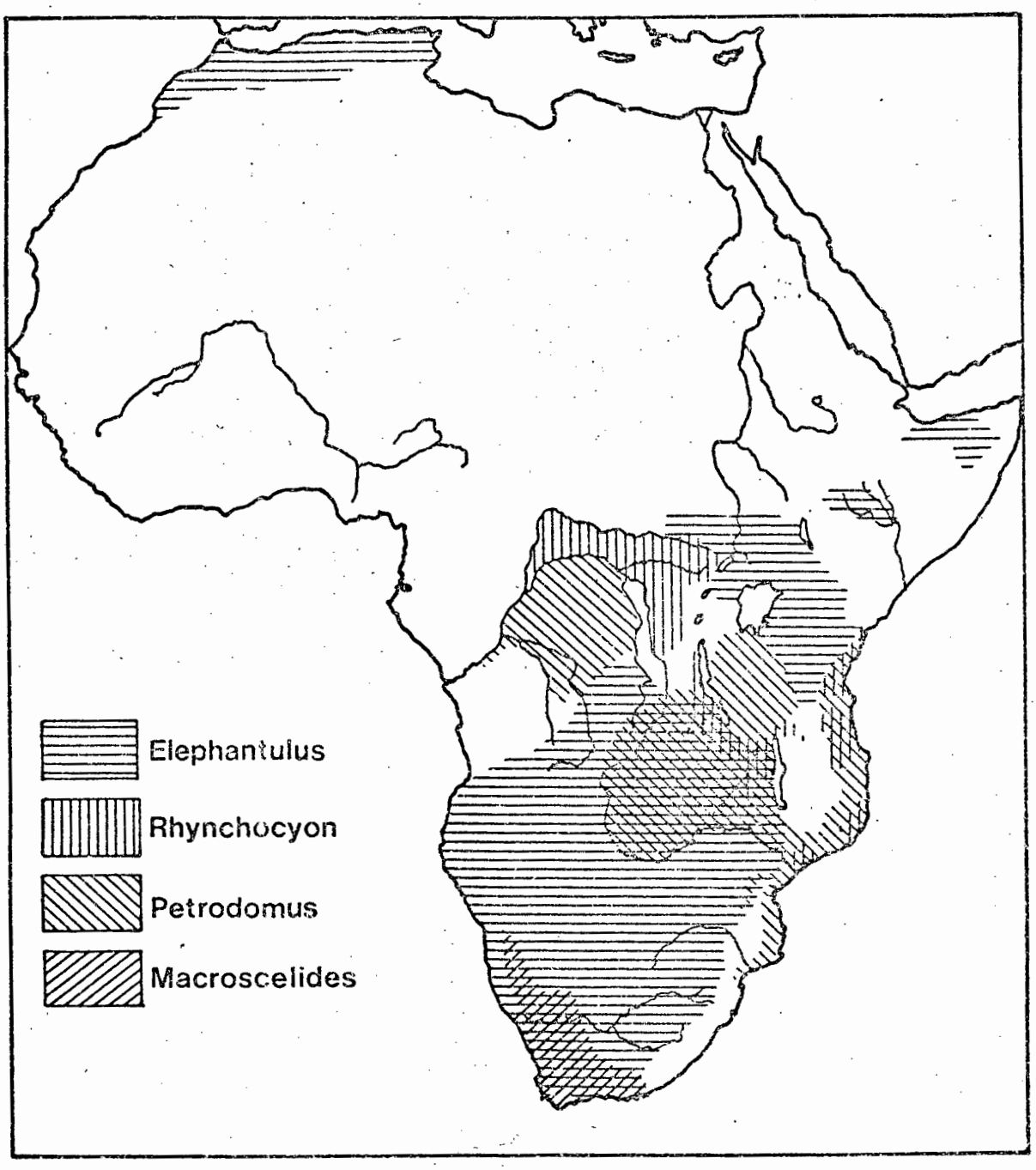

Fig. 1.3 Recorded distribution of the four genera of the Macroscelididae. (From Corbet & Hanks, 1968)

Hanks, 1968). The distribution of these four genera are shown in Fig. 1.3.

Elephantulus has the widest range of the four genera, being found in all provinces of South Africa, extending north into Angola, the Congo, Zambia and along the northeast of Africa through Mozambique, Malawi, Kenya, Uganda, Tanzania to Ethiopia, Somalia and the Sudan. They are also found in the northwest of Africa in Morocco, Tunisia and Algeria. The distribution of this genus is therefore that of the family Macroscelididae (Corbet & Hanks, 1968).

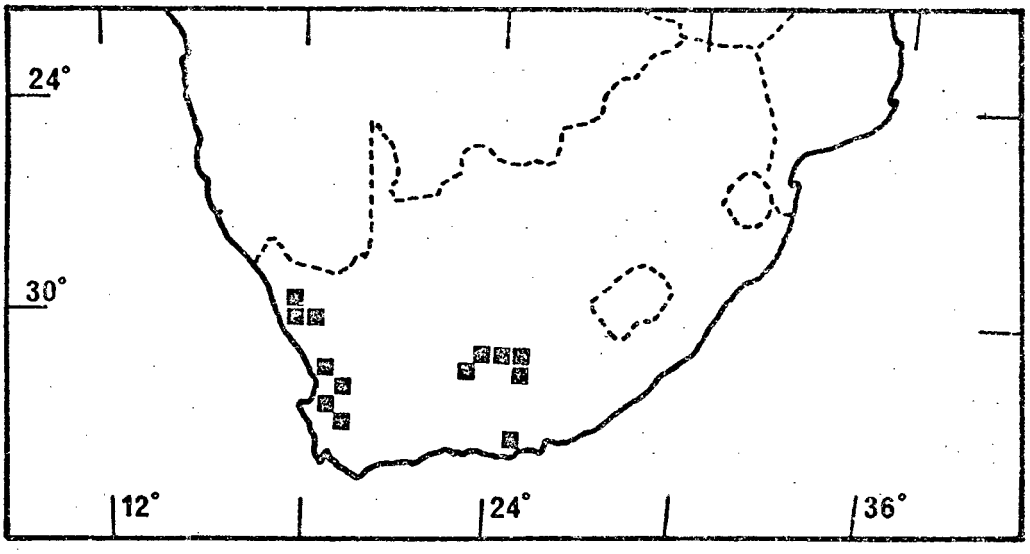

Fig. 1.4 Recorded distribution of *Elephantulus edwardi*. (From Corbet & Hanks, 1968)

Elephantulus edwardi, the species under study is restricted to the south and west of the Cape Province but extends east to Port Elizabeth, and north to the Upper Karroo in the Richmond district (Fig. 1.4). It is marginally sympatric with *E. rupestris* in the north and with *E. myurus* in the northeast, but overlaps more extensively with *Macroscelides proboscideus* (Corbet & Hanks, 1968).

1.2.3 Literature

Aside from the taxonomic studies and scant references to the habitat of *E. edwardi*, usually incorporated in articles on the systematics of the elephant shrews (e.g. Roberts, 1951; Corbet & Hanks, 1968) the only other published information on this species is concerned with its reproductive physiology (Tripp, 1971). My own information on the habits and habitat of the animal have been taken from trapping data or from observations of elephant shrews kept in captivity for the physiological studies documented later in this thesis. Therefore, the following introductory information is taken from ecological and behavioural reports of other species of *Elephantulus* and any data confirming my own observations have been noted.

1.2.4 Habitat and social structure

Within the semi-arid or arid environments inhabited by the different species of *Elephantulus*, burrows or rock crevices and fissures are used as shelters, with the exception of *E. rufescens* which was never observed using a burrow, but sheltered in dense thickets (Rathbun, 1979). In the laboratory, *E. edwardi* often retreated to the cardboard box provided and remained there for long periods of time. In the wild it is probable that they use rock crevices for the same purpose since they were always trapped in rocky areas with large boulders or rocky scree. The same habitat has been recorded for *E. myurus* which uses the rock crevices as shelter (van der Horst, 1946; Critch, 1969; Tripp, 1972). In common with all Macroscelidinae (Rathbun, 1979), the Cape elephant shrew was never observed using nesting material.

A solitary existence is common to all the members of the genus *Elephantulus* studied so far (several authors, reviewed by Rathbun, 1979). *E. edwardi* also appears to be solitary in view of the violent aggression (chasing and biting) observed between two animals of the same or opposite sex, placed in the same cage. Rathbun (1979), however, reported that *E. rufescens* forms a stable monogamous association which lasts for the duration of the life of each member - usually from two to three years. Each member of the pair defends its own territory of approximately 0,34 ha, but the territories of the male and female overlap almost completely. Within the territories

the pair bond is loose, interactions between individuals occurring predominantly for feeding or sexual purposes. Other contacts result in aggressive encounters more often than not (Rathbun, 1979). Pair bonding in species which occupy burrows has been described only in *E. brachyrhynchus* (Rankin, 1965). The male and female of this species apparently live together in the burrows with their young.

1.2.5 Activity and general behaviour

In the laboratory, *E. edwardi* tended to remain in their shelters for most of the daylight hours, though some occasionally used the activity wheels provided. If a lamp was provided as a heat source they would alternate between basking beneath it and lying in the shelter. Feeding appeared to be restricted to the evening, night or early morning, though this may have been due to the provision of fresh food in the evening. After feeding in the evening, however, the animals were seen more often outside the shelters, often using the activity wheels. These observations suggest that this species is crepuscular or nocturnal and examination of trapping data confirm this. In the Rooiberg mountains of the Cape Province, *E. edwardi* was found exclusively in traps set after 17.00h and checked at 07.30h (David, 1978). Tripp (1970) and Rathbun (1979) suggest that all species of *Elephantulus* are polycyclic. This may be true of *E. edwardi*, since they do show basking behaviour which

is likely to take place during the day, though peaks in activity would probably occur in the early morning and evening as has been found for *E. rufescens* (Rathbun, 1979). Behaviours such as foot-drumming with the hind feet (a threat behaviour), sand-rolling, grooming the face and nose with the forefeet and basking, which have been described for other species of *Elephantulus* (reviewed by Rathbun, 1979) have all been observed in captive *E. edwardi*.

Trails: *E. rufescens* appears to be the only member of this genus that uses and maintains an extensive trail system within its territory (Rathbun, 1979). Trails are maintained by clearing away leaves and small twigs with a lateral sweep of the forefoot. The same behaviour has been noted by Tripp (1970) in captive *E. intufi*. *E. edwardi* in captivity were often seen moving the cardboard boxes in their cages with a lateral sweep of the forefoot. Whether this behaviour of *E. edwardi* occurs in the wild is not known, but as Rathbun (1979) has pointed out, trails may be important for a rapid escape from predators and may allow the animals to cover their territories easily and rapidly thus increasing the likelihood of detecting food sources.

Gait: Despite the reference to elephant shrews as the "jumping shrew" (Fitzsimons, 1920), the continuous saltatory movement expected from the long hind-limbs and shorter fore-limbs, reminiscent of some gerbils, has not been reported. Brown (1964) has reviewed this aspect from various reports in the literature and it seems that a rapid quadrupedal motion is the normal gait, sometimes interrupted with short rapid jumps.

The same has been observed in *E. edwardi*.

1.2.6 Reproduction

Reproduction in *Elephantulus* is the only aspect of its physiology that has been studied in any detail. The numerous publications on this aspect by van der Horst, Gillman and co-workers (van der Horst published yearly from 1940 to 1951; van der Horst, 1954; McKerrow, 1954; Stoch, 1954) deal with reproduction in *E. myurus*, but this work has been extended to several other species by Tripp (1971). These studies show that polyovulation occurs in the females of only *E. myurus* and *E. edwardi*, releasing about 120 ova in *E. myurus* (van der Horst & Gillman, 1941) and 88 in *E. edwardi* (Tripp, 1971). Of these, many are fertilized but a maximum of two embryos develop, the number being restricted by the availability of only two implantation sites in the uterine horns (Tripp, 1971). In *E. myurus* post partum ovulation occurs and there is no lactation anoestrus (van der Horst, 1954; McKerrow, 1954). A true vagina is absent in the seven species of *Elephantulus* studied, in *Macroscelides* and in *Petrodomus*, and may be a characteristic of the family (Tripp, 1971).

The mating season of *E. myurus* in the Transvaal, begins in the middle to the end of July when the females come into oestrus. Two to three pregnancies can occur during the season of reproductive activity (mid July to January) (van der Horst, 1946). After a gestation period of eight weeks, long for an animal of this size, one or two precocial young are born. The young are weaned after four weeks and

reach sexual maturity within five to six weeks of age (McKerrow, 1954). A six month period of anoestrus occurs after the breeding season and van der Horst (1946) suggests that probably only three pregnancies occur in the life of *E. myurus* and that females cannot live beyond the completion of their sexual life.

All male Macroscelididae are testicond and in *E. myurus*, sexual activity coincides with the female oestrus period. Although testes are fully active throughout the year, the accessory sexual organs are fully active only from July to January (Stoch, 1954). This appears also to be true for the interstitial cells in the testes (Stoch, 1954).

The present study on *E. edwardi* was undertaken to provide some basic physiological information on the animal. While it is not the intention here to clarify the taxonomic position of this family, it is hoped that the information provided may aid others in doing so. The aspects of energy metabolism, temperature regulation and water metabolism examined are important in that they give some indication of how the animals cope with the arid and semi-arid conditions, the seasonal lack of water and the extremes of temperature encountered in their environment.

1.3 REMARKS ON COMPARATIVE ASPECTS OF *PROCAVIA CAPENSIS* AND *ELEPHANTULUS EDWARDI*

While a comparative study of the hyrax and elephant shrew was not the

primary intention of this thesis, in some respects the two animals are similar. The semi-arid to arid mountainous and rocky areas where they both live are rather extreme habitats with harsh environmental conditions such as large seasonal fluctuations in temperature and limitations in water availability. These conditions can also impose limitations on the availability of food, particularly for the herbivorous hyrax. A scarcity of water and nutrients in the soil (conditions particularly prevalent in the mountainous regions of the southern Cape - Joubert *et al.*, 1969) hamper primary productivity and tend to enhance the growth of plants of poor nutritional quality, often with defence mechanisms such as spines or secondary compounds. The situation is not as critical for the elephant shrew, however, as insects tend to be a fairly stable nutrient source throughout the year. Within this environment, both animals utilize the rock crevices as shelter, are at least partially diurnal and bask in the sun. With these features in common, it is possible that the animals may show similar adaptations in energy and water metabolism and thermoregulatory mechanisms. The differences between the two, however, such as the solitary and insectivorous nature of the small elephant shrew in contrast with the gregarious, herbivorous nature of the larger hyrax must affect the physiological mechanisms employed.

Thus, the present study illustrates some of the physiological mechanisms employed by the two different sized mammals and which are associated with life in the environment described above. In addition, in view of the different habits of *E. edwardi* and *P. capensis*,

the modifications in energy and water metabolism which have been adopted in association with either a solitary or gregarious existence and an insectivorous or herbivorous diet, have been examined.

SECTION 2

ASPECTS OF DIGESTION AND ENERGY ASSIMILATION IN THE ROCK HYRAX *PROCAVIA CAPENSIS*

2.1 INTRODUCTION

The complex nature of plant matter and the intrinsically different compositions of plant and animal bodies, require major modifications in the digestive system of an animal for it to be totally reliant on an herbivorous diet, as a source of nutrients and energy. The harbouring of symbiotic microorganisms in specialized, expanded regions of the gut, viz. the rumen and caecum, has been the general modification of the alimentary tract adopted by herbivorous mammals. These anaerobic microorganisms are capable of producing cellulases to break down the plant matter in a fermentation process. As by-products of the system energy, essential amino acids and vitamins which may be lacking in the food, are provided for the host. While the microorganisms play an essential role in the digestive processes of herbivores, the efficiency with which they are able to break down the plant matter and ultimately provide the host with energy, is dependent on several factors. These include the efficiency of the enzyme systems employed by the microorganisms, this in turn being dependent on the conditions within the alimentary tract with regard to pH, temperature and moisture; the nature of the plant matter (whether lignified or not) and the time over which the microorganisms are able to act on the food material. These factors prevent nutrient and energy release from the food being absolutely efficient. This, coupled with the relatively low yield of energy per unit mass of dry plant matter compared with food of animal origin (Lloyd *et al.*, 1978) necessitate a large food intake by herbivores to sustain the life processes.

Thus, herbivores generally spend 40 to 50 per cent of the day in feeding (Moen, 1973). The hyraces, however, are unusual in this respect, spending one to two hours per day feeding (Sale, 1965a; Hoeck, 1975). Their ability to crop food rapidly using the long cutting edge of the molar tooth row allows them to take in a large quantity of herbage in a short time (Sale, 1966b). Nevertheless, both Sale (1966b) from limited data, obtained from a single *Procavia johnstoni mackinderi*, and Hume *et al.* (1980) working on *P. habessinica*, have shown that the total intake of the hyrax is low for its size when compared with other herbivores.

Important implications arise from this, particularly concerning the energetics and digestive processes of the animal. In terms of energy consumption, a low food intake would necessarily mean that the hyrax has a low energy intake, which, in turn, must reflect a low energy expenditure by the hyrax. In this respect, it has been shown that the mass specific metabolic rate is low for most species of hyrax studied so far (Taylor & Sale, 1969; Bartholomew & Rainy, 1971; Rubsamen *et al.*, 1979; present study section 6). The energy derived from the food, however, is dependent on the efficiency of the digestive system in digesting and assimilating the food components. Generally, a highly efficient system obviates the need for a larger food intake, but in the case of herbivores, this must be considered within the confines of the limited energy available in plant matter. Thus in the overall examination of the energetics of the hyrax and in an attempt to explain the low food intake, the following hypotheses arise:

1) The digestive system of the hyrax is more efficient than that of other herbivores obviating the need for a larger food intake. This would be influenced by the extent to which the animal selects food with a high nutritive and low fibre content.

2) The low food and energy intake reflects a conservative energy expenditure in the daily life of the hyrax.

These hypotheses are not mutually exclusive, however, and they provide the basic concept with which the energy metabolism of the rock hyrax *Procavia capensis*, has been studied in the following sections.

2.2 METHODS

The food intake, digestibility of food components and energy assimilation by the hyrax, were evaluated in three digestion trials (Maynard & Loosli, 1962), using different feeds. All quantities were recorded on a dry matter basis.

2.2.1 Trial 1

Six adult male hyraces with a mean mass of 2,92 $\pm_{A}^{S.D.}$0,37 kg, were used in the trial. They had all been in captivity for at least six months

prior to the experiment during which time they were housed individually in cement enclosures with a sloping floor. The animals rested on a raised, slatted, wooden platform which retained the faeces while urine drained out of the cage. Over the six months prior to the experiment, which served as the preliminary period, they had been accustomed to daily handling, while the cages were cleaned, and were fed commercial rabbit pellets, the same ration used in the digestion trial. During the nine day trial, the body masses of the animals were recorded at the same time each day. A predetermined amount of food and a known volume of water was provided at the same time. Any remaining food was removed, dried and weighed, and the volume of water remaining was recorded after correcting for evaporation. Evaporation was assessed from a control dish in the room. Faeces were removed daily, dried, weighed, milled and stored for later analyses of the energy content. This trial was performed in September (winter-spring) during which time the animals were kept under conditions of natural light and indoor temperature fluctuations. A sample of food was retained for analysis of its composition.

2.2.2 Rate of passage of food through the alimentary tract

At the end of Trial 1, additional food in the form of a known mass of fresh chopped carrot tops was fed to the same animals for a further seven days. The same procedure was adopted as in Trial 1. The rate of passage was determined by visually comparing the colour of the milled faeces, from Trial 1 with the subsequent faecal samples

produced when greens were eaten. This method was possible since the colour varied markedly from a tan colour on a pelleted diet to a distinct green with additional greens. The time from the day on which greens were first given to the day on which the green colour appeared to be at its greatest intensity or a consistent intensity with subsequent faecal samples, was taken as the retention time.

In order to confirm the validity of this method, and to reduce any error which may have arisen due to the increased fibre intake with the greens, the animals were fed plastic particles 1-2 mm^3 in size. Faeces were collected twice a day, morning and afternoon, dried, crushed manually and examined for the presence of the particles. A comparative estimate of the quantity of particles in the daily faecal samples allowed a determination of the retention time for each animal.

2.2.3 Trials 2 and 3

Prior to the actual trials, the animals were kept in an outdoor pen for one month and fed the particular diet to be used in the trial. Thereafter they were placed indoors in individual cages at a constant temperature of 20°C and exposed to natural lighting. Each cage was placed above a stainless steel fine mesh tray and beneath this was a plastic funnel leading into a measuring cylinder. Faeces were retained on the mesh tray while urine drained into the measuring cylinder. After a preliminary period of seven days the actual digestion trial was conducted. The same procedure was employed as

in Trial 1, except the body masses of the animals were recorded only at the beginning and end of the trial. Both experiments were conducted during the months of April and May (autumn-winter).

2.2.3.1 *Trial 2*

Eight male hyraces with an initial mean mass of 2,12 $\pm_{A}^{S.D.}$0,40 kg were used. Five of these animals were under 2 kg in mass, and therefore probably sub-adult. The feed consisted of commercially prepared guinea pig pellets and the trial continued until data from five consecutive days were collected. Although the volume of urine excreted daily was recorded, samples were not kept for analysis of energy content.

2.2.3.2 *Trial 3*

Three male and two non-gravid female, adult hyraces of mean mass 2,38 $\pm_{A}^{S.D.}$0,44 kg were used. The feed consisted of lucerne hay chaff, milled in an attempt to prevent selection of leaves from stems. Since selection did occur, remaining food was collected daily, dried, weighed and analysed separately from the food given, to establish the correct intake of the food components. Only in this experiment was urine collected over ice and an aliquot (10% of the volume excreted) retained and stored frozen in sealed plastic bottles for later analysis of energy content. The digestion trial continued until data from 10 consecutive days were collected.

2.2.4 Field specimens

Dried, milled samples of stomach contents were available from wild *P. capensis*, shot on two adjacent farms in Nieuwoudtville, Western Cape. These were collected over six months from September to March (excluding November) thus covering the hottest and driest months of the year. The monthly samples consisted of combined stomach contents from 10 to 13 animals, but the total mass of the stomach contents and the mass of the animals shot, were not known. The composition of each sample was determined as outlined below.

2.2.5 Analytical methods

Food, remaining food and faeces were dried at 70°C to constant weight. An aliquot (10 per cent by weight) from each day of the experimental period was combined and milled. In the case of faeces, a two-day food retention time was allowed (see results) to minimise errors caused by a non-uniform food intake. As a check, a three day retention time was also used in the calculation of results from Trial 1. The final samples from Trials 2 and 3 were analysed for contents of protein, fibre, lipid and ash using standard methods for proximal analyses (A.O.A.C., 1960) except in the case of lipid extraction where hexane was used instead of ether.

The daily urine samples were combined and two samples of the pooled urine from each animal used for analysis. One sample was spun for

five minutes in a clinical centrifuge to separate the calcium carbonate precipitate from the fluid portion, and the supernatant freeze-dried (New Brunswick Scientific Co.). The second sample was freeze-dried inclusive of the precipitate. Since the oxidation of calcium carbonate involves an endothermic reaction, the two different methods were considered necessary to evaluate any discrepancy that may have arisen in determining the energy content of the urine. The freeze-dried samples were then analysed for heat of combustion using a bomb calorimeter.

All quantities were recorded on a dry matter basis and expressed as the mean with estimates of error given as the standard deviation (S.D.). Where applicable, results have been expressed on a metabolic body weight basis ($kg^{0,75}$) (Kleiber, 1961) to minimise errors due to differences in body mass of the animals. Significance of differences was estimated using the Student's t-test (Zar, 1974).

2.3 RESULTS

2.3.1 Composition of food and stomach samples

The major difference between the pelleted diets and the lucerne hay was the content of crude fibre (Table 2.1), both pelleted rations having a lower fibre content (7,7 and 10 per cent) than the lucerne hay (30%). Although the lucerne hay was coarsely milled, the animals still tended to select the leaves in preference to stalks

TABLE 2.1 Composition of the three diets used in three digestion trials and of wild hyrax stomach contents (% of dry matter)

TRIAL NUMBER	1	2	3			Stomach contents	
FEED	Rabbit Pellets	Guinea Pig Pellets	Lucerne Chaff			of wild hyraces	
			Given	Remains	Ingested	Mean*	± S.D.
Crude protein (%)	16+	21,04	18,46	15,82	19,23	11,15	0,74
Crude fibre (%)	10+	7,70	29,92	33,07	28,99	22,70	1,61
Protein: Fibre ratio	1,60	2,73	0,62	0,48	0,66	0,75	
Hexane extract (%)	<3+	1,28	1,37	1,16	1,43	2,48	0,84
Ash (%)	7-8+	7,58	9,50	8,69	9,74	7,89	0,40
Nitrogen-free extract (%)	64	62,40	40,75	41,26	40,60	55,79	1,34
Heat of combustion ($kJ.g^{-1}$)	18,60	18,28	16,46	16,14	16,60	16,33	0,96

* Mean of six, monthly samples from a total of 60 animals

+ Manufacturers' analysis

and thus the composition of that portion eaten was marginally higher in protein and lower in fibre content than that given (Table 2.1). Of the three feeds used in the trials, the lucerne hay was nearer in composition to the stomach contents (with respect to the protein to fibre ratio, Table 2.1), and therefore, the results from the trial using this food have been used to extrapolate to the situation in the field. There was no marked difference in the composition of the stomach contents over the six months of sampling.

2.3.2 Food and water intake

The differences in food intake between the hyraces on the pelleted diets (Trials 1 and 2) were significant ($p<0,01$) and both were significantly lower than the intake of the animals fed lucerne hay (Trial 1, $p<0,001$; Trial 2, $p<0,02$) (Table 2.2). The mean mass changes over the experimental periods, however, were low in all three trials. Water intake, expressed per gram of dry matter ingested, was similar for all three trials with a mean value of $2,10 \pm 0,13$ ml water. g^{-1} dry matter intake (Table 2.2).

2.3.3 Rate of passage of food through the alimentary tract

The time taken from the ingestion of food to its voidance from the alimentary tract of the hyrax was two to three days, based on the colour of the faeces, and 36 to 60 hours based on the particle study. Since the rate would depend on the composition of the food, as a

TABLE 2.2. Food and water intake of hyraces on three different diets

	TRIAL 1		TRIAL 2		TRIAL 3	
Feed	Rabbit Pellets Mean	± S.D.	Guinea Pig Pellets Mean	± S.D.	Lucerne Chaff Mean	± S.D.
Mass of hyraces (kg)	2,92	0,37	2,12	0,40	2,38	0,44
n	6		8		5	
Duration of trial (days)	9		5		10	
Mass change over trial period (% of initial mass)	-0,57		+1,09		+2,36	
Food intake ($g\,DM.kg^{-0,75}.day^{-1}$)*	20,03	6,21	32,60	5,75	40,80	2,94
Water intake ($ml.g^{-1}$ DM intake)	1,99	0,29	2,07	0,67	2,24	0,23

* DM: dry matter

best approximation, a two day rate was used for all the trials. To check the validity of this rate, the faecal samples from Trial 1 were combined using both a two day rate and a three day rate, the heat of combustion of each combined faecal sample measured, and the apparent digestible energy intake (DEI) calculated using the two results. Comparison of the DEI values for each rate showed no significant difference ($p > 0,1$). In Trial 3 where there may have been a longer rate of passage due to the high fibre content of the food, in view of the constancy of the food intake (low standard deviation - Table 2.2), a two day rate of passage was considered acceptable.

2.3.4 Dietary energy balance

The gross energy intake (GEI) of the hyraces in the three trials followed the same pattern as the food intake (Table 2.3). Although the GEI was significantly lower ($p < 0,01$) on the rabbit pellets than on the guinea pig pellets, faecal energy losses (FE) in both trials represented a similar proportion of the GEI (26,9 and 29,2 per cent respectively). Similarly, the difference in the apparent digestible energy ingested (DEI) in Trials 1 and 2 ($p < 0,01$), actually represented a similar proportion of the GEI (73,1 and 70,9 per cent, respectively) (Table 2.3). In Trial 3, with the markedly different composition of food, 48,6 per cent of the GEI was lost in the faeces and the efficiency of energy assimilation (DEI as a percentage of the GEI), 51,4 per cent, was lower than on the pelleted diets (Table 2.3).

TABLE 2.3 Dietary energy balances of hyraces in three digestion trials

Feed	Units	TRIAL 1 Rabbit pellets n = 6 Mean	± S.D.	TRIAL 2 Guinea pig pellets n = 8 Mean	± S.D.	TRIAL 3 Lucerne chaff n = 5 Mean	± S.D.
% Moisture in feed		7		7		9	
Gross energy of food (G.E.)	$kJ.g^{-1}$	18,60	-	18,28	-	16,60	± 0,17
Apparent digestible energy of food (D.E.)	$kJ.g^{-1}$	13,59	-	12,95	-	8,53	-
Apparent metabolizable energy of food (M.E.)	$kJ.g^{-1}$	-	-	-	-	4,08	-
Gross energy intake (GEI)	$kJ.kg^{-0,75}.day^{-1}$	372,56	115,45[a]	595,93	104,05[b]	677,25	31,62[b]
Energy lost in faeces (F.E.)	$kJ.kg^{-0,75}.day^{-1}$	100,26	43,32	173,71	22,12	329,16	42,97
Energy lost in urine (U.E.)	$kJ.kg^{-0,75}.day^{-1}$	-		-		28,84	7,89
Energy lost as methane (Me.E)*	$kJ.kg^{-0,75}.day^{-1}$	-		-		6,96	-
Apparent digestible energy ingested (D.E.I.)	$kJ.kg^{-0,75}.day^{-1}$	272,30	75,66[a]	422,22	88,98[b]	348,09	44,30[ab]
DEI as % of GEI (Assimilation efficiency)	%	73,09	4,64	70,85	3,56	51,40	6,02
Apparent metabolizable energy ingested (MEI)	$kJ.kg^{-0,75}.day^{-1}$	-		-		312,29	-
MEI as % of GEI	%					46,11	-
MEI as % of DEI	%					89,71	-

* Mean methane production in *Procavia habessinica* = 5,9 ± 2,56 ml $kg^{-1}.hr^{-1}$.
(von Engelhardt *et al.*, 1978) and heat of combustion of one litre methane = 39,54 kJ (from Kempton *et al.*, 1976).

a, b Means on the same line bearing different superscripts differ significantly ($p<0,01$).

There was no significant difference between the DEI in this trial and those in either Trials 1 or 2 ($p \geq 0,05$).

The heat of combustion of the urine, inclusive of the precipitate (6,404 ± 1,372 $kJ.g^{-1}$ dry matter) was significantly lower ($p < 0,02$) than that without the precipitate (8,932 ± 1,241 $kJ.g^{-1}$ dry matter). When these figures are adjusted to the total volume excreted, no significant difference ($p \geq 0,1$) in energy loss was apparent. Thus the energy lost in the urine represented 4,27 ± 1,23 per cent of the GEI and assuming that 6,96 $kJ.kg^{-0,75}.day^{-1}$ (1,03 per cent of GEI) was lost as methane (calculated from von Engelhardt *et al.*, 1978), the metabolizable energy intake (MEI) on a lucerne hay diet was 46,11 per cent of the GEI and 89,71 per cent of the DEI (Table 2,3).

2.3.5 Digestibility measurements

The apparent digestibility of all the components of lucerne hay measured, with the exception of crude protein and fibre, were significantly lower than those in the guinea pig pellets ($p < 0,001$) (Table 2.4). For comparative purposes, digestibility coefficients for kangaroos and sheep on a lucerne chaff diet (Kempton *et al.*, 1976) similar to that used in Trial 3, have been recorded in Table 2.4.

TABLE 2.4 Mean apparent digestibility coefficients of the food components eaten by hyraces in two digestion trials compared with those of kangaroos and sheep on a lucerne chaff diet.* (Values are expressed as a % of the component ingested.)

Feed	TRIAL 2 Guinea-pig Pellets		TRIAL 3 Lucerne chaff		KANGAROO* Lucerne chaff		SHEEP* Lucerne chaff	
	x	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.E.	$\bar{x}$	± S.E.
Dry matter %	70,61	3,67	57,33	5,11	55	1,1	62	0,3
Organic matter %	72,48	3,82	55,74	5,42	56	1,1	63	0,3
Crude protein %	63,68	6,78	58,11	8,62	73	0,1	76	0,4
Crude fibre %	31,01	11,21	37,80	6,23	36	1,8	48	0,7
Hexane extract %	-ve balance		-ve balance		-		-	
Nitrogen free extract %	82,41	2,19	69,76	3,68	-		-	
Energy %	70,85	3,56	51,40	6,02	56	0,5	61	0,9

* Composition of feed given to kangaroo and sheep: 36% crude fibre; 2,6% nitrogen (16,25% protein assuming protein contains 16% nitrogen); 8,5% ash on a dry matter basis. All values for these animals taken from Kempton *et al.* (1976).

2.4 DISCUSSION

2.4.1 Food intake

The chemical composition of a plant is one of the prime factors influencing its selection as food by herbivores, as well as influencing the quantity which will be ingested and its ultimate utilization by the animal. Given the wide variability in the composition of plants, the prediction of the quantity of food which would be ingested by an animal becomes a difficult task. Two generalized formulae that have been used to predict daily food intake in cattle are:

On green pastures - 3 kg dry matter per 100 kg live body mass
On dry pastures - 2 kg dry matter per 100 kg live body mass.
(van der Merwe, personal communication)

Using these figures, a hyrax of 2 kg body mass should consume 40 to 60 g dry matter daily. Although the food intake by *P. capensis* in the present study was of the same magnitude (Table 2.2), the food and therefore energy intake of an animal should be related to its metabolic rate. Thus the exponential increase in metabolic rate with decreasing body mass necessitates a concomitant increase in food and energy consumption as body mass decreases. Considering the small size of the hyrax compared to cattle therefore, the consumption of dry matter found in the present study must be considered low. This has been noted previously by Sale (1966b).

Both the intake of lucerne hay (32,86 g dry matter.kg^{-1}.day^{-1}) and of rabbit pellets (20,03 g dry matter.$kg^{-0,75}$.day^{-1}) by *P. capensis* accord respectively with the findings of Sale (1966b) for *P. johnstoni* on a similar diet to lucerne hay (33,6 g dry matter.kg^{-1}.day^{-1}) and with those of Hume *et al.* (1980) for *P. habessinica* on a low fibre and relatively high protein diet (18,6 g dry matter.$kg^{-0,75}$.day^{-1}).

In order to establish a rough estimate for the intake of hyraces in the wild, the data of Lensing (1978) have been used as follows: In his study of the feeding ecology of *P. capensis* in Namibia, he found the mean wet mass of stomach contents of wild hyraces, shot immediately after a feeding period, to be 108,39 ± 35,99 g (Appendix A). The data were obtained over 33 months from 255 hyraces of mean mass 2,259 ± 0,505 kg (Lensing, personal communication). Assuming the daily intake to be twice the mass of stomach contents, since the animals feed twice per day and assuming a moisture content of 67 per cent for the wet stomach samples (personal observations), the dry mass of the food intake would be 31,67 g dry matter.kg^{-1}.day^{-1} or 38,82 g dry matter.$kg^{-0,75}$.day^{-1}. These values are in good agreement with the present data (40,80 g dry matter.$kg^{-0,75}$.day^{-1}) for captive hyraces on a lucerne hay diet.

2.4.2 Factors affecting the quantity of food ingested by the hyrax

Sale (1966b) has suggested that the quantity of food ingested by the hyrax is determined by the dry matter content. This is certainly

true on a broad scale when quantities of fresh and dry food ingested are compared, but the dry matter intake itself also varies considerably depending on the composition of the food. This was clearly shown for *P. capensis* in Trials 1 and 3 where the major difference was the higher proportion of crude fibre in the lucerne hay. Thus the differences in dry matter intake between animals on this diet and those on the pelleted diets were expected. Considering the minor differences in the fibre content of the two pelleted diets, however, the different intakes in Trials 1 and 2 were unexpected. The discrepancy may have resulted from one of the following three factors:

a) The higher protein content of the diet in Trial 2 may have resulted in a higher intake (see below), although a substantial increase in body mass would have been expected as well.

b) The hyraces in Trial 2, being immature may have required a greater nutrient and energy intake for growth. Over the short experimental period of five days, the small increase in body mass (1 per cent of the original mass) may have been indicative of growth, but the significance of this increase in representing growth is questionable.

c) The animals in Trials 2 and 3 may have been more active than those in Trial 1. The additional energy expenditure associated with activity would explain the higher food intake without a substantial increase in body mass.

The final reason, of the three outlined above, seems to be the most acceptable in explaining the higher food intakes in Trials 2 and 3.

A variation in the dry matter intake by the hyrax *P. habessinica* with variations in the composition of the food was also shown by Hume *et al.* (1980). Although neither the latter study, nor the present were designed to determine factors affecting food intake, when the results of the two were combined, the following trends became apparent:

For animals on a relatively low fibre diet (10 per cent or less), the dry matter intake increased as the protein content increased (Fig. 2.1). However, on the high fibre diets, food intake was higher than on the low fibre diets when the protein levels were similar. Thus it is clear that the crude fibre content of the food also affected the quantity consumed. These results then suggest that an interrelationship between protein and fibre content of the food was a determining factor in the quantity of dry matter consumed.

Apart from the protein and crude fibre content of the food, the moisture content of the plants eaten may be an additional factor that influences the dry matter intake. This would be of particular significance in the natural environment if free water was unavailable. Certainly in the present study and in that of Hume *et al.* (1980) the water intake was clearly dependent on the dry matter intake, a relatively constant volume being drunk per mass of dry matter intake. Furthermore Louw *et al.* (1973) have shown that when water was withheld, *P. capensis*, fed on a dry diet, decreased their food intake to

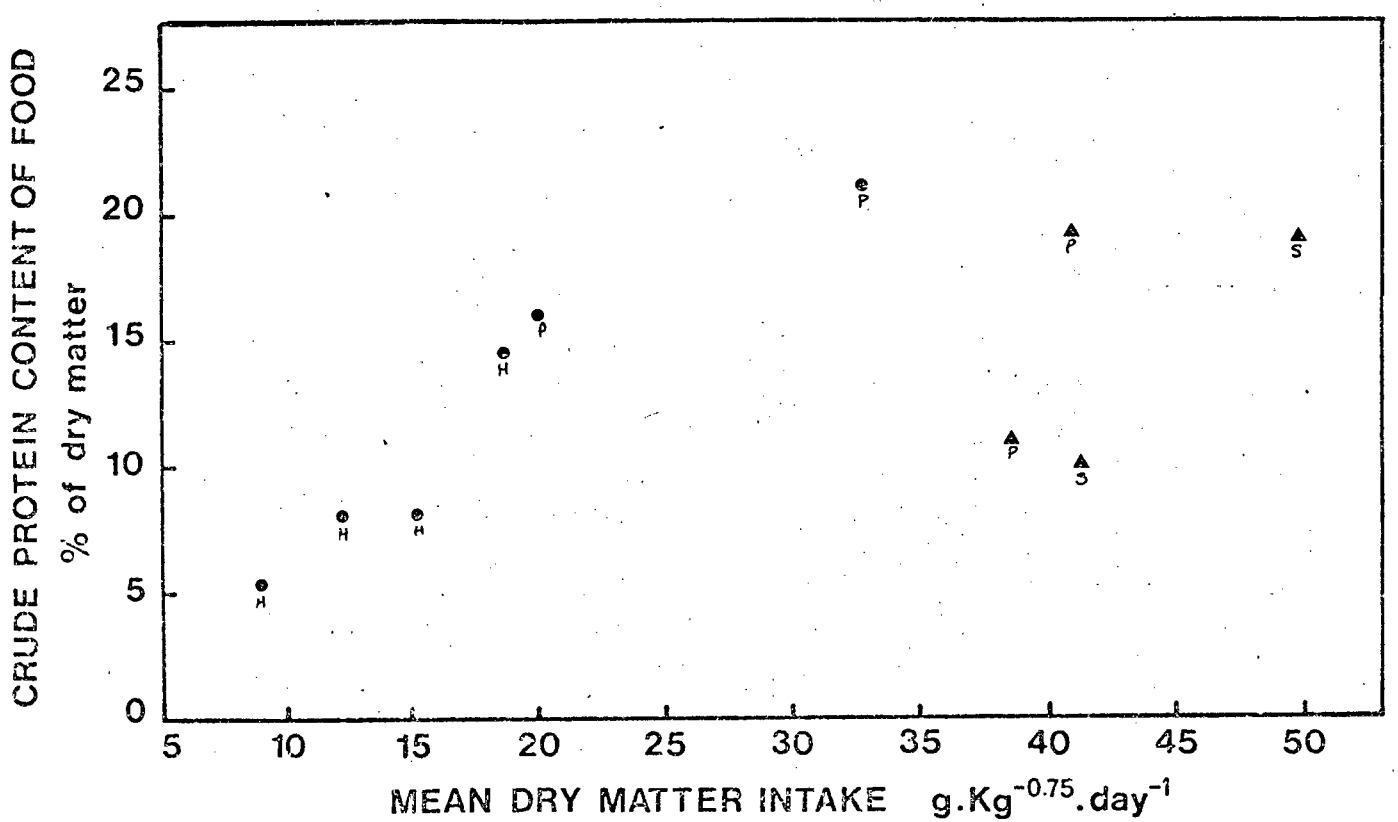

Fig. 2.1 The influence of crude protein content of food on the dry matter intake for various species of hyrax. Values are taken from the present study, (P) Hume *et al.* (1980) (H) and Sale (1966b) (S).

(●) Low fibre diet (< 10%)

(▲) High fibre diet (> 10%)

negligible amounts over a period of a week. Similar results were obtained by Maloiy and Sale (1976) and Rubsamen *et al.* (1979) for *P. syriacus* and *P. habessinica*. Lensing (1978), however, found that hyraces in the wild did not select food primarily on the basis of moisture content in any season despite the apparent lack of free water and suggested that this factor may have been of secondary importance in food selection. Meltzer (1976) has calculated the water requirements of the hyrax *P. syriacus*, and has concluded that even in the driest months of the year, the plants eaten in the wild would provide enough moisture to meet the animals' requirements. I would hesitate to draw the same conslusions for *P. capensis* without sufficient data on the moisture content of the plants eaten. Considering, however, that the urine osmolality of *P. capensis* was found to be higher than that of *P. syriacus* when dehydrated (Louw *et al.* 1973; Maloiy & Sale, 1976), the implications are that the South African hyrax is as tolerant to desiccation, if not more so, and given a minimum moisture content in the food, would be independent of free water in the wild.

Under natural conditions, then, a complex situation would undoubtedly exist where, at least, the interrelationship of protein, fibre and the water content of the plant matter eaten would determine the total quantity ingested, but other factors such as the availability of drinking water, the inclusion of secondary compounds in the plants and the general availability of edible plants would also be of crucial significance.

2.4.3 Digestibility of the food components

The high crude fibre content of the lucerne hay was probably the major factor contributing to the significantly lower ($p < 0,001$) digestibility coefficients found for all of its components, with the exception of crude protein and fibre, when compared to those of the pelleted ration. This is shown graphically in Fig. 2.2 where the coefficients of digestibility of energy, dry matter and soluble carbohydrates decreased with an increased fibre content of the food eaten. Since the nutrients would have been largely enclosed within the intact cellulose cell walls of the lucerne hay, the overall apparent digestibility of this food would depend, to a large extent, on the efficiency of the digestive system in breaking down the cellulose. An additional factor to be considered, however, with respect to the differing digestibilities of the feeds used in Trials 2 and 3, was the differing physical consistencies. The ground pellets would have been more easily digested than the coarse lucerne hay, presenting a larger surface area for enzymatic attack. On the other hand, the finer consistency would tend to increase the rate of passage of digesta through the alimentary tract, decreasing the efficacy of the microbial digestion of cellulose (Lloyd *et al.*, 1978). Finely ground food, therefore, would be expected to have a lower fibre digestibility, but in the present context, the low crude fibre content of the guinea pig pellets would have rendered this factor unimportant as far as its overall apparent digestibility and utilization was concerned.

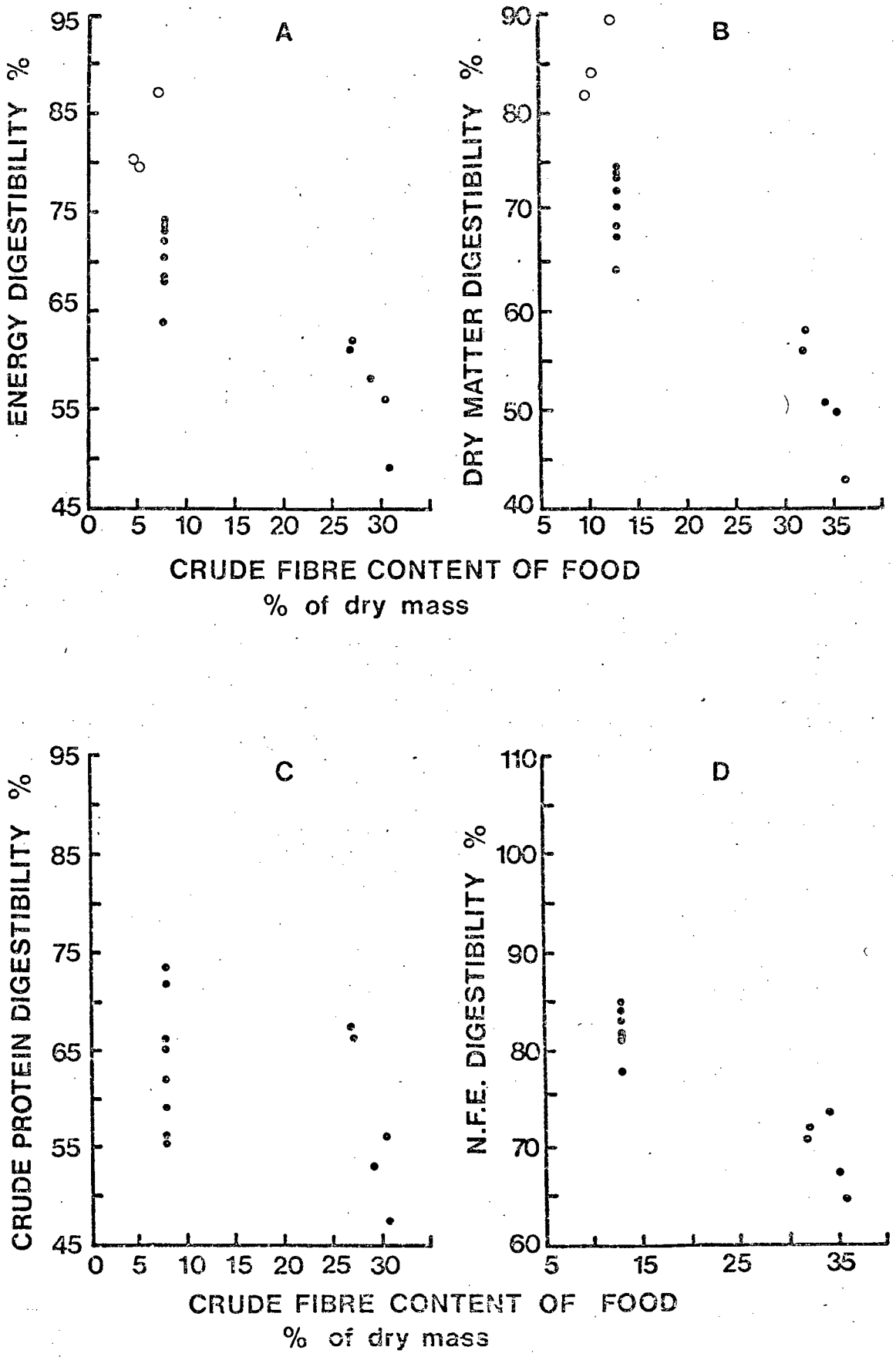

Fig. 2.2 Relation between crude fibre content of food ingested by hyraces and the coefficients of digestibility of A) energy, B) dry matter, C) crude protein, D) nitrogen-free extract (N.F.E.).

(o from Hume *et al.*, 1980)

On a feed with a high fibre content, the hyrax appeared to have as efficient a system in digesting fibre as the "ruminant-like" (Moir *et al.*, 1956) grey kangaroo, although true ruminants are undoubtedly superior (Table 2.4). The incorporation of the grey kangaroo in the category of "ruminant-like" mammals has been questioned by Kempton *et al.* (1976) on the basis of the low levels of methane production. Since the same is true of the hyrax (von Engelhardt *et al.*, 1978) the suggested inclusion of these animals in the same category (Moir, 1968) must also be questioned. This has received further attention in the following section. The lower protein digestibility by the hyrax (Table 2.4), even on a low fibre diet which would minimise the abrasive effect on the gut wall, may suggest a relatively greater loss of microbial protein from the hindgut than was found by Kempton *et al.* (1976) in the kangaroo and sheep. Hume *et al.* (1980) have shown, however, that the metabolic faecal nitrogen of *P. habessinica* is lower than in sheep. If this is true of *P. capensis* then apparently the hyrax is not as efficient in digesting protein. Considering that the size of the residual plant particles in the faeces of wild *P. capensis* were larger than in its food competitor, the ruminant klipspringer, *Oreotragus oreotragus* (Norton, 1980), the breakdown of food by the hyrax digestive system can not be as effective as in the ruminant. This could explain the lower protein digestibility found in the present study.

2.4.4 Energy assimilation by the hyrax

Despite the differing digestibility coefficients for energy in the three trials (73, 71 and 51 per cent - Table 2.3) none was exceptionally high and they were within the range found for several other herbivores (40 - 80 per cent, Davis & Golley, 1963). Thus with a comparatively low dry matter intake and an average digestibility of energy, the resultant amount of energy apparently assimilated by the digestive tract of the hyrax must have been low. The value of $272,3 \pm 75,7$ kJ.kg$^{-0,75}$.day^{-1} for the DEI from Trial 1 was similar to that found by Hume *et al.* (1980) for *P. habessinica* (279 ± 9 kJ. kg$^{-,75}$.day^{-1}). The higher values found in the subsequent trials were probably due to increased levels of activity of the animals. A nearer approximation of the energy available for use by the animals was given by the metabolizable energy intake (MEI) since urinary and gaseous energy losses were taken into account. Both the DEI and MEI of an animal can be predicted from the following equation relating the digestible energy requirements for maintenance to body mass:

Digestible Kcal per day = 98 ($W^{0,75}$) for humans, pigs and rats, where W = body mass in kg. (Lloyd *et al.*, 1978).

Metabolizable energy intake can be computed from this equation by assuming the energy lost in the urine and gases to be 7 per cent of the MEI (Lloyd *et al.*, 1978).

The equation above is based on the predicted metabolic rate derived

by Brody (1945) and Kleiber (1961). Since the basal metabolic rate (BMR) of *P. capensis* was lower than predicted (0,27 ml $O_2.g^{-1}.hr^{-1}$ - section 6) the actual values for DEI and MEI would obviously be lower than predicted as well. Therefore it is more appropriate, for comparative purposes, to express the DEI and MEI as a multiple of the actual BMR. Table 2.5 shows the DEI and MEI as a multiple of the BMR for hyraces in the three trials and for wild hyraces. The values for the latter animals have been calculated assuming that the energy value of the food eaten was constant throughout the year (16,33 $kJ.g^{-1}$ dry matter - Table 2.1), and that the dry matter intake was 31,67 $g.kg^{-1}.day^{-1}$ (from the data of Lensing, 1978). It was also assumed that the digestive and assimilative efficiency of the wild hyraces was the same as those of the animals in Trial 3. Furthermore, although the MEI was established experimentally only in Trial 3, I have assumed that the MEI represents the same proportion of the DEI for all the trials as well as for the wild animals. As the energy in the urine depends, to a large extent, on the protein ingested, the calculated MEI in Trial 1 and for the wild hyraces was probably an underestimate since the protein intake in both cases was lower than in Trial 3. However, the resulting error is likely to be insignificant as the urinary and gaseous energy losses were so small compared to the DEI.

For domestic cattle and sheep the daily digestible energy requirement for adult maintenance is normally calculated as 2,0 x BMR and 2,88 for pigs and rats (Lloyd *et al.*, 1978). The multiples for the hyraces were within this range, though for Trial 1 it was lower at 1,60 x BMR (Table 2.5).

TABLE 2.5 Digestible energy intake (DEI) and metabolizable energy intake (MEI) as multiples of basal metabolic rate (BMR) for *P. capensis* in three digestion trials, and in the wild.

	TRIAL 1	TRIAL 2	TRIAL 3	WILD*
Mass kg	2,92	2,12	2,38	2,26
BMR $kJ.day^{-1}$	380,55	276,29	310,18	294,41
DEI $kJ.day^{-1}$	608,30	741,81	667,00	600,40
MEI $kJ.day^{-1}$	545,71+	665,48+	598,37	538,62+
DEI as a multiple of BMR	1,60	2,68	2,15	2,04
MEI as a multiple of BMR	1,43	2,41	1,93	1,83

* Figures for the wild hyraces have been calculated from a dry matter intake of 38,82 $g.kg^{-0,75}.day^{-1}$, heat of combustion of food of 16,33 $kJ.g^{-1}$, and assuming DEI = 51,4% of GEI as in Trial 3.

\+ Assuming MEI = 89,71% of DEI as in Trial 3.

The MEI measured in the present three trials has also been termed "existence metabolism" (Gessamen, 1973), and is considered as a summation of the energy expended in basal metabolism, activity, thermoregulation and the specific dynamic action (SDA). Of these four components, that associated with thermoregulation was zero in Trials 2 and 3 since the experiments were conducted at temperatures within the thermoneutral zone (section 6). If SDA is calculated as 10 per cent of MEI (Lloyd *et al.*, 1978), the energy spent in activity can be calculated by difference. The partitioning of MEI into these three energy components is shown graphically in Fig. 2.3 for the three trials and for the wild hyraces.

The cost of free existence of an animal has been estimated as 3 x BMR, with a range of energy expenditure of 1,3 to 4 times BMR (Brody, 1945, from Gessamen, 1973) depending on the level of activity, production etc. Both the caged animals and the wild hyraces showed MEI as multiples of BMR, within this range and for the wild hyraces the calculated MEI can be assumed to be an estimate of the cost of free existence. Of particular interest was the fact that the multiple for the wild hyraces was within the range of the multiples for the caged animals. This is unusual considering that the wild hyraces would have had to expend energy for thermoregulation, production and activity in the wild, whereas the former two factors were negligible in the case of the caged animals. Furthermore the activity of the caged animals must have been curtailed by the limited space. Indeed, of the 33 monthly samples from wild hyraces, the calculated multiple of BMR was higher than that in Trial 2 (2,41 x BMR) for only 5 months

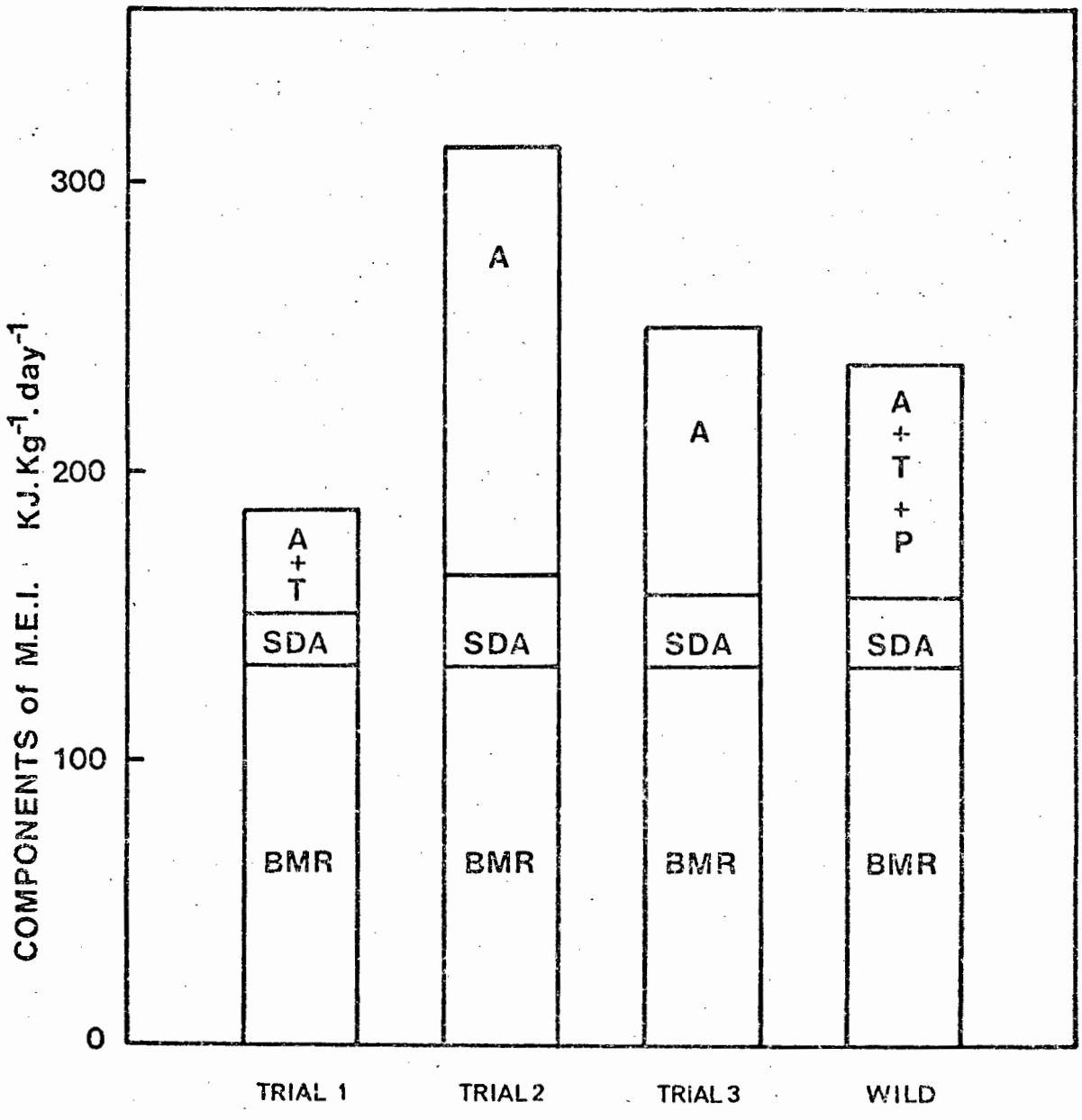

Fig. 2.3 Components of metabolizable energy intake of hyraces in three digestion trials and in the wild.

A = activity
T = Thermoregulation
P = Production
SDA = Specific dynamic action
BMR = Basal metabolic rate

(Appendix A). These figures calculated for the wild hyraces by extrapolation from laboratory studies, should be viewed with caution since they are based on several assumptions as outlined previously. A major source of error in these calculations could be the assumption that the moisture content of the stomach contents was 67 per cent, since this value was derived from captive animals fed lucerne hay, commercial pellets and water. However, even if a figure of 60 per cent was used to calculate the dry matter intake, the calculated MEI would be 2,21 x BMR, which would still be within the range of the values for the experimental animals. It should be noted too, that the moisture content of the stomach samples included saliva which was likely to be a substantial volume since the salivary glands are large in the hyrax (Grassé, 1956).

When allowing for the above assumed sources of error, from Fig. 2.3, the energy used by the wild hyraces for thermoregulation, production and activity was approximately 1,64 x BMR. Comparison between the caged and wild hyraces suggests that in the wild either one or all of these three factors demands a low energy expenditure. Since production would occur in a viable population to different extents throughout the year in the form of pregnancy and growth of young animals this factor cannot be considered negligible in terms of energy utilization. The energy expended on thermoregulation would depend on the ability of the hyraces to sun-bask, huddle or to select ambient temperatures as near to thermoneutrality as possible, thus minimising the cost of thermoregulation. This aspect has been investigated further in section 6. Finally the generally inactive

mode of life described for the hyrax (Sale, 1965a & 1969; Turner & Watson, 1965; Coe, 1962) would not demand a high level of energy expenditure and this observation would support the above suggestion.

2.4.5 Food Selection

Although food selection *per se.* was not investigated in the present study, selection for young shoots and leaves, normally higher in nutrients and lower in fibre was noted during casual observations made in captivity and in the field. In the wild, Acacia trees almost denuded of their foliage by hyraces suggest a preference for protein-rich herbage with a high moisture content. Several authors, however, have examined, in detail, food preferences and selection by the hyrax (Coe, 1962; Sale, 1965a; Turner & Watson, 1965; Hoeck, 1975; Lensing, 1978). Of these studies most are concerned with the various species of hyrax in Kenya and only Lensing (1978) has undertaken a comprehensive study of the feeding ecology of *P. capensis.* Nevertheless, there is general agreement that the rock hyraces are opportunistic feeders including a diverse selection of plants in their diet, of which 2 - 11 species form a major part of their diet (Hoeck, 1975). While there is some dispute as to whether several species of *Procavia* are predominantly grazers or browsers (Coe, 1962; Sale, 1965a; Turner & Watson, 1965; Hoeck, 1975), Lensing (1978) found that *P. capensis* both grazed and browsed, depending on the relative availability and possibly, the nutritive quality of the herbage. For all species, selection appears to be

dependent on the local and seasonal availability, with preferences for young shoots, leaves, twigs, flowers and fruits with high nutrient and incidentally high moisture content. Under severe drought conditions, when these are not available, less nutritious food is eaten, such as dry grasses and even the bark of trees (Hanse, 1962; Sale, 1965a; Turner & Watson, 1965; Hoeck, 1975; Lensing, 1978), together with an apparent preference for plants with a high moisture content if available (Sale, 1965a). During a severe drought in the Robertson district of the Cape Province, *P. capensis* were observed eating the latex-rich *Euphorbia mauritanica*, despite the ulcerated state of their lips. The drought had lasted for approximately four years and little vegetation was available besides these toxic plants (G.N. Louw, personal communication).

From the present analyses of the stomach contents of the wild hyraces (Table 2.6), the relatively constant composition over a period of six months indicates either an efficient system of selection, if not of plant species, then of plant parts, or alternatively that during these months, the composition of the herbage was relatively constant and abundant. Unfortunately, the seasonal composition and phenology of plants in the Nieuwoudtville area is unknown and also no data on stomach contents were available for the winter months, when the small amount of rain for the year falls. Thus it is not possible to ascertain whether the composition of the stomach contents was constant throughout the year and if this was so, whether this constancy was influenced by the uniformity of nutrient availability or selection by the hyraces.

TABLE 2.6 Monthly analyses of wild hyrax stomach contents (all figures are per cent by mass of dry matter)

	Crude Fibre %	Crude Protein %	Hexane Extract %	Ash %	N.F.E. %	Number of Samples Combined
September 1976	25,34	11,48	0,99	7,68	54,51	8
October 1976	21,29	10,53	2,67	7,34	58,17	11
December 1976	21,48	12,08	3,31	8,37	54,76	10
January 1977	23,32	10,95	2,25	8,35	55,18	13
February 1977	23,34	10,14	2,49	7,75	56,28	10
March 1977	21,40	11,70	3,18	7,87	55,85	8

In terms of nutrient and energy intake, food selection is important when viewed in conjunction with the quantity eaten and the efficiency with which it is digested - factors which change with seasonal changes in plant composition and phenology. Selection for nutrient-rich plants has obvious advantages considering that a high nutrient content is usually associated with a high energy content and furthermore, selection for food with a low fibre content minimises losses due to poor digestibility. An additional advantage gained through selection of low fibre food is the possible conservation of water. Withers (personal communication) has shown in rodents, that food with a low digestibility tends to increase faecal water loss by virtue of the greater quantity of waste products which must be voided, carrying moisture with it. This would be particularly relevant to *P. capensis* which must be totally reliant on moisture in the food during the frequent droughts in the Cape Province.

While selection may not be of great importance to an animal in a nutrient-rich environment, in nutrient-poor vegetation and under drought conditions, selection may be a factor determining whether the nutrient, energy and water requirements of the animal are met or not.

Thus returning to the two hypotheses originally posed, it appears that the hyrax, *P. capensis*, does not have a particularly efficient digestive system and the selective feeding habits serve to augment the energy assimilated, by virtue of the improved quality of herbage eaten. Although the food and energy intake of the hyrax is lower

than predicted for "standard" eutherian mammals, this comparison is deceptive since the deviation in the metabolic rate of the animals from that predicted, is not taken into account. When the energy assimilated is expressed as a function of the metabolic rate, the energy consumption of the hyrax falls within the range found for other eutherian mammals. The lower than predicted intake of energy is thus largely due to the low basal metabolic rate. The present study also indicates that in the wild the energy expenditure is reduced further by energy conservation in thermoregulation and in a conservative level of activity.

SECTION 3

FERMENTATION AND THE PRODUCTION OF VOLATILE FATTY ACIDS IN THE ALIMENTARY TRACT OF THE ROCK HYRAX *PROCAVIA CAPENSIS*

3.1 INTRODUCTION

The abundance of cellulose in the environment provides a rich source of energy for animals that are able, either directly or indirectly, to break the constituent 1-4, β-glucosidic linkages in this carbohydrate. In mammals this ability to digest cellulose resides in the bacterial population of the rumen or rumen-like structures and the caecum. It has been suggested by Kinnear *et al.* (1979) that the pre-gastric fermentation system of microbial digestion confers an advantage on mammals by expanding their nutritional niche and enabling them to consume food poor in nutrients, or containing toxic substances, thus avoiding competition with other mammals unable to utilize such foods. This advantage is readily demonstrated by the success of ruminants in nutrient poor environments. Although pre-gastric fermentation is usually associated with a complex voluminous stomach, a bacterial population may be able to reside in less complex structures, providing the conditions are hospitable, and in this respect the lack of proteolytic enzymes would be a prerequisite to bacterial survival.

The simple stomach of many granivorous and herbivorous mammals is divided into two distinct regions. The proximal region, termed the oesophageal or cardiac region, is lined by stratified squamous epithelium and is separated from the normal glandular pyloric region by a ridge, comparable to the margo-plicatus of the horse. The simple stomach of the hyrax has the same structure, the cardiac region being a highly distensible sac, slightly larger than the

pyloric region and completely covered with stratified squamous epithelium (Elias, 1946 and personal observations). The lack of glandular epithelium in this proximal region implies that it is a storage organ, where stasis of contents could occur. Thus depending on the length of time of storage, fermentation of the contents would be possible due to the accumulation of micro-organisms (Bauchop, 1971). In the hyrax, feeding is restricted to two main periods of the day, one in the morning and one in the evening, both of which are less than 1 hr (Sale, 1965a; Millar, 1972). Sporadic feeding may occur throughout the day, however. The plant material eaten is stored between these periods, for 4 hr in the cardiac stomach with some of the ingesta remaining in the whole stomach for 24 hr or more (Clemens, 1977). In addition, stasis of digesta and fermentation occurs in the proximal and distal caeca (Clemens, 1977; von Engelhardt *et al.*, 1978), the latter being an unusual feature of the alimentary tract of the hyrax.

Unlike ruminants and ruminant-like herbivores where the major site of microbial fermentation is the fore-stomach, monogastric herbivores rely more on the hind-gut for cellulose digestion. This has been quantitatively established for the horse, pig, rabbit and rat by Elsden *et al.* (1946). In the East African hyrax, *Procavia habessinica*, fermentation with high concentrations of total volatile fatty acids (VFA) occurs in the cardiac stomach, and the proximal and distal caeca (Clemens, 1977; von Engelhardt *et al.*, 1979). Information on the concentrations and relative proportions of individual VFA along the length of the alimentary tract of any hyrax species is lacking, however.

Since fore-stomach fermentation is considered to be a feature of ruminant-like metabolism, it seems likely that the hyrax would be included in this group of herbivores. In order to establish ruminant-like metabolism in the hyrax, it is necessary to demonstrate a high content of stearic rich, saturated fatty acids in the depot fat and a low glucose level in the blood, which are additional characteristics of ruminants.

In view of the unusual feeding behaviour, the peculiar anatomy and evidence of fermentation in the alimentary tract of the hyrax, the purpose of this investigation was to determine whether the rock hyrax *Procavia capensis* has ruminant-like metabolism. Since studies on cellulose digestion in *P. capensis* have not been undertaken previously, the concentrations and proportions of VFA in the different regions of the alimentary tract have been examined, as well as the lactic acid content of the cardiac stomach, the composition of the depot fat and the glucose level in the plasma.

3.2 PROCEDURE

Six adult hyraces were killed between 2 and 7 hr post-feeding, by an intra-peritoneal injection of Nembutal (Abbot Laboratories). The alimentary tracts were ligatured at the distal ends of the oesophagus and rectum, removed and stored at -20°C until analysis. These

animals had been fed on lucerne hay and commercial guinea pig pellets with water *ad lib.* Additional tracts were obtained from two hyraces killed in the wild approximately 2 hr post morning feeding and one approximately 10 hr post morning feeding.

3.2.1 Contents of the alimentary tract

In a preliminary study the alimentary tract of 10 hyraces was divided into several regions (Fig.3.1) and the pH of the contents estimated using universal indicator pH paper. The contents of each region were weighed and a representative portion dried at 70°C and reweighed for dry matter estimation.

3.2.2 VFA determination

A sample of wet gut contents from each region was homogenised with an appropriate volume of distilled water. An aliquot of the homogenate was weighed and dried at 70°C. The rest of the homogenate was weighed and between 1 and 2 ml of iso-butyric acid added as an internal standard since it had been established that iso-butyric acid was not detectable in the gut with this method of extraction. The mixture was centrifuged at 1000 *g* for 20 min and the supernatant again centrifuged at 65 000 *g* for 15 min. The final supernatant was stored, frozen, in sealed glass vials until used for column chromatography. The supernatant was injected directly onto a glass spiral column (2,6 m x 3 mm) containing Chromosorb 101 (80 - 100 mesh)

in a Hewlett Packard 5750 Research Chromatograph with dual flame ionization detectors. Nitrogen was used as the carrier gas (40 ml/min). The signal was processed on an H.P. 3352A laboratory data system. The performance of the column was monitored by regular analysis of a standard mixture of volatile fatty acids. VFA concentrations were expressed as mg/g dry matter and converted to mmol/g dry matter using the molecular weight of the individual acids.

3.2.3 Lactate analysis

Extracts of the cardiac stomach contents used for VFA analysis were also analysed for lactate using the method of Gutman and Wahlefeld (1974). In an additional alimentary tract, the contents of all the regions were separated and squeezed through cheesecloth. The liquid recovered was then analysed for lactate using the same method.

3.2.4 Depot fat analysis

Subcutaneous fat obtained from the pelvic region was minced and the lipid extracted with chloroform/methanol using the method of Bligh and Dyer (1959). The extracted lipid was converted to methyl esters with 14 per cent boron trifluoride in methanol (Metcalfe *et al.*, 1966; AOAC methods, 1975). The esters were analysed in a 3 m x 6 mm glass column packed with 5 per cent DEGS on 100 - 120 mesh Chromosorb W. The signal was processed on an HP 3352 laboratory data system.

3.2.5 Analysis of blood glucose

Blood was taken from the femoral vein of eight hyraces that had been starved for 12 hr. The glucose content of the plasma was then analysed using the method of Werner *et al.* (1970) (Boehringer Mannheim Test-Combination).

3.3 RESULTS

3.3.1 Structure and contents of the alimentary tract

The structure of the alimentary tract of the hyrax is unusual, particularly because it bears a second caecum and the relative stomach size is larger than that of other monogastric herbivores (Fig. 3.1). The proximal caecum (PC), termed the proximal sacculation by Clemens (1977), is a large sacculated organ separated from the small intestine by a sphincter. A second sphincter occurs close to the first and separates the caecum from the colon. The colon (Co) however, is proximally distended and sacculated and does not differ in appearance from the caecum itself. This proximal part of the colon (PCo) has been referred to as the distal sacculation by Clemens (1977). A sphincter does not separate this expanded portion of the colon from the narrower tube-like continuation and is thus referred to here as the proximal colon. The ascending colon forms an expanded, non-sacculated region, referred to by several authors (George, 1874;

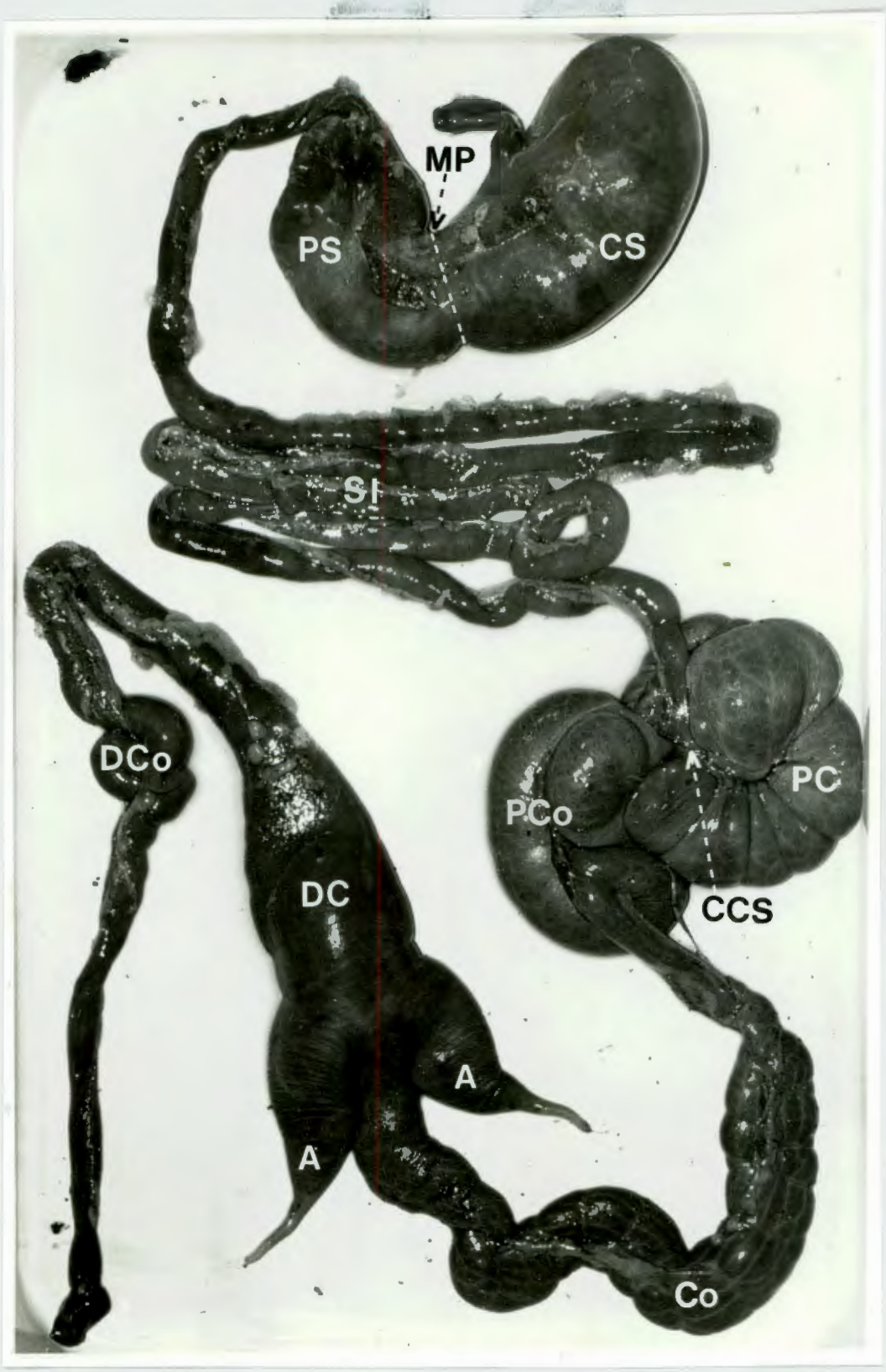

Fig. 3.1 The alimentary tract of *P. capensis*

A - appendices; Co - colon;
CCS - caeco-colonic sphincter; CS - cardiac stomach;
DC - distal caecum; DCO - distal colon and rectum;
MP - position of margo-plicatus;
PC - proximal caecum; PCo - proximal colon;
PC - pyloric stomach; SI - small intestine.

Grassé, 1956; von Engelhardt *et al.*, 1978) as the distal caecum (DC). It bears two "horns" or appendices (A) referred to by Clemens (1977) as the "caeca".

The contents of the different regions in relation to the body mass are shown in Table 3.1. The total stomach contents constituted 3,9 per cent of the body mass with a range of 2,4 - 7,1 per cent. The two portions of the stomach contents differed slightly in moisture content, the cardiac stomach being dryer than the pyloric stomach (approximately 80 per cent and 83 per cent moisture respectively) but this difference was not statistically significant (Table 3.2). The contents of the proximal caecum and proximal colon together also constituted 4,1 per cent of the body mass with a moisture content of approximately 85 per cent, while the distal caecum and its appendices contained 3,1 per cent of the body mass with a moisture content of approximately 82 per cent. The digesta reaching the descending colon and rectum were dryer with a moisture content of approximately 80 per cent (Table 3.2).

3.3.2 pH of gut contents

The pH of the cardiac stomach contents varied between 4 and 6. In both of the wild hyraces killed about 2 hr after feeding, the cardiac stomach contents had a pH of 5,5. The animal shot 10 hr post feeding had a lower pH of 4,5.

TABLE 3.1 Mass and proportion of contents in the various portions of the alimentary tract of *P. capensis* (mean body mass = 2,21 kg ± 0,44)

Region	n	Mean wet mass of contents		Mean wet contents as % of body mass		Mean % of total gut contents	
		g	±S.D.	%	range	%	±S.D.
Stomach	10	92,0	55.8	3,9	2,4-7,1	28,3	6,8
Proximal caecum + proximal colon	10	88,7	15,9	4,1	3,2-5,7	30,1	7,4
Distal caecum + appendices	10	67,3	19,0	3,1	1,8-4,0	23,1	6,4
Distal colon + rectum	10	28,6	13,5	1,3	0,8-1,8	9,5	1,8

TABLE 3.2 Mean VFA concentrations in different regions of the alimentary tract of *P. capensis*

Region	n	Dry mass contents as % of wet mass		pH range	Total VFA Concentration			
		g dry mass/ 100g wet mass	± S.D.		mg/g dry matter	range	mmoles/g dry matter	range
Cardiac stomach	9	20,3	7,6	4-6	22,2	5,3-46,3	0,4	0,09-0,77
Pyloric stomach	9	16,7	4,6	3-4	5,3	0,8-22,4	0,1	0,01-0,37
Proximal caecum	9	14,9	3,5	6-8	39.2	8,9-101,1	0,6	0,15-1,85
Proximal colon	9	14,9	2,9	6-8	31,6	3,9-71,2	0,5	0,06-1,12
Distal caecum	9	15,9	2,0	6-7	17,1	2,7-37,7	0,3	0,04-0,58
Appendices	9	17,8	1,9	6-7	18,3	5,2-32,1	0,3	0,08-0,50
Descending colon + rectum	9	20,2	7,6	6-7	7,9	1,1-15,6	0,1	0,02-0,26

Lower pH values were found in the pyloric stomach (range 3 - 4), while in the rest of the alimentary tract the contents were at a near neutral pH (Table 3.2).

3.3.3 Concentrations of volatile fatty acids

The major sites of fermentation in the alimentary tract of *P. capensis* were found to be the proximal caecum and proximal colon with mean VFA concentrations of 39,2 and 32,6 mg/g dry matter content respectively (Table 3.2). Both the cardiac stomach and distal caecum with its appendices contained appreciable concentrations of 22,2 and 17,1 mg/g dry matter content, respectively. The concentration in the stomach however, was not always higher than that in the distal caecum. In the two wild hyraces killed 2 hr after feeding, the VFA concentration in the cardiac stomach was high (43 and 21 mg/g dry matter) and the stomachs were full. A lower concentration (14 mg/g dry matter) occurred in the stomach of the animal shot approximately 10 hr post feeding, with very little plant matter remaining in the cardiac stomach.

Lower concentrations of VFA were recorded in the pyloric stomach. The mean concentration was found to be 5,3 mg/g dry matter which is significantly lower ($P < 0,01$) than that in the cardiac stomach. The contents of all but one of the pyloric stomachs had concentrations of approximately 6 mg/g dry matter or less, although there was one rather high value of 22 mg/g dry matter. High VFA concentrations

in the proximal caecum and proximal colon were recorded with a small but significant ($P < 0,05$) difference between them, the concentration in the proximal colon being lower. In the distal caecum and appendices concentrations of 17,1 and 18,3 mg/g dry matter respectively, were recorded, although no significant difference was found between these two regions. This was expected since the two compartments are continuous. The final region of the alimentary tract, the descending colon and rectum, had a mean concentration of 7,9 mg/g dry matter. Since the last region contained both pelleted and unpelleted material, variations in the concentration would be expected.

3.3.4 Proportions of individual volatile fatty acids

The proportions of individual VFA in the alimentary tract of *P. capensis* are shown in Table 3.3. In the cardiac stomach, acetic acid was found to be predominant constituting 87 per cent of the total VFA with low proportions of propionic and butyric acids (9 per cent and 3 per cent respectively). In the pyloric stomach, the only detectable VFA was acetic acid, and this was in low concentrations. The proportions of VFA in the proximal caecum and proximal colon were identical. Acetic acid dominated but a higher proportion of both propionic (22 per cent) and butyric (8 per cent) acids was present here than in the cardiac stomach. In the distal caecum and the appendices, the distal colon and rectum, acetic acid varied from 75 per cent - 78 per cent while the proportions of propionic acid

TABLE 3.3 Molar proportions of individual VFAs in different regions of the alimentary tract of *P. capensis*

Region	n	Acetic	Propionic	Butyric	Valeric
		%	%	%	%
Cardiac stomach	9	87	9	3	1
Pyloric Stomach	9	100	-	-	-
Proximal caecum	9	69	22	8	0,3
Proximal colon	9	69	22	8	-
Distal caecum	9	75	20	4	0,1
Appendices	9	77	20	2	0,02
Distal colon + rectum	9	78	17	4	-

were between 17 per cent - 20 per cent and butyric acid between 2 per cent - 4 per cent.

3.3.5 Lactate concentrations

A high mean lactate concentration of 1,9 mg/g of contents (wet) was found in the cardiac stomach, with lower concentrations occurring in the rest of the tract (Table 3.4). For comparative purposes, these concentrations have been converted to mmol/100 g dry matter in Table 3.4.

3.3.6 Analysis of depot fat

The depot fat of *P. capensis* was found to have a high proportion of linolenic and linoleic acids characteristic of non-ruminant herbivores (Table 3.5).

3.3.7 Blood glucose

A mean glucose level of 77,3 mg/100 ml was found in the plasma with a wide variation of 44,0 - 103,2 mg/ml. These values may be higher than normal since the animals were somewhat stressed by the procedure employed in blood sampling. Nevertheless they fall within the range established for non-ruminant herbivores (Moir, 1968).

TABLE 3.4 Lactic acid concentrations in different regions of the alimentary tract of *P. capensis*

Region	n	mg lactate/g wet contents		mmoles lactate/100g dry matter	
		mean	range	mean	range
Cardiac stomach	10	1,85	0,15-4,66	27,0	5,0-42,0
Pyloric stomach	1	0,85	-	6,0	-
Proximal caecum	1	0,04	-	0,3	-
Proximal colon	1	0,03	-	0,3	-
Distal caecum	1	0,20	-	1,0	-
Appendices	1	0,25	-	1,0	-

TABLE 3.5 Proportions of major fatty acids in the subcutaneous fat from the pelvic region of *P. capensis* (*cis* and *trans* acids not distinguished).

Fatty Acid		% of total fatty acids
Myristic	(C14:0)	5,5
Palmitic	(C16:0)	22,3
Palmitoleic	(C16:1)	4,5
Stearic	(C18:0)	10,2
Oleic	(C18:1)	37,8
Linoleic	(C18:2)	4,7
Linolenic	(C18:3)	10,3

3.4 DISCUSSION

The possibility that the hyrax may be a ruminant-like herbivore has been suggested by Moir (1968), but evidence to support this has been largely lacking. The data presented here indicate that the digestive system of the hyrax has features of both monogastric and ruminant-like herbivores.

Structurally, the stomach of the hyrax does not resemble the large sacculated stomach of ruminant-like herbivores. Although the stratified epithelium lining the cardiac pouch of the stomach is

similar to the rumen epithelium, several monogastric herbivores have a constricted stomach with a part bearing this type of epithelium. These include several rodents, the tapir, rhinoceros (Bensley, 1902) and the horse (Sisson & Grossman, 1953). In addition, a reticular groove, which Black and Sharkey (1970) have considered to be an obligatory adaptation in ruminant-like herbivores, is absent in the stomach of *P. capensis*. Although George (1874) has described a structure resembling a rudimentary reticular groove in the cardiac stomach of *P. capensis*, I have not observed this feature and histologically the dorsal aspect of the cardiac pouch does not differ from the rest of this region (unpublished data). Nevertheless, considering the close proximity of the oesophageal entrance to the glandular pyloric stomach an oesophageal groove may not be necessary to divert liquids (especially milk) away from the fermentative region. The same has been described in the potorine marsupial, *Bettongia penicillata* (Kinnear *et al.*, 1979).

Whereas the contents of the large, compartmented stomach of ruminant-like herbivores constitute approximately 15 per cent of the body mass (Moir, 1968), the contents of the simpler stomach of the hyrax constitute 3 - 7 per cent of the body mass, a similar proportion to that in the pig and rabbit (3 - 4 per cent and 4 - 9 per cent respectively) (Elsden *et al.*, 1946). These percentages, however, are higher than those of other monogastric herbivores such as the horse and the rat (approximately 2 per cent and 1 per cent respectively (Elsden *et al.*, 1946). Nevertheless, within the simple stomach of the hyrax, fermentation of the ingesta occurs, as shown by the higher concentrations

of VFA here. The average concentrations in the cardiac stomach (2,2 g/100 g dry matter, 0,4 mmol/g dry matter or approximately 101 mmol/l) are high when compared to other monogastric herbivores such as the horse (0,45 g acetic acid/100 g dry matter), pig (1,52 g acetic acid/100 g dry matter) and rabbit (0,3 g acetic acid/100 g dry matter) (Elsden *et al.*, 1946), and are similar to those found in the stomachs of ruminant-like herbivores. For example, Bauchop and Martucci (1968) found the concentrations of VFA in the stomach of ruminant-like monkeys *Presbytis entellus* and *Presbytis cristatus* to range from 0,5 - 1,4 mmol/g dry matter and in the Quokka, *Setonix brachyurus* concentrations of 18 - 147 mmol/l of ingesta have been found (Moir, 1965). Although rumination in the hyrax has been described by Hendrichs (1963), I have never observed hyraces to ruminate in the wild or in captivity, even when fed a high fibre diet. Hyraces do, however, often grind their molar teeth, a behaviour that gives the illusion of rumination.

The regions of the alimentary tract of *P. capensis* in which pH values are higher correspond to those regions of higher VFA concentrations. The pH variation found in the cardiac stomach seems to indicate that the low acidity normally required for efficient cellulose fermentation is not continuously maintained. Fermentation in the cardiac stomach appears to be unusual in that acetic and lactic acids predominate. This suggests the presence of fermentative micro-organisms which are tolerant to relatively acid conditions. A pH of approximately 5, however, would permit the growth of lactic acid producing bacteria as shown by Bauchop (1971) in the rhesus monkey. Lactic acid also

occurs in high concentrations in the stomach of the rabbit (Griffiths and Davies, 1963), but the production of lactic acid is dependent on the ingestion of faecal pellets. Since no hyrax stomachs have been found to contain faecal pellets and coprophagy is a rare occurrence in the hyrax, the production of lactic acid in this animal differs from that in the rabbit.

Barnett (1952) and Barnett and Duncan (1953) found that both acetic and lactic acids tend to predominate in the anaerobic fermentation of grass/water mixtures, analogous to silage fermentation. In the cardiac stomach of *P. capensis*, the anaerobic condition, the pH, temperature and moisture content of the ingesta, as well as the predominance of acetic and lactic acids, indicate that silage-like fermentation occurs. It cannot be determined from the present study whether a resident microbial population or bacteria ingested with the vegetation are responsible for this fermentation.

Fermentation does not take place to any appreciable extent in the pyloric stomach as is evident from the low concentrations of VFA. This is consistent with the low pH and the secretion of proteolytic enzymes by the glandular epithelium which would be detrimental to bacterial survival. The concentration of acetic acid found in the pyloric stomach was low enough to assume that this acid was not completely absorbed in the cardiac stomach and was carried with the ingesta into the pylorus.

The proportions of individual VFA found in the proximal caecum and

proximal colon are similar to those found in the stomachs of most ruminants and ruminant-like herbivores (Moir, 1968). They are also similar to those found in the colon of the horse and the caecum of the pig (Elsden *et al.*, 1946). In this region the pH remains near neutral and probably a more stable and diverse microbial population exists than in the cardiac stomach. In the more distal fermentation regions the proportions of propionic and butyric acids decreased while acetic acid increased. This may indicate either a preferential absorption of propionic and butyric acids along the colon and in the distal caecum or a greater production of acetic acid in the distal caecum and appendices. In the absence of data on relative production and absorption rates of these acids an explanation for this observation is not possible.

The nutritional importance of the products of stomach fermentation to the hyrax remains speculative. Fermentation could aid later enzymatic digestion by initiating the breakdown of carbohydrates as well as providing a protein source in the microbial population carried through to the pyloric stomach. In view of the high concentrations of VFA found in the proximal caecum and proximal colon, these regions are probably responsible for the major part of carbohydrate digestion. The function of the distal caecum and appendices in relation to fermentation remains uncertain. It seems probable, however, that microorganisms are carried with the digesta from the proximal caecum and proximal colon and continue their fermentative activity in the distal caecum and appendices. Since the concentrations of VFA and the moisture content of the digesta decreased in this distal expanded

region, absorption of the end products of fermentation together with some water probably takes place here and in the distal colon and rectum.

If a definite category of ruminant-like herbivores is to be used, then the hyrax *P. capensis* must be excluded from the group of truly ruminant-like herbivores since the hindgut, particularly the proximal caecum and proximal colon, appears to be the major site of fermentation, with concentrations of VFA higher than in the cardiac stomach. Furthermore the concentrations of plasma glucose are similar to those found in monogastric herbivores, and the high proportions of unsaturated linoleic and linolenic acids in the depot fat indicate that the hyrax does not have a ruminant-like metabolism. Kinnear *et al.* (1979) have expressed the futility of describing animals as "more or less ruminant-like", since the variability in digestive systems precludes categorization of this kind. With this, I am in total accord, the hyrax being an example of such variation.

Compared with ruminants, however, the specialized digestive system of the hyrax appears to have several advantages. The possession of both a pregastric and a caecal fermentation system allows them to exploit the benefits of both. The ability of the stomach bacteria to use non-protein nitrogen in the form of recycled urea (Hume *et al.*, 1980) for the subsequent production and use by the host of high quality microbial protein is clearly advantageous, particularly when coupled with the low nitrogen requirements of the hyrax (Hume *et al.*, 1980). Furthermore, the stomach fermentation of cellulose or any carbohydrate

resistant to enzymatic digestion by the host, producing volatile fatty acids is as advantageous to the hyrax as it is to ruminants in exploiting an energy source otherwise unavailable. However, one of the disadvantages of this pathway of carbohydrate digestion for the ruminant is that the amount of glucose available for the animal is curtailed, and of the volatile fatty acids, only propionate acts as a gluconeogenic precursor, another source being amino acids. Yet glucose is necessary in ruminants for the production of $NADPH_2$ for lipogenesis from acetate and butyrate (Lindsay, 1970; Annison & Armstrong, 1970). Lactate, however, can be used as a source of glucose and thus, in the hyrax, the relatively high levels of this acid in the stomach could explain the higher blood glucose levels. Glucose could then be considered as important a source of energy for the hyrax as the fatty acids and the carbohydrate metabolism rather more stable than in the ruminant.

Caecal fermentation in the hyrax would further reduce the fibrous food which escaped digestion in the stomach due to the shorter time exposed to bacterial action and the larger particle size in the absence of rumination. The digestion here would furnish the animal with additional fatty acids and vitamins and the smaller particle size of the waste material would reduce the abrasive effect of the faecal pellets on the gut lining. At the same time, however, microbial protein lost through the lack of subsequent enzymatic digestion would be an unavoidable disadvantage of caecal fermentation.

SECTION 4

CALCIUM, MAGNESIUM AND PHOSPHORUS EXCRETION IN THE ROCK HYRAX *PROCAVIA CAPENSIS*

4.1 INTRODUCTION

Among the cliffs and rocky screes inhabited by the rock hyrax or dassie, a white accretion is often found, sometimes associated with a brown tar-like substance, the latter commonly known as "klipsweet". Both the white and brown accretions are urinary products, the latter sometimes combined with faecal matter.

Louw *et al.* (1973) noted that the "klipsweet" occurred when the communal urinating sites were sheltered from the rain, usually beneath an overhang, whereas the white precipitate, sometimes forming stalagmites, occurred when the urinating sites were on a steep rock face. In the latter situation the rain had leached out the soluble salts leaving the white precipitate. Their analysis of this precipitate revealed a predominance of calcium carbonate.

Hyrax urine, collected in the laboratory, divides into two distinct portions: a precipitate, mainly calcium carbonate and the supernatant, which often turns a dark rust colour on exposure to air. Urine taken directly from the bladder contains the calcium carbonate in suspension, a precipitate forming after exposure to air.

Urinary excretion of calcium carbonate has been observed in several other animals such as rabbits (Cheeke and Amberg, 1973) and pack rats (Shirley and Schmidt-Nielsen, 1967) - both these animals excrete a rust coloured urine. Shirley and Schmidt-Nielsen (1967) reported

that the urine of hamsters was "thick and creamy", a description that accords with our own observations of guinea pig urine. The creaminess in the urine of the guinea pig is also due to a calcium carbonate precipitate. White encrustations on rocks, assumed to be the urinating sites of *Petromus typicus* (Petromyidae) (Jarvis & Withers, personal communication), were found to contain calcium carbonate.

Since calcium excretion takes place mainly via the gastro-intestinal tract in most mammals, it is remarkable that such apparently large quantities of undissolved calcium carbonate appear in the urine of the above-mentioned animals. The present investigation was therefore undertaken to examine this unusual feature and to establish the major pathways of calcium, phosphorus and magnesium excretion in the hyrax, using two diets with different levels of the three elements. Since the diets used were very different, only general tendencies have been examined. The experiments were not designed to determine the interrelationships between the elements though some speculations in this respect have been made.

In addition, the levels of the three elements in body tissues and plasma have been determined to establish whether they occur at similar levels to those found in other mammals. Stomach contents of hyraces shot in the wild have been similarly analysed in an attempt to relate the experimental results to field conditions.

4.2 MATERIALS AND METHODS

4.2.1 The balance trials

Two experiments were conducted using rations with different levels of calcium, phosphorus, magnesium, crude fibre, crude protein, hexane extract and ash. Prior to the balance trials, the two groups of experimental animals were each kept in out-door pens for about a month, during which time they received the ration to be used in that trial. Thereafter, they were kept indoors in individual cages, for seven days, to become accustomed to the experimental procedure. A balance trial was then conducted over five days in the first experiment and over ten days in the second.

During the course of the balance trials, the following regime was employed. All data were collected in the morning at 0800h. On the morning of day 2 the food and water intake and the urine produced during day 1 (the first experimental day) was measured. Faecal collection was started only on day 4, i.e. that produced during day 3, thus allowing for a two day rate of passage (section 2).

4.2.1.1 *Experiment 1*

Nine adult male hyraces of average mass 2,3 kg were used. Each cage was placed on a stainless steel fine-mesh tray, beneath which was a PVC funnel leading into a glass measuring cylinder. Faeces were

retained on the mesh tray and urine was collected in the measuring cylinder.

Each animal was given a predetermined amount of food daily and a known volume of water. The ration given consisted of commercially prepared pelleted food containing 0,88 per cent calcium, 0,88 per cent phosphorus, 0,24 per cent magnesium, 7,7 per cent crude fibre, 21,0 per cent crude protein, 1,3 per cent hexane extract and 7,6 per cent ash on a moisture free basis. Food left from the previous day was removed, dried and weighed to determine the intake. Water intake was recorded.

Each day the volume of urine excreted was recorded, the PVC funnel rinsed with dilute hydrochloric acid and distilled water and the urine sample and washings retained in a sealed plastic container and frozen. At the end of the experimental period, the daily urine samples from individual animals were pooled, made up to a known volume with hydrochloric acid and distilled water and an aliquot retained and frozen for later analysis.

Similarly, faeces collected daily were stored in plastic containers in a freezer until the end of the experiment when the daily samples collected from each animal, were combined and frozen. The experiment was terminated when five consecutive urine and faecal specimens had been taken. A collection period of only three days was possible for one animal. The results for this animal have been included with the rest. At the end of the experimental period, the animals were

anaesthetised with an intra-peritoneal injection of pentobarbitone sodium (Nembutal, Abbot). A blood sample was taken from the heart of each animal, centrifuged in a clinical centrifuge for 15 min and the plasma stored in vials and frozen. After death, the kidneys, liver, seft semimembranosus muscle and the nineteenth left rib were removed, placed in plastic bags and frozen for later analysis.

4.2.1.2 *Experiment 2*

In this experiment, three adult male and two adult non-gravid female hyraces of average mass 2,4 kg were used.

Lucerne hay was used as the feed. It was coarsely ground in an attempt to prevent selection of leaves and not stems. Analysis showed this ration to contain 1,41 per cent calcium, 0,20 per cent phosphorus, 0,36 per cent magnesium, 29,9 per cent crude fibre, 18,5 per cent crude protein, 1,4 per cent hexane extract and 9,5 per cent ash on a moisture free basis.

The procedure used in the first experiment was repeated, but the collection period was extended to ten days. No tissue or blood samples were taken.

On completion of this balance trial it was discovered that one animal was in severe negative calcium and magnesium balance. The results from this animal have not been included and the results shown are those obtained from only four animals.

4.2.2 Field specimens

Samples of stomach contents were available from wild animals shot on two adjacent farms in Niewoudtville (Western Cape 3119 C.A.). The samples collected every month over a period of a year were dried, milled and analysed for calcium, phosphorus and magnesium content. Six pooled monthly samples were analysed for crude fibre, crude protein, hexane extract and ash.

4.2.3 Chemical analyses

An aliquot of feed, refused feed, faeces and body tissue was dried, milled and then again dried to a constant mass at 103°C. A 2 g sample of each was ashed at 540°C for five hours. The ash was dissolved in 5 ml 20 per cent hydrochloric acid and made up to 100 ml. This stock solution was suitably diluted for calcium and magnesium determinations by atomic absorption spectrophotometry. A nitrous oxide flame and potassium for ionization suppression was used (Varian Techtron, 1972). Phosphorus was determined using the photometric method of Hanson (1958). Standard A.O.A.C. (1960) methods were used for the proximal analyses, except in the case of fat extraction where hexane was substituted for ether.

Urine and serum samples were analysed for calcium and magnesium by atomic absorption (Varian Techtron, 1972) while inorganic phosphates were determined using the photometric method of Delsal and Manhouri (1958).

Total plasma protein was determined using the biuret method of Weichselbaum (1946).

4.3 RESULTS AND DISCUSSION

4.3.1 Calcium

4.3.1.1 *Balance trials*

On the pelleted ration, the mean mass gain over the experimental period was 1,1 per cent of the original mass (range - 6,6 per cent to + 6,2 per cent) while a mean mass gain of 2,6 per cent was obtained on the lucerne ration (range 0 - 4,4 per cent).

Table 4.1 shows a net negative balance for calcium on the pelleted diet, the excess excreted representing 20,7 per cent of the calcium intake per day. The animals on the lucerne ration appeared to be in better calcium balance with a positive balance of 7,8 per cent of the intake per animal per day being recorded (Table 4.1).

The distribution of calcium between the urine and faeces did not closely follow the pattern found in most other mammals. More calcium was found in the urine than in the faeces in both experiments, although differences between the two experiments were apparent in the percentage of ingested calcium appearing in urine and faeces.

TABLE 4.1 Results of calcium, phosphorus and magnesium balance trials using hyraces fed two different feeds

	Commercially prepared pellets n = 9						Lucerne hay n = 4					
	Mean intake		Mean output		Balance		Mean intake		Mean output		Balance	
Element	mg/animal day^{-1}	±SD	mg/animal day^{-1}	±SD	mg/animal day^{-1}	±SD	mg/animal day^{-1}	±SD	mg/animal day^{-1}	±SD	mg/animal day^{-1}	±SD
Calcium	500	125	603	149	-103	78	1192	136	1099	141	+93	59
Phosphorus	510	124	481	100	+28	55	176	28	174	19	+2	12
Magnesium	139	35	151	29	-12	24	300	33	281	44	+19	21

TABLE 4.2 Distribution of calcium, phosphorus and magnesium between urine and faeces from hyraces fed two different diets

Element	Experiment No.	n	Diet	Content of feed %	Mean intake (food + water) (mg/animal day^{-1})	±SD	Mean amount excreted in urine (mg/animal day^{-1}	±SD	Urine content as % of intake %	Mean amount in faeces (mg/animal day^{-1})	±SD	Faecal content as % of intake %
Calcium	1	9	Commercial pellets	0,88	500	125	332	78	68,4	271	125	53,2
Calcium	2	4	Lucerne hay	1,41	1192	136	992	168	83,0	106	48	9,1
Phosphorus	1	9	Commercial pellets	0,88	510	124	78	41	16,9	404	126	78,6
Phosphorus	2	4	Lucerne hay	0,20	176	28	3	0,7	1,5	171	19	97,9
Magnesium	1	9	Commercial pellets	0,24	139	35	70	20	50,3	81	20	58,5
Magnesium	2	4	Lucerne hay	0,36	300	33	194	38	64,6	87	11	28.9

For example, Table 4.2 shows that on the pelleted ration with a calcium content of 0,88 per cent, approximately 68 per cent of ingested calcium was excreted in the urine with 53,2 per cent appearing in the faeces. If expressed as a fraction of total output, then 55,1 per cent appeared in the urine and 44,9 per cent in the faeces. However, on the lucerne ration with a higher calcium content of 1,41 per cent approximately 83 per cent of ingested calcium appeared in the urine with only 9 per cent in the faeces. This is even more marked if expressed as a fraction of total output with 90,3 per cent appearing in the urine and only 9,7 per cent in the faeces.

From the two balance trials, it is clear that the renal pathway is the major route for calcium excretion in the hyrax. From absolute figures, (Table 4.2), it is evident that the dietary intake affects urinary calcium levels. This substantiates the findings of Louw *et al.* (1973). They noted, during the course of dehydration experiments on hyraces, that the urinary precipitate disappeared when feed intake was reduced to negligible amounts, but reappeared when normal feed intake was resumed.

The renal pathway as the major pathway for calcium excretion is a remarkable feature of the hyrax. However, they are not alone in this respect. Cheeke and Amberg (1973) have shown that rabbits on a high calcium diet (4,44 per cent calcium) excreted about 60 per cent of that ingested, in the urine. On a diet of 0,69 per cent calcium, only 23 per cent of the calcium intake appeared in the urine. This too, indicates a dietary dependent response, but is not as

marked as the response of the hyrax. Shirley and Schmidt-Nielsen (1967) noted that the urine of pack rats (*Neotoma albigula*) and hamsters appeared creamy from a calcium carbonate precipitate when fed calcium oxalate. The calcium levels in the urine of these animals represented only about 13 per cent (pack rats) and about 8 per cent (hamsters) of the average intake. The calcium of the feed in their experiments was predominantly in the form of calcium oxalate and thus these results may not reflect the true pattern of calcium excretion. Our own preliminary experiments using guinea pigs suggest that these animals also have high levels of calcium in the urine.

If it can be assumed that urinary calcium excretion gives some indication of the superfluous amount absorbed by the digestive tract then these experiments suggest that the hyrax has an efficient calcium absorptive mechanism operating in the alimentary tract with any excess calcium appearing in the urine. The faecal calcium then presumably represents unabsorbed calcium in part at least.

The marked differences between the two experiments as far as calcium partitioning in the excreta is concerned (Table 4.2) may have several explanations, probably attributable to the different compositions of the two diets. Table 4.3 shows that the major differences in organic matter content of the rations were the fibre and protein content, with the lucerne hay having a much higher fibre content but slightly lower protein content than the pellets. It may be of significance in this respect that proper faecal pellets were not formed on the commercial pelleted ration but were on the lucerne hay ration.

TABLE 4.3 Comparison between composition of feeds used in two balance trials and composition of stomach contents of wild hyraces

	Commercially prepared pellets (expt 1)	Lucerne hay (expt 2)	n	Stomach contents Mean	± SD	Range
Calcium %	0,88	1,41	103	0,56	0,27	0,36 - 0,69
Phosphorus %	0,88	0,20	114	0,14	0,05	0,09 - 0,19
Magnesium %	0,24	0,36	103	0,19	0,10	0,13 - 0,20
Crude fibre %	7,70	29,90	6[X]	22,70	1,60	-
Crude protein %	21,00	18,50	6[X]	11,20	0,70	-
Hexane extract %	1,30	1,40	6[X]	2,50	0,80	-
Ash %	7,60	9,50	6[X]	7,90	0,40	-
Nitrogen free extract %	62,40	40,70	6[X]	55,80	1,30	-

[X]Each sample analysed was a combination of 10-13 individual stomach contents from 1 month.

For this reason, the latter diet probably approximated the natural diet of the hyrax more closely than the commercially prepared pellets. This is further verified by a comparison of the proximal analyses of the two feeds with that of the stomach contents of field animals (Table 4.3). An additional difference between the two diets was that the pelleted ration had been ground before pelleting while the lucerne hay had been only coarsely chopped. Both a low fibre content and a fine consistency of feed allow a rapid passage through the alimentary tract of herbivores. It is possible that these two factors contributed to the decreased calcium absorption of the animals on the pelleted diet.

Apart from differences in organic content and physical properties of the feeds used in the two experiments the inorganic composition differed considerably, not only in calcium content but in phosphorus content as well with only a small difference in magnesium (Table 4.3). Since the pelleted ration contained 0,88 per cent phosphorus compared with the 0,20 per cent phosphorus content of the lucerne hay, the high phosphorus levels of the pelleted diet may have inhibited calcium absorption by forming insoluble calcium triphosphate. This would result in a higher faecal calcium content. The negative calcium balance in the first experiment (Table 4.1) is unexpected when the calcium content of the diet fed is compared with the calcium levels of stomach contents from wild hyraces (Table 4.2). Since it is unlikely that the wild hyraces were in negative calcium balance, it would be expected that an uptake greater than 0,69 per cent calcium would result in a positive balance, unless part of the intake

was unavailable for absorption. This would result in a higher calcium level in the faeces and possibly a negative calcium balance.

4.3.1.2 *Field samples*

The calcium levels of the samples of stomach contents (Table 4.3) may not be a true reflection of dietary intake since salivary calcium may have been included. Although these values vary considerably they are lower than those of the different feeds used in the two experiments. One would expect to find, therefore, that hyraces in the field have a lower urinary calcium content than found in the two balance trials. Nevertheless, under field conditions, hyraces do excrete much calcium in the urine, since the rocks which form the urinating sites are always marked by a white calcium carbonate precipitate. This fact re-emphasizes the efficient calcium absorption mechanism in the alimentary tract, with large amounts appearing in the urine.

4.3.2 Phosphorus

4.3.2.1 *Balance trials*

Positive phosphorus balances were shown in both experiments, representing 5,6 per cent and 1,3 per cent of the phosphorus intake in experiments 1 and 2 respectively (Table 4.1).

Urinary phosphorus levels in the hyraces, measured in the two experiments, tended to be low. With an intake of 0,88 per cent phosphorus

in the feed, approximately 16 per cent of that ingested appeared in the urine, but this latter value fell to about 1,5 per cent with a diet containing 0,20 per cent phosphorus (Table 4.2). As with calcium, urinary phosphorus appears to be dietary dependent. This is clearly shown when absolute intake is compared with the urinary output (Table 4.2). As expected, the urinary phosphorus content is much lower than the calcium content. In their experiments on rabbits, Cheeke and Amberg (1973) found a low urinary phosphorus output. However, the dietary levels did not seem to influence the urinary levels with approximately 6 per cent of the ingested phosphorus appearing in the urine on diets containing either 0,36 per cent or 0,72 per cent phosphorus.

A low urinary phosphorus excretion is a common feature of many herbivorous animals. Sheep, on a pelleted grass diet excrete less than 8 per cent of the phosphorus intake in the urine and similar levels have been found in the urine of young calves and red deer. Steers on a roughage diet have been found to excrete only 2 - 4 per cent of the phosphorus intake in the urine (quoted by Scott, 1972).

The major pathway for phosphorus excretion in the hyrax appears to be through the gastrointestinal tract with approximately 78 per cent of the ingested phosphorus appearing in the faeces on a diet containing 0,88 per cent phosphorus. Of the total output 83,8 per cent appeared in the faeces and 16,2 per cent in the urine. On the lower phosphorus content diet (0,20 per cent) almost 98 per cent of that ingested appeared in the faeces (Table 4.2). In this case 98,3 per

cent of total output appeared in the faeces and only 1,7 per cent in the urine. When absolute amounts excreted are considered, although more phosphorus is absorbed and excreted in the urine on a high phosphorus intake, it appears that absorption is limited by the intestine resulting in a higher faecal loss on a higher dietary intake.

Although a calcium to phosphorus ratio between 2:1 and 1:2 in the feeds of domestic animals is considered to be optimal for absorption of both these elements (Maynard & Loosli, 1962) this does not seem to be true for hyraces, since interference with calcium absorption seems to have occurred on the pelleted ration. Although other factors, such as a rapid passage of digesta through the gastro-intestinal tract, may have contributed to reduced absorption, a ratio as low as 1:1 was not found in the stomach contents of the wild animals. The lowest ratio found was 2,4:1 and the highest 7,0:1.

4.3.2.2 *Field samples*

From the field samples, a range of 0,09 per cent to 0,19 per cent phosphorus was recorded in the stomach contents (Table 4.3). Although saliva may have contributed in part to these values, they are much lower than the 0,88 per cent phosphorus contents of the commercial pelleted ration. The 0,20 per cent phosphorus content of the lucerne hay feed was closer to the phosphorus content of the stomach contents and it is probable, therefore, that the urinary phosphorus excretion is low under field conditions. The low phosphorus content of much

of the South African herbage is well known and phosphorus deficiency symptoms are common in domestic animals that do not have supplementary feeds (Theiler *et al.*, 1928 *et seq*).

4.3.3 Magnesium

4.3.3.1 *Balance trials*

Similar to the calcium balances, a net negative magnesium balance of 8,8 per cent of the intake was found in the first experiment (pelleted ration containing 0,24 per cent magnesium), but a positive balance representing 6,3 per cent of the intake was found on the lucerne hay diet (0,36 per cent magnesium) (Table 4.1). Although the feeds did not differ much in magnesium content, it is interesting to note that the distribution of this element varied considerably, with 50,3 per cent ingested magnesium appearing in the urine and 58,5 per cent in the faeces in the first experiment, while in the second 64,6 per cent was found in the urine and 28,9 per cent in the faeces (Table 4.2). A similar variation is found in the fractions of total output with 26,4 per cent appearing in the urine and 53,6 per cent in the faeces in the first experiment and 69,0 per cent in the urine and 31,0 per cent in the faeces in the second experiment. Thus, no conclusions as to the major route of magnesium excretion can be made from the two balance trials.

A similar pattern of magnesium excretion was found by Cheeke and Amberg (1973) in rabbits. On a 0,21 per cent magnesium intake (with

4,4 per cent calcium and 0,36 per cent phosphorus) 55,2 per cent of ingested magnesium appeared in the urine and 17,2 per cent in the faeces. On a 0,19 per cent magnesium intake (with 0,69 per cent calcium and 0,72 per cent phosphorus), 37,2 per cent of ingested magnesium appeared in the urine and 47,1 per cent in the faeces. In both the hyrax and rabbit it appears that the pattern of magnesium excretion is linked with that of calcium. When absolute values are considered, it is seen that although the hyraces had a higher magnesium intake on the lucerne hay diet, approximately the same amount appeared in the faeces in both experiments (Table 4.2). It is possible, that, as with calcium, the higher phosphorus levels of the pelleted diet inhibited magnesium absorption. When the magnesium intake was increased there was a concommitant rise in urine magnesium. As urinary levels are plasma dependent (Belonje, 1978; Nordin, 1976) there must have been an increased absorption of this element.

4.3.3.2 *Field samples*

The stomach contents from field animals showed a range of magnesium content from 0,13 per cent to 0,20 per cent. Again the experimental rations were higher than the natural diet (Table 4.3). From the present study it is expected that an almost equal distribution of magnesium in the urine and faeces would occur in the wild.

4.3.4 Mineral content of tissues and plasma

The calcium phosphorus and magnesium content of bone, soft tissues and plasma in the hyrax show some differences from sheep (Table 4.4). The values for bone were higher in the hyrax, but since these animals were fed on a diet with higher content of the three elements, the differences in bone composition are to be expected.

The differences in some of the soft tissues are difficult to explain but may be a species specific feature. Generally, the values for all elements in the tissues fall within the normal range expected for mammals.

The levels of the three elements in the plasma did not show any deviation from those normally found in mammals (Table 4.4). In rabbits the plasma calcium level reflects the dietary level (Chapin & Smith, 1967 from Cheeke & Amberg, 1973) and in view of the similarity in patterns of calcium excretion between the hyrax and the rabbit, it is possible that the same may be true of the hyrax.

4.3.5 Ecological significance

The adaptive value of a high calcium excretion in the urine is enigmatic. A common feature of the animals known to excrete or that possibly excrete unusually large amounts of calcium in the urine viz. hyraces, rabbits, pack rats, hamsters, guinea pigs and the dassie-rat (*Petromus typicus*) is that they are small herbivores. Other than

TABLE 4.4 Mean calcium, phosphorus and magnesium content of tissues and plasma in hyraces and sheep Ø (% of dry mass - g/100g).

	CALCIUM				PHOSPHORUS				MAGNESIUM			
	Hyrax		Sheep		Hyrax		Sheep		Hyrax		Sheep	
	Mean	± SD	Mean	± SD	Mean	± SD	Mean	± SD	Mean	± SD	Mean	± SD
Total dry bone (rib) %	23,82	0,74	18,76	1,21	10,48	0,31	8,99	0,60	0,57	0,16	0,42	0,04
Kidney %	0,05	0,01	0,07	0,02	0,95	0,09	1,17	0,06	0,07	0,01	0,08	0,004
Liver %	0,02	0,01	0,02	0,01	0,90	0,12	1,18	0,05	0,05	0,005	0,06	0,01
Muscle %	0,03	0,007	0,02	0,004	0,89	0,05	0,72	0,06	0,09	0,005	0,09	0,009
Plasma %	11,10	0,97	10,60	0,59	5,32	2,39	7,62	1,11	2,87	0,85	1,93	0,08
Mineral content of ration%	0,88	-	0,62	-	0,88	-	0,27	-	0,24	-	0,13	

Total plasma protein of hyrax = 7,09 ± 0,54 g/100 ml. Total plasma protein of sheep = 6,23 ± 0,22 g/100 ml, Ash % of bone in hyrax = 62,66 ± 1,20, Ash % of bone in sheep = 52,03 ± 3,43.

Ø Belonje, P.C. (1978).

the hamsters and pack rats which belong to the same subfamily (Cricetinae) (Shirley & Schmidt-Nielsen, 1967) there is no taxonomic similarity. Urinary excretion of calcium may be of no adaptive significance, but rather an obligatory process arising from the mechanism of calcium absorption in the digestive system. Shirley and Schmidt-Nielsen (1967) have suggested that efficient calcium absorption in the pack rat may be an adaptation to a low calcium, high oxalate diet. While hamsters too can absorb and excrete calcium from calcium oxalate (Shirley & Schmidt-Nielsen, 1967), the rabbit cannot (Cheeke & Amberg, 1973). In this respect it should be noted that on occasion, a layered stone, composed predominantly of calcium and magnesium oxalate with a trace of phosphate, has been found in the stomach of wild hyraces (personal observation). This suggests that a diet containing oxalic acid (presumably with a high concentration) may have a detrimental effect on the absorption of calcium magnesium and phosphorus. Beyond this, however, the oxalate metabolism of hyraces, guinea pigs and dassie-rats is not known but an efficient absorption of calcium under any conditions of low calcium availability would certainly be advantageous, particularly for young growing animals and lactating females. It is difficult to accept that the calcium metabolism of the above animals has no adaptive significance and that none of them can regulate their calcium absorption (Trout, 1954 from Shirley & Schmidt-Nielsen, 1967).

Whether the availability of calcium in the natural diets of these animals is low is difficult to asses, since the diet may vary considerably in the various regions the animals inhabit. Hyraces inhabit

areas with widely differing vegetation types but are reputed to feed frequently on plants high in oxalic acid in certain habitats within their distribution. From the data available on the hyrax, it seems that the calcium content of the diet is not particularly low. Thus the efficient calcium absorbing mechanism might have evolved at a time when calcium was scarce and readaptation has not occurred.

Whatever the advantage may be of this ability to absorb calcium, the resulting calcium load presented to the kidneys is certainly potentially hazardous, since the risk of renal calculi is increased. Although the calcium finally appears in the urine as a calcium carbonate precipitate it is unlikely that this forms in the kidney itself but probably in the ureter or bladder where it is kept in suspension.

The ability of the renal system of the hyrax to cope with a high calcium load presumably with no malfunction is of medical interest and deserves further investigation.

SECTION 5

WATER METABOLISM IN THE ROCK HYRAX *PROCAVIA CAPENSIS*

5.1 INTRODUCTION

The rock hyrax *Procavia capensis*, being of an intermediate body size, employs behavioural and physiological means similar to those used by both small and large mammals to dissipate heat. High ambient temperatures are avoided by retreating into rock crevices which have smaller fluctuations in temperature and humidity than the outside environment (section 6; Turner & Watson, 1965; Bartholomew & Rainy, 1971). In addition they are able to use evaporative cooling for heat dissipation. Bartholomew and Rainy (1971) have observed sweat droplets on the soles of the feet in *Heterohyrax brucei* under heat stress, and Taylor and Sale (1969) have described panting, salivating and grooming in hyraces exposed to high temperatures.

Irrespective of the body size, however, a mammal living in arid areas must have an economic water expenditure. The most common lines of research related to water economy have been investigations of water turnover, water balance and renal function of an animal under normal, heat-stressed or water-deprived conditions. Usually, these have been done in conjunction with metabolism studies. The hyrax has received some attention in this respect. The renal function of *P. capensis* in the laboratory has been examined by Louw *et al.* (1973) and that of *P. syriacus* by Meltzer (1976), with a comparison between the two reported by Maloiy and Sale (1976). Extensive studies on the water turnover and water balance of *P. habessinica* in the laboratory have been reported (Rubsamen *et al.*, 1979; Rubsamen & Kettembeil, 1980) together with the urea kinetics of this species (Hume *et al.*, 1980).

The water turnover of *P. capensis*, however, has not been studied either in the laboratory or in the field. In view of the known influence of different climatic conditions on the physiology of species living in different geographical regions, the present work was undertaken to examine the water turnover of *P. capensis* under simulated field conditions and to compare this situation with the laboratory studies reported for other species.

5.2 PROCEDURE

5.2.1 'Field' studies

Ten hyraces (4 males, 6 females) were trapped in the Robertson district of the Cape Province and subsequently maintained in an outdoor cage at the 'Vrolijkheid' Nature Conservation Research Station for two months prior to the study. None of the females was gravid and several of the animals were sub-adult. The mean mass of the ten hyraces was 1,14 ± 0,31 kg. The dimensions of the cage were 5 m x 6 m x 3 m (L x B x H) and it contained a stone shelter into which the animals could retreat. They were thus subject to natural sunlight, temperature and humidity fluctuations with a moderate amount of space in which to move. For a month prior to initiating the experiment, they were fed chopped lucerne hay and given drinking water *ad lib*.

5.2.2 Water turnover rates using tritiated water (TOH)

Two estimates of the water turnover rate (WTR) were made, one with drinking water provided *ad lib.* (hereafter termed 'hydrated' animals), and the other with no drinking water (hereafter termed 'dehydrated' animals). The animals were weighed and injected (I.P.) with tritiated water (approximately 40 uCi/kg) diluted in sterile saline. An equilibration time of 18 hours was allowed before the first blood sample was taken by heart puncture. Owing to the risk of trauma involved in this method of sampling, only one other blood sample was taken after 9 days when the animals were weighed again. Water was then removed from the cage and the animals dehydrated for a further five days. Only four of the animals could be used in the dehydration experiment and it was logistically impossible to repeat it using more animals. After five days the four remaining hyraces were weighed again and a final blood sample taken.

During the two periods of experimentation, daily maximum and minimum ambient temperatures were recorded, as well as the relative humidity at 13.00 h. Although the experiments were conducted during the winter months of June-July, no rain fell during the two experimental periods though heavy dew falls were common. To assess the increased moisture content of the food after a dew fall, a known mass of lucerne hay with known water content was left outside in a mesh container, overnight. The next morning just after sunrise, it was reweighed, dried at 70°C and the gain in water content calculated.

5.2.3 Treatment of blood samples

All blood samples were processed immediately. A 25 to 50 microlitre sample was first taken from the one millilitre blood sample for haematocrit determination and the remaining volume was centrifuged in a clinical centrifuge. The plasma was separated and 200 µl of plasma added to 400 µl trichloroacetic acid to precipitate the plasma proteins. After centrifuging this mixture, the clear supernatant was stored frozen in sealed vials until the radioactivity could be determined.

5.2.4 Determination of radioactivity

The radioactivity of all the processed blood samples and the original TOH solution was assessed at the same time. 100 µl of the solution to be counted was added to 10 ml Packard Instagel scintillation cocktail and the radioactivity measured using a Packard liquid scintillation counter (model 3385). A Wang 700 bench top computer, programmed to correct for quenching was used to convert CPM to DPM. The DPM values were converted to µCi/ml correcting for all dilutions and the final values for each animal plotted on semilogarithmic graph paper against time as the abscissa. The rate constant (k), biological half-life ($t_{\frac{1}{2}}$) total body water (TBW) and water turnover rate (WTR) were calculated according to the method outlined by Yousef *et al.* (1974). To calculate the WTR of a dehydrated animal, TBW was assumed to be the same as that when hydrated. This assumption would be true only at the beginning of the dehydration period and thus the WTR presented is probably an overestimation. WTR has been expressed per $kg^{0,8}$ to eliminate the variations due to body size (Richmond *et al.*, 1962).

5.2.5 Urine and plasma analysis; kidney morphology

To assess the effect of dehydration on the plasma and urine electrolytes, urea content and osmolality, eight hyraces (5 females, 3 males) of mean body mass 2,21 ± 0,96 kg were used. They had been in captivity for over a month and were maintained in an outdoor cage with a sheltered section. During the period of captivity they were fed lucerne hay, commercial rabbit pellets and occasional fresh greens. Water was provided *ad lib.* Four of these animals, presumably normally hydrated, were killed with an I.P. injection of Euthabarb (pentobarbitone sodium, Lennon Laboratories) a blood sample from the heart was withdrawn while under deep anaesthesia and after death, a sample of urine was withdrawn from the bladder by syringe. The kidneys were removed and their individual masses recorded. The other four hyraces were deprived of free drinking water for five days and fed only lucerne hay and the pelleted food. Thereafter, blood, urine and kidneys were removed as described above.

All blood and urine samples were centrifuged to obtain the plasma and, in the case of the urine, to remove the calcium carbonate precipitate. The osmolality of all samples was determined immediately using a Wescor microosmometer and the sodium and potassium content was determined using a flame photometer (Instrumentation Laboratory, model 243). Urea and chloride concentrations were measured in a Beckman Astra 8 automated Stat/Routine analyser.

The dimensions of the kidneys were measured and each sectioned medially.

The relative medullary thickness was calculated as described by Sperber (1944).

5.2.6 Statistical tests

Mean values for all measurements were calculated with the estimate of error expressed as the standard deviation, unless otherwise stated. Whenever appropriate a Student's 't' test was performed to determine the significance of differences (Zar, 1974). Occasionally it was necessary to perform a paired 't' test (Zar, 1974) when the variation between individual animals was large. This has been noted whenever it was used. The minimum level of significance considered acceptable throughout was $p < 0,05$ (95%).

5.3 RESULTS

5.3.1 Total body water (TBW) and tritiated water turnover rate (WTR)

The TBW, biological half-life ($t_{\frac{1}{2}}$) and WTR recorded in the hydrated and dehydrated animals are shown in Table 5.1. During both experiments, the variations in temperature and relative humidity of the air were similar and have been summarized in Table 5.2. The TBW of the hydrated animals (70,7%) was within the range expected for mammals (Richmond *et al.*, 1962; Hulbert & Gordon, 1972; Holleman & Dieterich, 1973; Yousef *et al.*, 1974). The values given for TBW of the dehydrated animals

(Table 5.1)were estimated at the beginning of the period of dehydration and thus do not reflect the effect of water restriction on this parameter.

As would be expected, the WTR of the hydrated hyraces was significantly higher ($p < 0,001$) than those of the dehydrated hyraces, the mean value for each being 85,1 ± 7,2 and 27,7 ± 12,5 $ml.day^{-1}.kg^{-0,8}$ respectively. The turnover rate for the hydrated animals was 69,5 per cent of that predicted according to body mass, using the equation:

$$WTR\ (ml.day^{-1}) = 0,4894\ (mass\ g.)^{0,8}$$

(Richmond *et al.*, 1962)

A similar comparison with predicted values was not made for the dehydrated animals as they were in negative water balance. The values for $t_{\frac{1}{2}}$ shown in Table 5.1 are a reflection of the WTR, a high $t_{\frac{1}{2}}$ reflecting a low WTR.

5.3.2 Haematocrits

The mean haematocrit value for the eight hyraces with water provided *ad lib.* was 31,3 ± 7,3 per cent. Of these animals, the four that were dehydrated subsequently, had a mean haematocrit value of 32,3 ± 8,7 per cent which increased to 40,3 ± 5,7 per cent when dehydrated. This increase was significant ($p < 0,02$) when tested with a paired 't' test and the mean of the differences between the values for each animal was 8,0 ± 2,9 per cent.

TABLE 5.1 Water turnover rate (WTR), biological half-life ($t_{\frac{1}{2}}$) and total body water (TBW) measured with tritiated water in hydrated and dehydrated rock hyraces *P. capensis* in an outdoor cage.

	Mean Mass	n	Duration of expt	Change in Body mass	$t_{\frac{1}{2}}$	TBW	Water content of body mass	WTR	
	g		days	% of initial mass	days	ml	%	$ml.day^{-1}$	$ml.kg^{-0,8}.day^{-1}$
HYDRATED									
$\bar{x}$	1139	10	9	+2,1	5,91	803	70,7	94,8	85,1
± S.D.	307	-	-	(-4,6 to +6,6)‡	0,60	210	4,0	24,7	7,2
DEHYDRATED									
$\bar{x}$	946	4	5	-25,0	22,6	753x	70,0x	25,8	27,7
± S.D.	178	-	-	(-21,0 to -28,1)‡	8,8	130	5,4	9,9	12,5

x These values are for animals at the beginning of the dehydration period.

‡ Figures in parentheses represent range

TABLE 5.2 Air temperatures and relative humidities recorded during the evaluation of the water turnover rates of *P. capensis*.

	Maximum Temperature °C		Minimum Temperature °C		Relative Humidity %	
	Mean	range	Mean	range	Mean	range
Hydration period	19,6	15-25	5,6	1-8	62,8	37-82
Dehydration period	21,4	16-24	5,1	2-10	60,6	48-91

5.3.3 Composition of plasma and urine

The different concentrations of sodium (Na^+) potassium (K^+), chloride (Cl^-) and urea, as well as the osmolality of plasma and urine in the four hydrated and four dehydrated hyraces are shown in Table 5.3. The mean mass of the four hydrated animals was 2,56 ± 0,74 kg and that of the dehydrated animals was initially 2,27 ± 0,32 kg. After five days without water the mean mass of the latter group was reduced by 17,7 ± 0,73 per cent. Although the actual amounts of food ingested, faecal matter voided and urine volumes excreted over the period of water deprivation were not measured, the small quantity of faecal matter in the cage and the apparent lack of a calcium carbonate precipitate in the urine samples of all except one animal on the fifth day, were indicative of a large reduction in the food intake.

Dehydration did not significantly alter the Na^+ and K^+ concentrations in the plasma ($p \geq 0,1$) although both chloride and urea concentrations increased significantly ($p < 0,05$ and $p < 0,01$ respectively). Despite the almost doubled concentration of the plasma urea, dehydration did not cause a statistically significant increase in the plasma osmolality ($p \geq 0,10$). While the concentrations of the measured components of the plasma did not show a marked individual variation (shown by the low standard deviations in Table 5.3) the urinary concentrations did. In general, the concentrations of the urine electrolytes in the dehydrated hyraces decreased when compared with those of the hydrated hyraces, but only the K^+ concentration was significantly lower ($p < 0,05$).

TABLE 5.3 The composition of urine and plasma in four hydrated and four dehydrated[x] *P. capensis* (mean mass of 8 = 2225 ± 624 g).

	Na^+ meq/l		K^+ meq/l		Cl^- meq/l		Urea mmoles/l		Osmolality mosm.kg^{-1}	
	$\bar{x}$	±SD	$\bar{x}$	±SD	$\bar{x}$	±SD	$\bar{x}$	±SD	$\bar{x}$	±SD
PLASMA										
Hydrated	136,5	7,1	3,3	0,2	107,3	8,1	7,1	2,5	254	26
Dehydrated	150,8	16,6	4,3	1,1	120,0	1,8	14,0	2,5	273	58
p[+]	>0,10	NS	>0,10	NS	<0,05	S	<0,01	S	>0,10	NS
URINE										
Hydrated	81,3	56,9	246,0	33,9	230,0	23,0	548,0	170,0	1365	120
Dehydrated	16,8	(2-54)[‡]	184,3	31,9	113,0	(16-244)[‡]	1018,0	89,2	1621	192
p	>0,05	NS	<0,05	S	>0,05	NS	<0,005	S	>0,05	NS
U/P ratio										
Hydrated	0,61	(0,17-1,10)	74,88	6,13	2,16	0,34	78,85	16,08	5,42	0,78
Dehydrated	0,10	(0,01-0,33)	44,82	11,11	0,95	0,88	75,62	20,76	6,20	1,79
p	>0,05	NS	<0,005	S	<0,05	S	>0,10	NS	>0,10	NS

x Dehydrated for 5 days

\+ S = significant difference NS = no significant difference

‡ Figures in parentheses represent range

Urinary urea concentrations increased significantly ($p<0,005$) when the animals were dehydrated. Although the osmolality of the urine increased after dehydration, it is unlikely that the maximum osmolality recorded (1823 mosm.kg^{-1}) represented the maximum attainable, since the animals had reduced their food intake. These results will be discussed later in conjunction with those of Louw *et al.* (1973) and Maloiy and Sale (1976).

The urine:plasma ratio for each of the above constituents have been compared in Table 5.3. The ratio for K^+ and Cl^- was significantly lower in the dehydrated animals ($p<0,005$ and $p<0,05$ respectively), but no difference was shown in the ratios for Na^+, urea or osmolality (all $p>0,05$).

5.3.4 Relative medullary thickness of the kidneys

The relative medullary thickness of the kidneys of an animal gives an indication of the maximum concentration of the urine that can be produced (Schmidt-Nielsen & O'Dell, 1961). The mean relative medullary thickness for *P. capensis* measured in 16 kidneys (mean mass 7,37 ± 1,96 g) was 6,64 ± 0,73 and the highest ratio obtained was 7,90. This corresponds to a maximum urine concentrating ability of between 3000 and 4000 mosm.kg^{-1} when compared with other mammals (Yaakobi & Shkolnik, 1974).

5.4 DISCUSSION

5.4.1 Water turnover rate

5.4.1.1 Hydrated hyraces

The water turnover rate (WTR) of an animal under controlled conditions in the laboratory can be expected to differ from that of an animal in the wild. This is because the latter measurement is subject to the influences of the animal's activity, social behaviour, the availability of food and water and changing climatic conditions such as temperature and humidity. In the present experiments, the conditions under which the outdoor hyraces were studied approximated natural conditions in winter as the animals were subjected to the daily changes in temperature and humidity. Moreover, their activity was only partly curtailed and because a whole colony was studied, the effects of a gregarious life-style were operative. I expected therefore to find that the mean WTR for the outdoor animals would be higher than those values found in the laboratory for other species of hyrax. For example Rubsamen *et al.* (1979) found the WTR of *Procavia habessinica* to be 61,4 44,1 and 55,1 $ml.kg^{-0,82}.day^{-1}$ at laboratory temperatures of 20, 27 and 35°C respectively with food and water provided *ad lib.* Rubsamen and Kettembeil (1980) working with the same species, found a similar WTR of 61 $ml.kg^{-0,82}.day^{-1}$ with laboratory temperatures varying between 20 and 30°C. The thermoneutral zone of *P. habessinica* extends from 27 to 35°C and the relative humidities in these two experiments varied but were lower than in the present study. Air temperatures in

the present study never exceeded the thermoneutral zone of *P. capensis* (19 to *ca.* 28°C - section 6) but did fall below 19°C. Therefore, for comparative purposes the WTR found by Rubsamen and Kettembeil (1980) is the more appropriate here. This assumes that *P. capensis* would have a similar WTR to *P. habessinica* under the same conditions, an assumption that may be justified considering that their basal metabolic rates are the same (0,27 $ml O_2.g^{-1}.h^{-1}$ - section 6, and Rubsamen *et al.*, 1979). Thus the ratio between the WTR of *P. capensis* outdoors, and those of *P. habessinica* in the laboratory would be *ca.* 1,4, relatively low considering that the outdoor animals were subject to more variable climatic conditions and their activity was not as restricted as the laboratory animals. A closer examination of the possible avenues of water loss in the outdoor animals does explain the low ratio, however.

In the present study, since air temperatures did not exceed thermoneutrality, there was little or no necessity to use water for heat dissipation. Evaporative water loss (EWL) for metabolic heat dissipation would then depend on the level of activity, but it is unlikely that a large volume of water would have to be used for cooling as heat would be lost passively from the body to the cooler air at these temperatures. At night, however, temperatures were low, reaching 1°C. At low ambient temperatures, metabolism and therefore heat production increases in order to maintain a stable body temperature (section 6). This process involves the catabolism of the energy stores in the body producing waste products which must be eliminated via the urine, thereby losing water. Thus the higher the metabolic rate, the more

water would be lost in the urine. Since the metabolic rate is dependent on the ambient temperatures and on the behaviour of the animals with respect to air temperatures, in an outdoor or wild situation, behaviour is of critical significance in the assessment of the water demands of the hyrax.

Here the effects of utilizing environmental conditions such as solar heat or creating a favourable microclimate by huddling in the crevices to minimise metabolic heat production are operative (see section 6). In the present context it would seem that the hyraces expended relatively little energy in activity and particularly at night when temperatures were so low and the metabolic rate would be expected to be high, huddling in the crevices created an ambient temperature and humidity such that water losses and heat production were minimised. The low level of activity and energy expenditure in the wild, as suggested in section 2 by comparison of the food intake in the wild and in the laboratory are therefore supported here.

5.4.1.2 *Dehydrated hyraces*

The WTR of the dehydrated hyraces was low (27,7 $ml.kg^{-0,8}.day^{-1}$) but was accompanied by a large reduction in mass (25% of initial mass). This value, although similar, is not directly comparable to the WTR of *P. habessinica*, found by Rubsamen and Kettembeil (1980) or Rubsamen *et al.* (1979), on a reduced water intake. In the former study, the animals initially lost 15 per cent of their body mass but thereafter maintained a stable mass with a WTR of 37 $ml.kg^{-0,82}.day^{-1}$. The latter

authors found a lower WTR of 25,8 $ml.kg^{-0,82}.day^{-1}$ also on a reduced water intake and a reduced body mass. Possibly, the low WTR found in the present study could have been maintained and the body mass stabilized at the reduced level, if *ca.* 28 $ml.kg^{-0,8}.day^{-1}$ of drinking water had been provided after the dehydration period.

Since the water component of the body mass lost in the present experiment is not known, it is difficult to correct the WTR. However, the water content of the mass lost probably lies between 71 and 100 per cent. The former per cent is the value for the TBW in hydrated animals, and the use of this value assumes that the TBW to body mass ratio remains constant during dehydration. Hulbert and Dawson (1974) found that during water restriction, the body water pool size in relation to the body mass was not changed in bandicoots, but this would depend on the fat content of the animals. In acute water restriction, it is probable that the loss in mass would involve a greater loss in water initially, however, and the use of 71 per cent would therefore give an underestimate. Assuming that all the mass lost was in the form of water (i.e. 100%) would obviously give an overestimate of WTR. Thus, using both these values, the corrected WTR, without a loss in mass would lie between 50,0 and 60,4 $ml.kg^{-0,8}.day^{-1}$, and is lower than found in the hydrated hyraces in the present study.

It is clear, therefore, that water losses in *P. capensis* can be reduced when water is restricted or unavailable. Reductions in metabolism, EWL, urine volume and faecal water are the possible avenues through which this could be achieved, but from other studies, it appears that

acute and chronic dehydration have different effects on some of the above avenues of water loss. For example, in the jackrabbit *Lepus californicus* (Reese & Haines, 1978) and Sinai goats *Capra hircus* Shkolnik *et al.*, 1972) acute dehydration did not result in a reduction in oxygen consumption although EWL in the latter species was reduced. Apparently the reduction of metabolism in response to dehydration takes several days to develop in the jackrabbit (Reese & Haines, 1978). Chronic dehydration in the jackrabbit, however, caused a decrease in both metabolic rate and EWL. A reduction in EWL with acute dehydration appears to be common in different mammals (the camel - Schmidt-Nielsen *et al.*, 1956; African goats and sheep - Maloiy & Taylor, 1971; bandicoots - Hulbert & Dawson, 1974; *Antechinus stuartii*, a dasyurid marsupial - Nagy *et al.*, 1978) and this probably occurred in *P. capensis* too. Although chronically dehydrated, *P. habessinica* also showed a reduction in EWL (Rubsamen & Kettembeil, 1980). Of particular interest in the latter study was the increased lability in the body temperature of *P. habessinica* in response to water restriction. At high ambient temperatures the thermolability was mediated, in part at least, through a reduction in EWL so that the animals became hyperthermic but were tolerant of the higher body temperature. At low ambient temperatures, the hyraces became hypothermic with a decrease in metabolic rate and in EWL. Rubsamen and Kettembeil (1980) have suggested that the increased thermolability may be explained by the shifting apart of the threshold levels for evaporative heat loss and for activation of heat production, as outlined by Bligh (1972). In view of the stability of body temperature in *P. capensis* over a wide range (6 to 28°C - section 6) which is not shown by *P. habessinica*

very low electrolyte intake in the food. Even though plant matter is low in Na^+ and Cl^-, it does provide animals with a source for the replenishment of these essential electrolytes. Thus the overall response to dehydration was the maintenance of osmotic equilibrium and stable electrolyte concentrations in the plasma, an essential response for the survival and normal functioning of an animal in unfavourable conditions.

The haematocrit of *P. capensis*, however, increased by 25 per cent in response to dehydration. This does not necessarily mean that of the body fluid compartments, the plasma was the major source of water loss, since there may have been an equal reduction in all fluid compartments, as was shown in acutely dehydrated jackrabbits (Reese & Haines, 1978). Further work is needed to establish whether the hyrax responds to dehydration by maintaining plasma volume constant as in the camel (Macfarlane *et al.*, 1963), desert kangaroos (Denny & Dawson, 1975), jackrabbits (Reese & Haines, 1978) and the burro (Yousef *et al.*, 1970) or follow the pattern of Merino sheep (Macfarlane *et al.*, 1961) and the Guanaco (Rosenmann & Morrison, 1963) where the plasma volume is reduced by 40 to 50 per cent with a 20 per cent loss in body mass.

Any alteration in the fluid volumes of an animal necessitates an adjustment in the electrolyte distribution and concentration in order to re-establish osmotic equilibrium. Louw *et al.* (1973) have shown that in response to dehydration, the urine osmolality and urinary concentrations of Na^+ and K^+ in *P. capensis* initially increased for the first two days and subsequently dropped as feed intake dropped.

Chloride concentrations in the urine decreased with dehydration while urea concentration increased reaching a peak, five days after water was first withheld. These changes were accompanied by a reduction of urine volume from *ca.* 45 $ml.day^{-1}$ to the lowest volume of *ca.* 15 $ml.day^{-1}$ after a week without water. In the present study only one urine sample was taken from each animal after five days of dehydration and thus these values can be compared only with those of Louw *et al.* (1973) on the same day of dehydration since the pattern of urinary components change daily. Thus on the fifth day of dehydration, urinary electrolyte concentrations either decreased or remained near the 'hydrated' level, but the absolute amount of the ions Na^+, K^+ and Cl^- must have been reduced as urine volumes declined (Louw *et al.*, 1973; Maloiy & Sale, 1976). In the present study, this was most marked in the case of Na^+ where three of the four dehydrated animals had urinary concentrations of 2,2 and 9 $meq.l^{-1}$. The single animal that was still feeding and had a calcium carbonate precipitate in the urine had a far higher value of 54 $meq.l^{-1}$. This latter value was probably the cause of the insignificant statistical difference between the hydrated and dehydrated hyraces with respect to Na^+ excretion. The extremely low concentration of Na^+ and reduced Cl^- concentration in the urine is indicative of an efficient countercurrent system in the kidney whereby Na^+ and Cl^- ions are efficiently recycled, reabsorption of water following passively (Schmidt-Nielsen, 1975). The efficiency of Na^+ retention by the body or reduction in its excretion would presumably also be advantageous for hyraces faced with a lack of sodium in the diet. Extremely low levels of sodium in the urine have also been found in the camel and sheep when dehydrated (below 1 $meq.day^{-1}$

- Macfarlane, 1964) and in the ground squirrel *Xerus inauris* where levels as low as 1 and 6 meq.l^{-1} have been found in the field (Marsh *et al.*, 1978). Maloiy and Sale (1976) have shown that Na^+ excretion increased on dehydration in *P. capensis*, though they did not specify the length of the dehydration period when this was measured. Comparison with the study of Louw *et al.* (1973) would suggest that the period was two to three days since Na^+ initially increases and with it the highest osmolality is usually recorded (Louw *et al.*, 1973).

The higher concentration of K^+ than Na^+ in the urine of *P. capensis* is indicative of an increased secretion of adreno-corticosteroids and their effect on renal function. Potassium, however, is more abundant in plant matter than sodium, and the need therefore to conserve this ion is less critical. Macfarlane (1964) found that sheep excreted more Na^+ than K^+ in the urine and noted an increased disparity between the excretion of the two ions with more rapid dehydration and a high heat load. He related this disparity to the production of sweat with a predominance of potassium and bicarbonate ions derived from the plant food. Thus the Na^+ to K^+ ratio in the plasma was kept stable by the elimination of Na^+ in the urine. It would be interesting to determine the predominant ions in hyrax sweat in view of the large amount of carbonate ions which are incorporated into the urinary precipitate.

Judging from the relative medullary thickness of the kidneys of *P. capensis* an osmolality of 3000 mosm.kg^{-1} would be expected, a value which was recorded by Louw *et al.* (1973) and Maloiy and Sale (1976). The lower urine osmolality in the present dehydrated hyraces occurred

despite the higher urea concentration when compared with the two previous studies mentioned - (1018 mmol.l^{-1} - present vs. 836 mmol.l^{-1} - Maloiy & Sale, 1976). However, the present urine osmolality was in keeping with that of the hyraces in the study of Louw *et al.* (1973) on the fifth day of dehydration and supports the view of these authors that the electrolyte content of the urine was the major factor determining osmolality.

With the increase in urinary urea concentration on dehydration, the plasma urea of *P. capensis* increased by 100 per cent (from 7 to 14 mmol . l^{-1}). Both the hydrated and dehydrated plasma urea concentrations were higher in the present study than the highest levels found in *P. habessinica* (6 mmol . l^{-1} - Hume *et al.*, 1980). In both studies the highest concentrations of plasma urea occurred during dehydration with a low energy intake and therefore the body tissues were probably catabolised resulting in the production of high levels of urea. From these results, it appears that *P. capensis* may be more tolerant of plasma urea loading than *P. habessinica*. A marginal advantage in terms of water economy and nitrogen conservation would result, assuming that *P. capensis* recycles urea in the same way as *P. habessinica*.

5.4.3 Ecological considerations

The low basal metabolic rate, the gregarious, semi-fossorial existence and the mechanisms of behavioural thermoregulation of *P. capensis* are advantageous in terms of energy utilization and have manifold effects on

other aspects of the physiology of this animal. One of these is a low turnover rate of water. Even though the WTR of *P. capensis* was measured under free-living conditions, it was still below the predicted rate for eutherian placentals of comparable size. Although the low WTR may be a secondary effect of the frugal energy expenditure and the low BMR, common to the order Hyracoidea, rather than an ecologically determined character, as suggested by Rubsamen *et al.* (1979), it still has beneficial survival value. The low WTR would be an obvious advantage for this species living in an arid environment where free water is scarce and the main source of water is in the food eaten.

It is generally believed that the hyrax can exist without free drinking water in the wild and the calculations of Meltzer (1976) show this to be true of *P. syriacus*. A similar calculation can be made for *P. capensis*, assuming the minimum water requirement, on a relatively high protein diet, to be 50 to 60 $ml.kg^{-0,8}.day^{-1}$ with no change in body mass (calculated from the WTR of the dehydrated hyraces in the present study). For a 2,3 kg animal, the water intake would have to be 97 to 117 $ml.day^{-1}$, less approximately 20 ml of water produced by the oxidation of the food. From the data on stomach contents of *P. capensis* (Lensing, 1978) the wet food intake of a 2,3 kg hyrax would be roughly 216 g wet $mass.day^{-1}$, a slight overestimate since this figure includes moisture from digestive and salivary secretions. Nevertheless omiting the oxidative water from the food and the moisture of the digestive secretions, 216 g of wet food would provide 97 to 117 ml of water if the moisture content was 45 to 54 per cent.

Lensing (1978) has compiled a list of the seasonal moisture contents of selected plant species which occurred in the habitat of *P. capensis* in two areas in Namibia during 1975 and 1976. These have been condensed in Table 5.4 to give a mean moisture content of the plants available to the hyrax as food, although not all would have been eaten. It can be seen that during the wet season, the available plants would readily supply enough water for the hyraces without additional drinking water, assuming the Namibian hyraces and Cape hyraces have the same minimum water requirements. In the drier seasons, however, only those plants with the highest moisture content would supply the animals with enough water. Thus, the hyraces would have to feed selectively on plants with the highest moisture content. Alternatively, the water turnover could be reduced together with a loss in mass so that the water demands were kept in line with that available in the food.

It is recognised that the numbers of animals used in this study were small, particularly in the dehydration and renal function experiments, and therefore the results should be viewed with caution. However, in as far as the results appear to corroborate other studies on the hyrax, there is some justification in their acceptance.

acute and chronic dehydration have different effects on some of the above avenues of water loss. For example, in the jackrabbit *Lepus californicus* (Reese & Haines, 1978) and Sinai goats *Capra hircus* Shkolnik *et al.*, 1972) acute dehydration did not result in a reduction in oxygen consumption although EWL in the latter species was reduced. Apparently the reduction of metabolism in response to dehydration takes several days to develop in the jackrabbit (Reese & Haines, 1978). Chronic dehydration in the jackrabbit, however, caused a decrease in both metabolic rate and EWL. A reduction in EWL with acute dehydration appears to be common in different mammals (the camel - Schmidt-Nielsen *et al.*, 1956; African goats and sheep - Maloiy & Taylor, 1971; bandicoots - Hulbert & Dawson, 1974; *Antechinus stuartii*, a dasyurid marsupial - Nagy *et al.*, 1978) and this probably occurred in *P. capensis* too. Although chronically dehydrated, *P. habessinica* also showed a reduction in EWL (Rubsamen & Kettembeil, 1980). Of particular interest in the latter study was the increased lability in the body temperature of *P. habessinica* in response to water restriction. At high ambient temperatures the thermolability was mediated, in part at least, through a reduction in EWL so that the animals became hyperthermic but were tolerant of the higher body temperature. At low ambient temperatures, the hyraces became hypothermic with a decrease in metabolic rate and in EWL. Rubsamen and Kettembeil (1980) have suggested that the increased thermolability may be explained by the shifting apart of the threshold levels for evaporative heat loss and for activation of heat production, as outlined by Bligh (1972). In view of the stability of body temperature in *P. capensis* over a wide range (6 to 28°C - section 6) which is not shown by *P. habessinica*

(Rubsamen & Kettenbeil, 1980; Taylor & Sale, 1969), and since the mechanism is clearly adaptive in terms of energy and water conservation, it would be of interest to test if *P. capensis* responded similarly to chronic dehydration.

Water loss through the urine and faeces is definitely reduced when *P. capensis* is dehydrated (Louw *et al.*, 1973; Maloiy & Sale, 1976). In the study of Louw *et al.* (1973), acute dehydration caused *P. capensis* to decrease its food intake with a consequent reduction in faecal output. The water content of the faecal pellets was also lower than when hydrated. Urine volumes decreased by approximately half (Louw *et al.*, 1973; Maloiy & Sale, 1969).

5.4.2 Blood and urine analyses

The water lost from mammals in response to dehydration can be derived from any of the fluid compartments within the body, the blood being one. Removal of water from the blood can lead to imbalances in the osmotic concentration and to greater viscosity, both of which can ultimately lead to death.

In the present study, the osmolality of the plasma and the concentrations of the Na^+ and K^+ remained fairly stable, with significant increases only in Cl^- and urea concentrations on dehydration. Considering that three of the four dehydrated hyraces had reduced their food intake to very small amounts on the last day of dehydration, there must have been

very low electrolyte intake in the food. Even though plant matter is low in Na^+ and Cl^-, it does provide animals with a source for the replenishment of these essential electrolytes. Thus the overall response to dehydration was the maintenance of osmotic equilibrium and stable electrolyte concentrations in the plasma, an essential response for the survival and normal functioning of an animal in unfavourable conditions.

The haematocrit of *P. capensis*, however, increased by 25 per cent in response to dehydration. This does not necessarily mean that of the body fluid compartments, the plasma was the major source of water loss, since there may have been an equal reduction in all fluid compartments, as was shown in acutely dehydrated jackrabbits (Reese & Haines, 1978). Further work is needed to establish whether the hyrax responds to dehydration by maintaining plasma volume constant as in the camel (Macfarlane *et al.*, 1963), desert kangaroos (Denny & Dawson, 1975), jackrabbits (Reese & Haines, 1978) and the burro (Yousef *et al.*, 1970) or follow the pattern of Merino sheep (Macfarlane *et al.*, 1961) and the Guanaco (Rosenmann & Morrison, 1963) where the plasma volume is reduced by 40 to 50 per cent with a 20 per cent loss in body mass.

Any alteration in the fluid volumes of an animal necessitates an adjustment in the electrolyte distribution and concentration in order to re-establish osmotic equilibrium. Louw *et al.* (1973) have shown that in response to dehydration, the urine osmolality and urinary concentrations of Na^+ and K^+ in *P. capensis* initially increased for the first two days and subsequently dropped as feed intake dropped.

Chloride concentrations in the urine decreased with dehydration while urea concentration increased reaching a peak, five days after water was first withheld. These changes were accompanied by a reduction of urine volume from *ca.* 45 $ml.day^{-1}$ to the lowest volume of *ca.* 15 $ml.day^{-1}$ after a week without water. In the present study only one urine sample was taken from each animal after five days of dehydration and thus these values can be compared only with those of Louw *et al.* (1973) on the same day of dehydration since the pattern of urinary components change daily. Thus on the fifth day of dehydration, urinary electrolyte concentrations either decreased or remained near the 'hydrated' level, but the absolute amount of the ions Na^+, K^+ and Cl^- must have been reduced as urine volumes declined (Louw *et al.*, 1973; Maloiy & Sale, 1976). In the present study, this was most marked in the case of Na^+ where three of the four dehydrated animals had urinary concentrations of 2,2 and 9 $meq.l^{-1}$. The single animal that was still feeding and had a calcium carbonate precipitate in the urine had a far higher value of 54 $meq.l^{-1}$. This latter value was probably the cause of the insignificant statistical difference between the hydrated and dehydrated hyraces with respect to Na^+ excretion. The extremely low concentration of Na^+ and reduced Cl^- concentration in the urine is indicative of an efficient countercurrent system in the kidney whereby Na^+ and Cl^- ions are efficiently recycled, reabsorption of water following passively (Schmidt-Nielsen, 1975). The efficiency of Na^+ retention by the body or reduction in its excretion would presumably also be advantageous for hyraces faced with a lack of sodium in the diet. Extremely low levels of sodium in the urine have also been found in the camel and sheep when dehydrated (below 1 $meq.day^{-1}$

- Macfarlane, 1964) and in the ground squirrel *Xerus inauris* where levels as low as 1 and 6 meq.l^{-1} have been found in the field (Marsh *et al.*, 1978). Maloiy and Sale (1976) have shown that Na^+ excretion increased on dehydration in *P. capensis*, though they did not specify the length of the dehydration period when this was measured. Comparison with the study of Louw *et al.* (1973) would suggest that the period was two to three days since Na^+ initially increases and with it the highest osmolality is usually recorded (Louw *et al.*, 1973).

The higher concentration of K^+ than Na^+ in the urine of *P. capensis* is indicative of an increased secretion of adreno-corticosteroids and their effect on renal function. Potassium, however, is more abundant in plant matter than sodium, and the need therefore to conserve this ion is less critical. Macfarlane (1964) found that sheep excreted more Na^+ than K^+ in the urine and noted an increased disparity between the excretion of the two ions with more rapid dehydration and a high heat load. He related this disparity to the production of sweat with a predominance of potassium and bicarbonate ions derived from the plant food. Thus the Na^+ to K^+ ratio in the plasma was kept stable by the elimination of Na^+ in the urine. It would be interesting to determine the predominant ions in hyrax sweat in view of the large amount of carbonate ions which are incorporated into the urinary precipitate.

Judging from the relative medullary thickness of the kidneys of *P. capensis* an osmolality of 3000 mosm.kg^{-1} would be expected, a value which was recorded by Louw *et al.* (1973) and Maloiy and Sale (1976). The lower urine osmolality in the present dehydrated hyraces occurred

despite the higher urea concentration when compared with the two previous studies mentioned - (1018 mmol.l^{-1} - present vs. 836 mmol.l^{-1} - Maloiy & Sale, 1976). However, the present urine osmolality was in keeping with that of the hyraces in the study of Louw *et al.* (1973) on the fifth day of dehydration and supports the view of these authors that the electrolyte content of the urine was the major factor determining osmolality.

With the increase in urinary urea concentration on dehydration, the plasma urea of *P. capensis* increased by 100 per cent (from 7 to 14 mmol . l^{-1}). Both the hydrated and dehydrated plasma urea concentrations were higher in the present study than the highest levels found in *P. habessinica* (6 mmol . l^{-1} - Hume *et al.*, 1980). In both studies the highest concentrations of plasma urea occurred during dehydration with a low energy intake and therefore the body tissues were probably catabolised resulting in the production of high levels of urea. From these results, it appears that *P. capensis* may be more tolerant of plasma urea loading than *P. habessinica*. A marginal advantage in terms of water economy and nitrogen conservation would result, assuming that *P. capensis* recycles urea in the same way as *P. habessinica*.

5.4.3 Ecological considerations

The low basal metabolic rate, the gregarious, semi-fossorial existence and the mechanisms of behavioural thermoregulation of *P. capensis* are advantageous in terms of energy utilization and have manifold effects on

other aspects of the physiology of this animal. One of these is a low turnover rate of water. Even though the WTR of *P. capensis* was measured under free-living conditions, it was still below the predicted rate for eutherian placentals of comparable size. Although the low WTR may be a secondary effect of the frugal energy expenditure and the low BMR, common to the order Hyracoidea, rather than an ecologically determined character, as suggested by Rubsamen *et al.* (1979), it still has beneficial survival value. The low WTR would be an obvious advantage for this species living in an arid environment where free water is scarce and the main source of water is in the food eaten.

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It is recognised that the numbers of animals used in this study were small, particularly in the dehydration and renal function experiments, and therefore the results should be viewed with caution. However, in as far as the results appear to corroborate other studies on the hyrax, there is some justification in their acceptance.

TABLE 5.4 Mean seasonal moisture percentages of plants occurring in two areas of Namibia (S = Sandmodder and W = Warmfontein) which *P. capensis* inhabits. (From Lensing, 1978.)

Season	March 1975 Wet		July 1975 Cool dry		Oct. 1975 Transition		Dec. 1975 Hot dry		March 1976 Wet		July 1976 Cool dry	
Area	S	W	S	W	S	W	S	W	S	W	S	W
No. of plant spp.	39	23	54	41	41	35	43	42	65	68	64	59
Moisture $\bar{x}$ %	60	62	47	39	33	34	38	31	64	64	47	42
content ±SD	18	16	22	18	20	16	21	21	19	19	26	24

SECTION 6

THE ROLE OF THERMOREGULATION IN THE ENERGY METABOLISM OF THE ROCK HYRAX *PROCAVIA CAPENSIS*

6.1 INTRODUCTION

The survival and success of an animal in any environment is dependent on a number of factors, one of the most important being the degree to which the energy demands of the animal are met, commensurate with the varying environmental conditions. Thus a reasonable balance must be achieved between energy expenditure and energy conservation. The mechanisms employed by mammals to achieve this balance involve both behavioural and physiological adjustments such as in activity, body temperature, insulation and metabolic rate. In homeotherms a large part of energy expenditure is involved in the maintenance of a stable body temperature and consequently regulation of energy expenditure is intimately associated with thermoregulation.

The behavioural component of thermoregulation involves the modification of the thermal environment while the physiological component involves predominantly, autonomic responses within the animal. They are, however, complimentary in the maintenance of a stable body temperature (Cabanac, 1972). The importance of thermoregulatory behaviour to ectotherms has long been recognised since they do not have the complex physiological mechanisms of thermoregulation characteristic of endotherms. Behaviour, however, is an extremely efficient mechanism of thermoregulation in endotherms as well (Hardy, 1961), since in adverse temperature conditions, physiological reactions alone would not prevent a mammal from dying. The complimentary rôles of these two aspects of thermoregulation are therefore evident, and it appears that the

neuronal mechanisms controlling the two types of response may be identical (Cabanac, 1972). It has been proposed that two levels of thermoregulatory control exist, a 'broad band' and a finer level (Bligh, 1966), and some evidence suggests that behaviour constitutes the former and physiological responses the latter (Ingram & Legge, 1970). Cabanac *et al.* (1970), however, have shown that in some dogs, the same is not necessarily true and fine behavioural control was used rather than resorting to physiological methods of thermoregulation, such as shivering in the cold and panting in the heat. Thus, Cabanac (1972) suggested that both behavioural and physiological mechanisms of temperature control are equally important and the use of either depends on the particular situation.

The rock hyrax *P. capensis* is extremely successful in southern Africa, despite the harsh climatic conditions prevalent in the arid areas they inhabit. A factor contributing to the success of the species may be an efficient use of energy, particularly with respect to thermoregulation. Indeed, much of its behaviour appears to be determined by the environmental temperature, viz. basking at moderate temperatures, avoiding intense solar radiation by retreating to the shade, shuttling between the sun and shade, and finally huddling in a rock crevice when temperatures are low or conditions are unfavourable. However, limited information on the energy metabolism of *P. capensis* is available and those studies concerned with physiological thermoregulation are conflicting (Louw *et al.*, 1973; McNairn & Fairall, 1979; Taylor & Sale, 1969). At best, the role of behaviour in thermoregulation and energy metabolism for any *Procavia* species is speculative, though Bartholomew

and Rainy (1971) have included thermoregulatory behaviour in their study on the more tropical species of hyrax, *Heterohyrax brucei*. Differences in environment, however, have significant effects on energy metabolism. Thus, the present investigation was conducted to evaluate the rôle of some aspects of behavioural and physiological thermoregulation together with a study of energy metabolism in the arid-adapted hyrax, *P. capensis*.

6.2 PROCEDURE

The nine hyraces (5 males, 4 females, mean mass 2,94 ± 0,43 kg) used for this study had been in captivity for at least six months prior to experimentation. They were housed in an outdoor run with access to an adjoining small indoor shelter and thus subjected to natural temperatures and lighting. During the period of experimentation the animals were housed indoors with three animals per cage. Water and food consisting of commercial rabbit pellets, lucerne hay and fresh leaves were provided *ad lib*. No artificial heating or lighting was imposed. Experiments were performed from March to June (autumn to winter).

6.2.1 Oxygen consumption

Experiments on oxygen consumption were performed in a temperature controlled room (accuracy 1°C). A flow-through respirometry system was used. At least five hours after feeding, animals were placed either

individually or in groups of three (huddled) in a sealed wooden metabolic chamber with a clear perspex front. Room air was drawn through a large tube of silica gel before entering the metabolic chamber, thereby maintaining the inflowing air at a constant humidity at different room temperatures. Air flow was maintained at 2 l/min for single animals and 6 l/min for three animals. Outflowing air was dried over silica gel before passing through a calibrated flow-meter (G.E.C. Elliott Rotameter) and then on to the vacuum pump. An hour was allowed for equilibration of the animal within the system and thereafter samples of outflowing air were drawn into 50 cm^3 syringes every five minutes for a duration of three to six hours. The animals were watched continuously and air samples were taken for analysis only when the animals were inactive. The oxygen content of the sampled air was measured using a Beckman OM14 polarographic oxygen analyser. Carbon dioxide and water were first removed by injecting the sample through ascarite and drierite. The oxygen analyser was calibrated every 30 min using room air.

Oxygen consumption for six single and six groups of three hyraces was measured at different air temperatures ranging from 5°C to 28°C. A copper-constantan thermocouple, connected to a Bailey Bat 4 thermocouple meter, placed in the temperature controlled room measured the temperature of the inflowing air (Tr). A second thermocouple sealed into the outflow port of the chamber measured the temperature of the outflowing air (Tch) (accuracy 1°C). Basal metabolic rates were calculated and converted to S.T.P. Oxygen consumption (VO_2) expressed as $ml O_2$ per gram body mass per hour, was plotted against Tr and Tch on

separate graphs for single and huddled hyraces. For each, a least squares regression line was fitted to points recorded at temperatures below the lower critical temperature. The four regression lines were compared using a two-tailed 't' test for differences between slopes and intercepts (Zar, 1974).

6.2.2 Temperature Telemetry

The deep body temperatures (T_B) of hyraces were recorded using radio telemetry, both in the laboratory and in an outdoor enclosure, simulating field conditions. Prior to implantation in the peritoneal cavity of each hyrax used, the transmitters were sealed using beeswax and an outer coating of silicone rubber, soaked in an antiseptic solution and calibrated. Animals were anaesthetized with an I.P. injection of pentobarbitone sodium (Nembutal, Abbot Laboratories), and penicillin introduced at the site of implantation. A week recovery period was allowed after the operation.

6.2.2.1 *Laboratory experiments*

Four adult, non-gravid female hyraces of mean mass 2,73 ± 0,33 kg were used in the laboratory experiments. They were captured in November from Montague (Robertson district, Cape), and transferred to individual cages in a temperature controlled room at 22°C with a 12 hour light:dark photoperiod. Each cage was fitted with an antenna which extended to the receiver outside the room, thus causing no disturbance to the animals. After three weeks a transmitter was implanted in each animal,

and during the recovery period of one week, body temperatures (T_B) were monitored to ensure that they were stable before continuing with recordings at different ambient temperatures. Thereafter, 24, hourly measurements of the deep body temperature of individual animals were recorded to establish the circadian pattern of temperature fluctuations and to establish the times when further recordings could be made without the interference of normal temperature fluctuations. Ambient temperatures were then varied between 4° and 39°C and body temperatures recorded after exposure to the particular temperature for at least four hours. An exposure time of only two hours was allowed at the ambient temperature of 34°C and one hour at 39°C. Finally, the four animals were allowed to huddle together in a ventilated wooden box, overnight at 4°C and body temperatures recorded to monitor the effect of huddling in the cold.

6.2.2.2 *'Field' experiments*

Prior to implantation of the transmitters all of the four male hyraces (A, B, C & D, mean mass 2,50 ± 0,86 kg) used in this study were maintained in an outdoor run with other hyraces. The temperature recordings for animals A, B and C were run concurrently during September, and those for D, during December under diffferent conditions.

After recovering from the operation, the body temperatures of the hyraces were recorded at room temperature (22°C) and animals A, B and C were then introduced into an outdoor run with a stone shelter

(approximate dimensions, 1,0 x 0,5 x 0,3 m^3 with three entrances) at Vrolijkheid Nature Conservation Research Station in the Robertson district, Cape. Since this run was occupied by an established colony of seven hyraces, the three experimental animals were allowed two days to integrate. One experimental animal (C) was not accepted by the colony and thus, was isolated in a separate small cage, exposed to fluctuating environmental conditions, with no shelter. Deep body temperatures of the three experimental animals were recorded at 15 min to one hour intervals for 51 hours, with concurrent hourly measurements of the following environmental parameters:

Air and crevice temperature (Thermistor probes connected to a Y.S.I. telethermometer); solar radiation (Middleton solarimeter, sensitivity 0,223 $mV.mW^{-1}.cm^{-2}$, connected to a microvoltmeter. Readings were converted to $W.m^{-2}$); air humidity (whirling hygrometer); wind speed (Wallac-thermo-anemometer); cloud cover (estimated as a fraction of 8).

After recovering from the operation, hyrax D was returned to its original colony of five animals in a run at the University of Cape Town. The shelter consisted of a wooden compartmentalized box (approximately 0,9 x 0,6 x 0,4 m^3 with two entrances), insulated with polystyrene and covered with heavy duty tar impregnated paper. This also served as a surface on which the animals basked. Deep body temperature of hyrax D was recorded hourly for various periods of time over six days. Only air temperature was recorded concurrently, and activity noted.

6.3 RESULTS

6.3.1 Oxygen consumption

The lowest value of oxygen consumption for both solitary and huddled hyraces was 0,27 ± S.D. 0,03 $ml O_2.g^{-1}.h^{-1}$ within the thermoneutral zone (Fig. 6.1). The lower critical temperature for single animals was 18,7°C but 16,9°C for huddled animals. These temperatures, however, were of the inflowing air (Tr), chamber temperature (Tch) being 1°C higher for single animals and 3°C higher for huddled animals. Thus, the actual lower critical temperatures for both isolated and huddled animals would be 19,7 and 19,9°C, respectively. Oxygen consumption, at Tr below thermoneutrality, increased according to the regression equations:

$$y = -0,0137\ x\ (\pm 0,0019) + 0,5260\ (\pm 0,0228)$$

for single hyraces ($r = 0,802$)

$$y = -0,0120\ x\ (\pm 0,0014) + 0,4730\ (\pm 0,0161)$$

for huddled hyraces ($r = 0,856$)

This is shown graphically in Fig. 6.1.

Comparison of the two regression equations showed no statistical difference in slope, but a significant difference in the intercept values ($ts = 3,49$, $p < 0,001$ with 57 degrees of freedom). Extrapolation of the regression line for single hyraces intercepted the x-axis at 38,4°C which was higher than T_B recorded in the laboratory at thermoneutrality, but was within the range of deep body temperatures found telemetrically

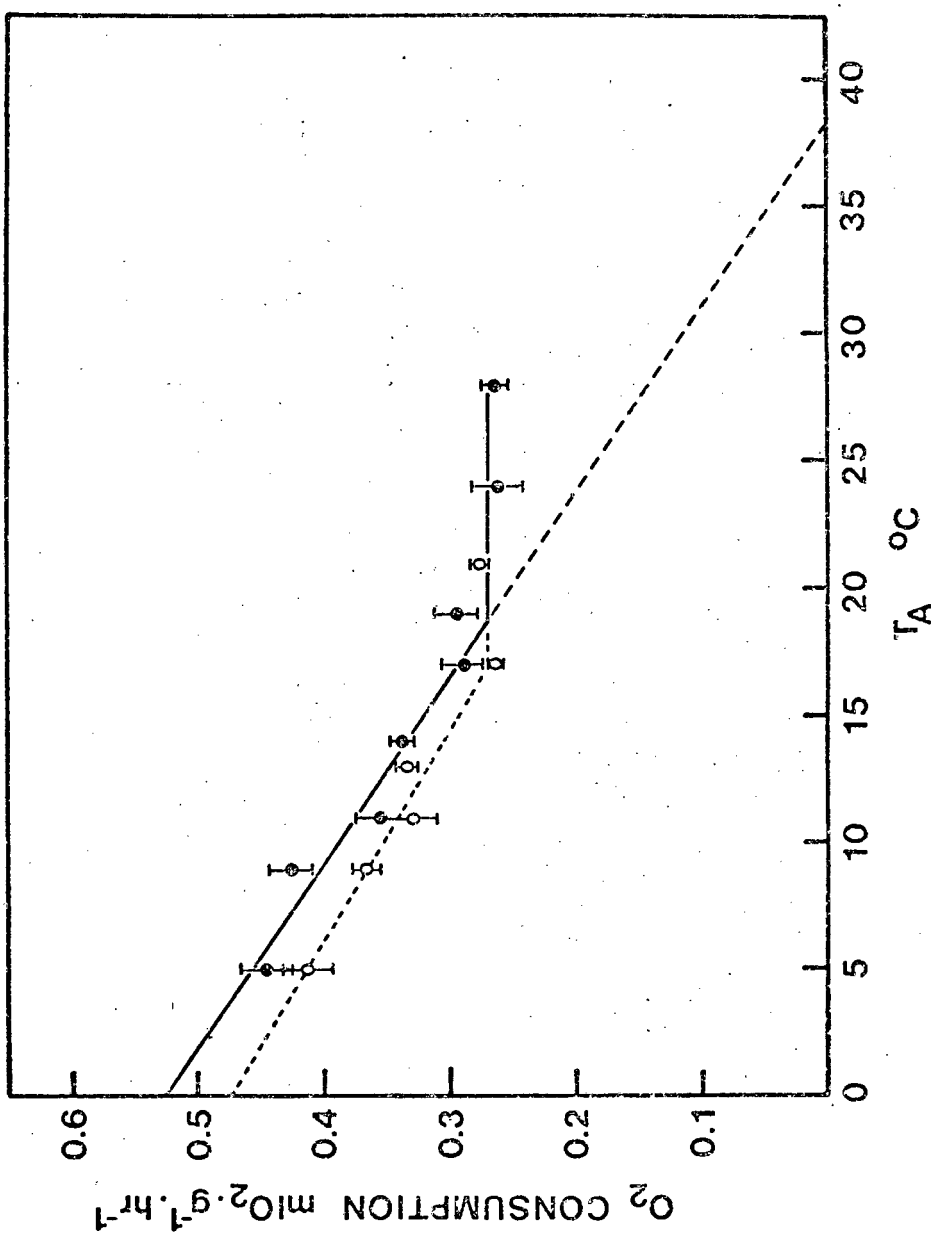


Fig. 6.1 Relationship between inflowing air temperature (T_r) and oxygen consumption in single (●) and huddled (○) hyraces. Values are means ± 1S.E. of 6 individuals or groups.

in *P. capensis* under free living conditions (see temperature telemetry, this section). Comparison of the regression equations for single and huddled hyraces using chamber temperatures rather than Tr showed no statistical difference in slope or intercept ($p \geq 0,05$).

6.3.2 Thermal conductance

At ambient temperatures below thermoneutrality, the minimal wet thermal conductance (0,0137 $ml O_2.g^{-1}.h^{-1}.°C.^{-1}$ - the slope of the regression line) was 21 per cent lower than predicted for an animal of mass 2,94 kg (MacMillen & Nelson, 1969). However this method of determining the minimal thermal conductance tends to underestimate the actual value unless extrapolation of the regression line meets the abscissa at a value equal to the body temperature, when metabolism is zero (McNab, 1980). Using the correction factor given by McNab (1980) the mean minimal thermal conductance would be 0,0147 $ml O_2.g^{-1}.h^{-1}.°C.^{-1}$. Within the thermoneutral zone at 22°C, with a body temperature between 37 and 38°C and oxygen consumption 0,27 $ml O_2.g^{-1}.h^{-1}$, the calculated value of mass specific, wet, conductance lies between 0,018 and 0,017 $ml O_2.g^{-1}.h^{-1}.°C.^{-1}$ which is similar to the predicted value of 0,0173 $ml O_2.g^{-1}.h^{-1}.°C.^{-1}$.

6.3.3 Temperature telemetry

6.3.3.1 *Laboratory study*

A clearly defined, diurnal rhythm was not apparent in the body temperatures

(T_B) of the four female hyraces when ambient temperature was kept constant, but a small rise in T_B could be detected a few hours prior to each change in lighting (Fig. 6.2). The maximum individual variations recorded over 24 hours were 0,95, 0,8, 0,8 and 0,6°C, with a maximum inter-animal variation of 1,90°C.

From Fig. 6.3, *P. capensis* was shown to have a remarkably stable body temperature (mean of 37,23 ± SD. 0,12°C) at ambient temperatures between 5 and 28°C. Below 5°C, T_B dropped slightly and increased above 28°C. T_B could not be maintained below ambient at high air temperatures. After an hour at 39°C, two animals lay prostrate but no nasal secretion or moisture droplets on the feet were observed. When huddled at 4°C, despite the wooden box being ventilated, the temperature around the animals rose to 10°C, and thus the mean T_B was higher (37,24 ± SE.0,36 °C) than found for solitary animals at 4°C.

6.3.3.2 *'Field' study*

The deep body temperatures (T_B) of hyraces A, B, C and D recorded at room temperature and at rest were 37,68 ± 0,10, 37,53 ± 0,24, 36,82 ± 0,14 and 37,20 ± 0,15 respectively. In the outdoor colony (see Figs 6.4 and 6.5), with air temperature (T_A) fluctuations of 7,6 to 32,7°C (for hyraces A and B) and 12,0 to 25,0°C (hyrax D) the maximum ranges of T_B recorded were 37,3 to 39,4°C (A), 37,6 to 39,2°C (B) and 37,0 to 38,7°C (D). The mean T_Bs during daylight hours (06h00 - 19h00) were 38,50 ± 0,44°C (n=65, A) and 38,37 ± 0,34°C (n=66, B) with temperatures at night being slightly lower - 37,74 ± 0,43°C (n=45, A) and 38,03 ± 0,21°C (n=49, B), though not statistically different

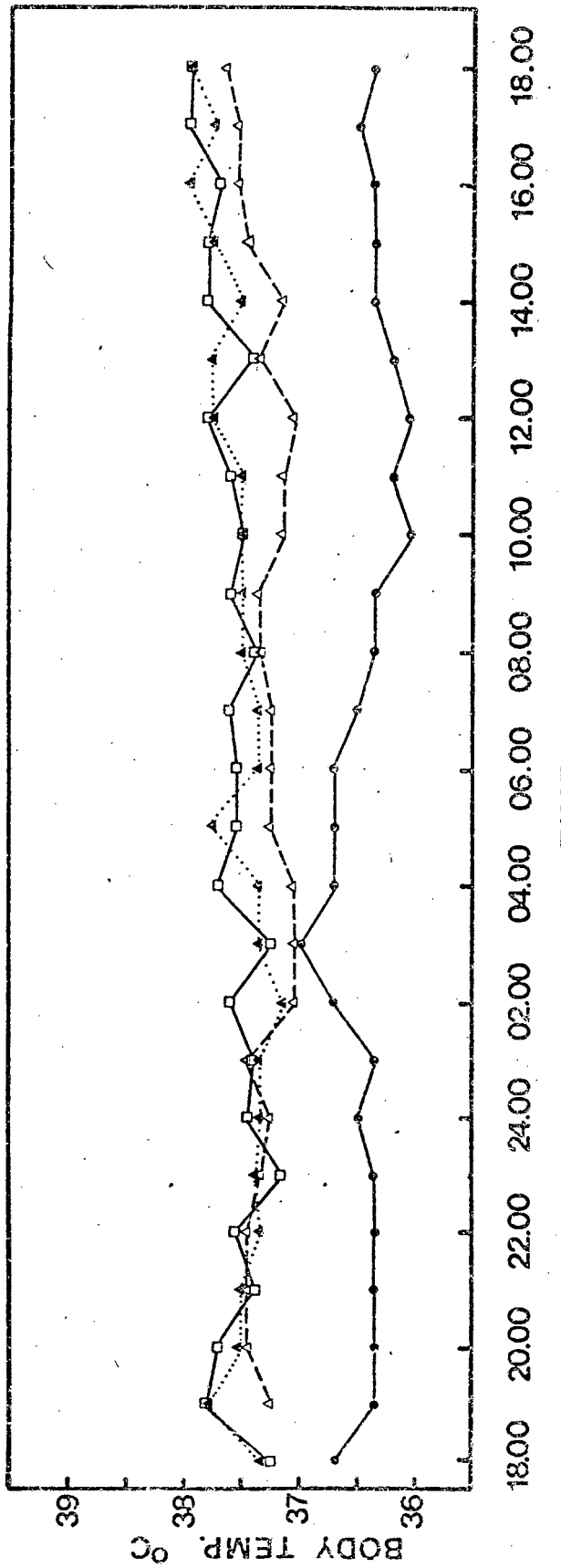


Fig. 6.2 Diurnal fluctuations in the deep body temperature (T_B) of four female hyraces recorded at a constant ambient temperature of 23°C

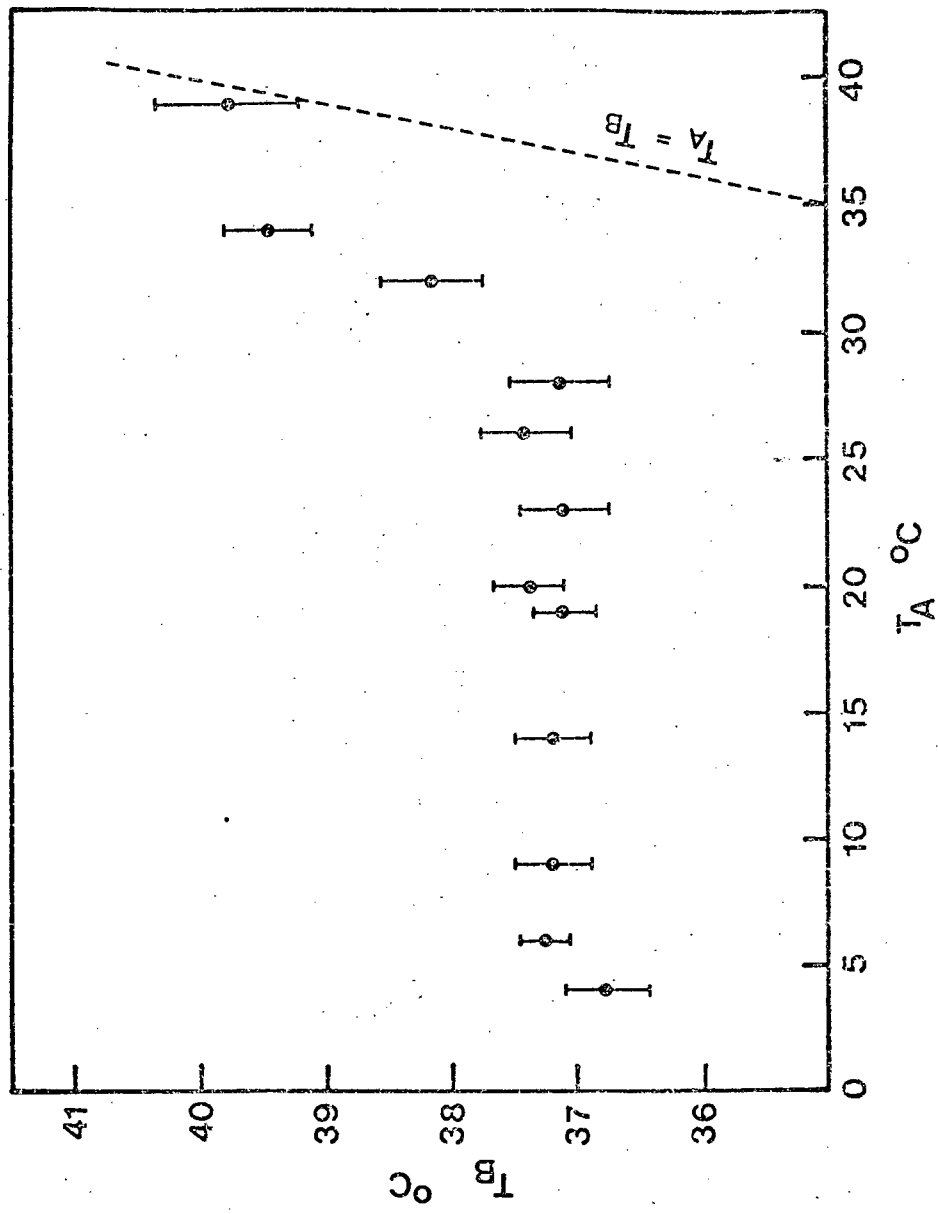


Fig. 6.3 Response of deep body temperature (T_B) of hyraces to different ambient temperatures (T_A) (mean ± 1S.E.)

Fig. 6.4 24 hr telemetered body temperature of a male hyrax (hyrax A) in an outdoor run in relation to environmental parameters. (Relative humidity of air at 11.00h = 39%, 02.00h = 64%, 06.00h = 82%)

Key:


sunny


sun obscured by cloud


intermittent sun for short periods

o hyrax in sun


hyrax in shade or shelter

A period of activity

F beginning of feeding period


sunrise


sunset

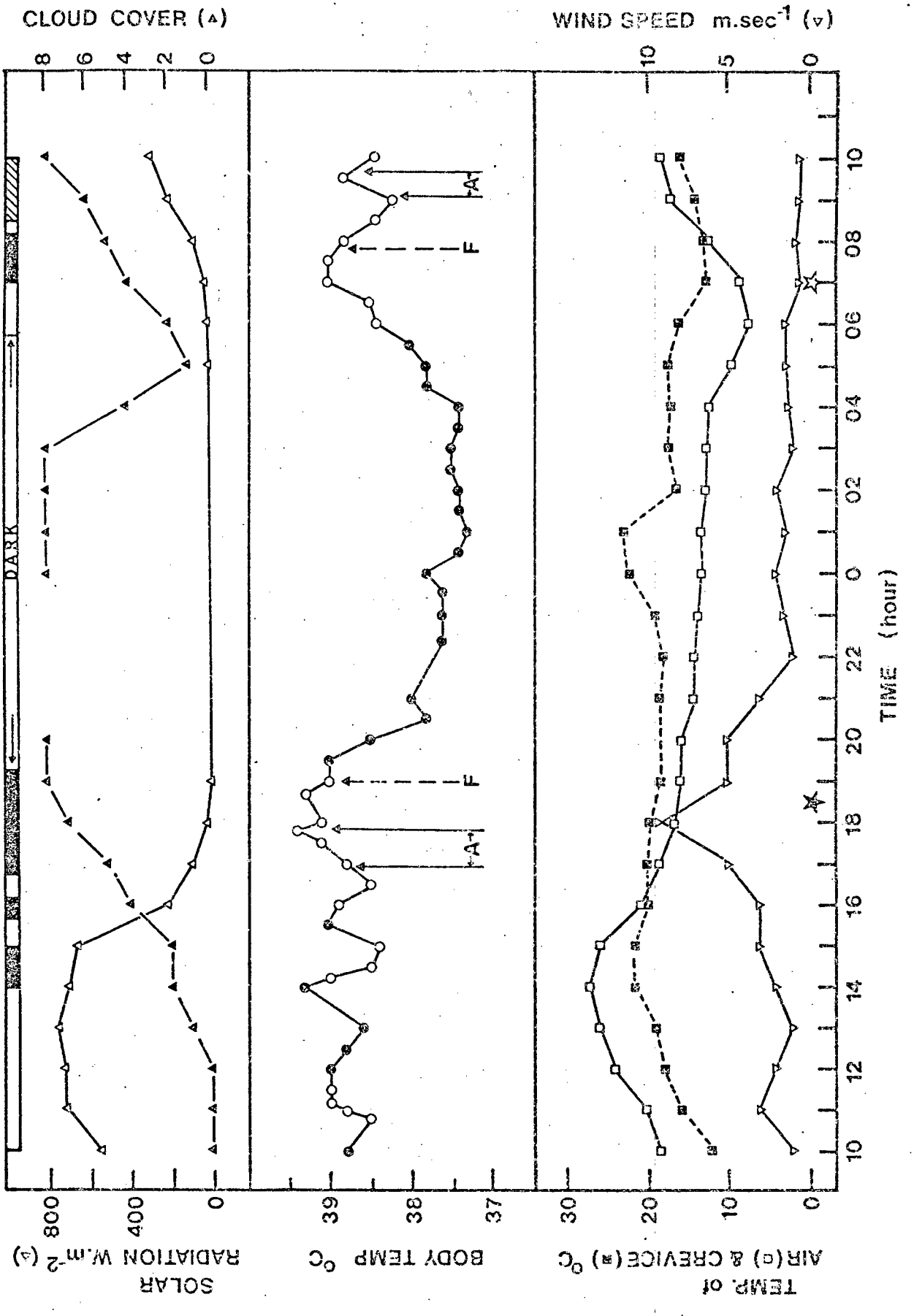

CLOUD COVER (▲)
WIND SPEED m.sec⁻¹ (▽)
DARK
A
F
TIME (hour)
SOLAR RADIATION W.m⁻² (△)
BODY TEMP °C
TEMP. of AIR(○) & CREVICE(■) °C

Fig. 6.5 Telemetered body temperatures of free (hyrax B) and caged (hyrax C) hyraces in an outdoor run in relation to environmental parameters. (Relative humidity of air at 11.00h = 70%, 03.00h = 88%, 13.00h = 40%)

Key:


sunny


sun obscured by cloud

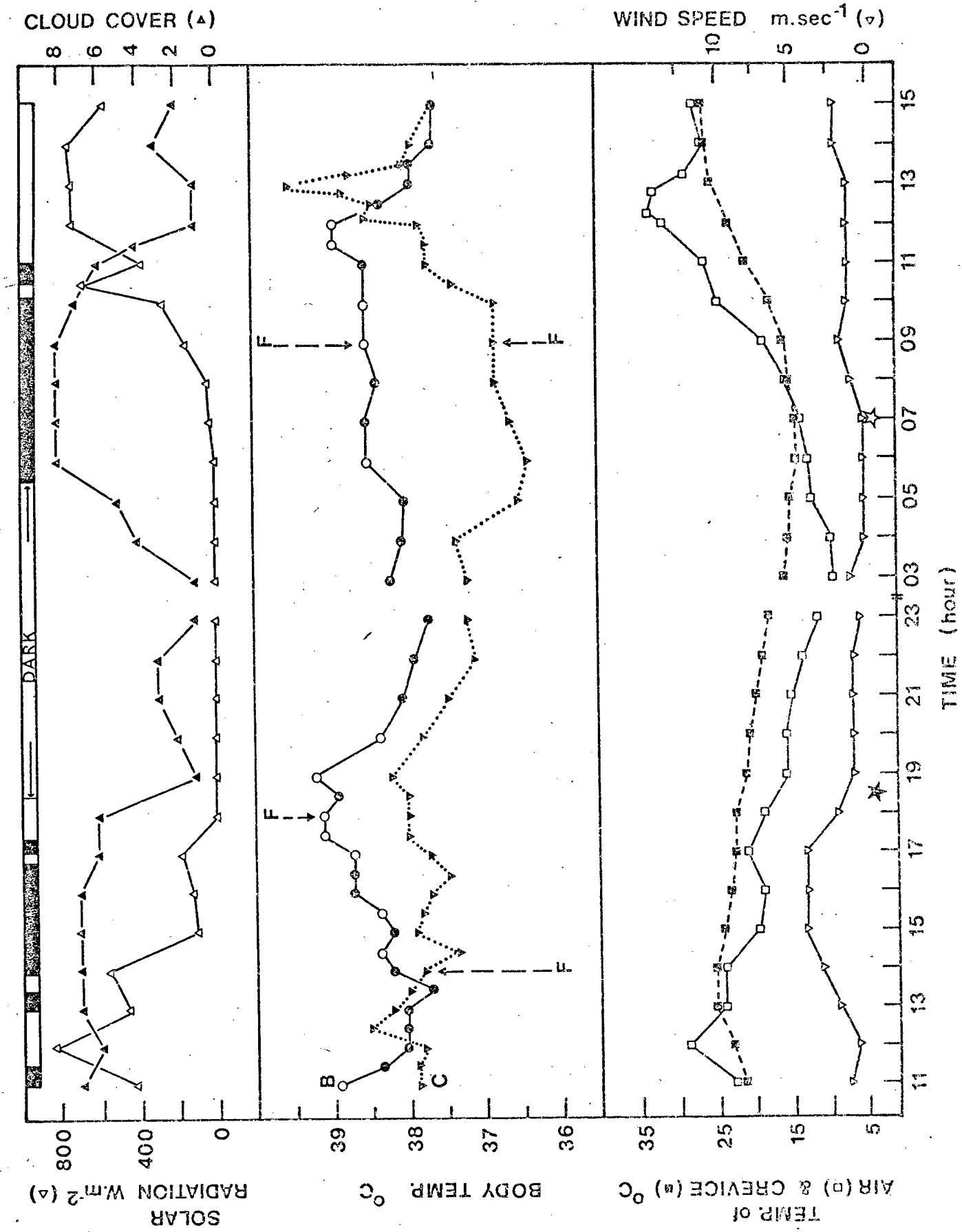

hyrax in sun


hyrax in shade or shelter

F beginning of feeding period


sunrise

sunset


CLOUD COVER (▲)
WIND SPEED m.sec-1 (▽)
DARK
F
B
C
E
TIME (hour)
SOLAR RADIATION W.m-2 (▲)
BODY TEMP °C
TEMP. of AIR (□) & CREVICE (■) °C

($p>0,05$). The highest T_Bs were recorded when the animals were either basking or were extremely active (running) and lowest in the early morning while huddled in the shelter (Fig. 6.4). The isolated animal (C) whose movement was restricted showed an overall lower range of body temperatures, the minimum being 36,40°C and a maximum, without any sign of distress, of 38,5°C (Fig. 6.5).

6.3.4 Factors affecting body temperature

6.3.4.1 *Crevice and ambient temperature*

The general pattern shown in the results was that of a relatively high T_B during daylight hours thus correlating with the higher ambient temperatures (T_A) and a nocturnal decline in T_B when T_A was low. The temperature of the shelter did not show as marked fluctuations as did the T_A, being cooler in the day and warmer at night. Thus it was used as a retreat during extremes of T_A and periods of intense solar radiation (Fig. 6.4).

6.3.4.2 *Solar radiation*

High levels of solar radiation recorded under a full sun with low wind speed (0,5 $m.sec^{-1}$) caused an increase in T_B. This was shown in hyrax C when escape from intense solar ratiation (717 $W.m^{-2}$) was prevented (Fig. 6.5, 10h00 - 13h00, day 2). During this time T_B and breathing rate increased exponentially over a period of an hour. The first sign of distress was apparent when T_B reached 38,4°C, 2°C higher than the

minimum recorded over 24 hours. The animal drank water and struggled to get under cover of the food dish. At a T_B of 39,4°C, breathing rate had increased from 48 to 172 breaths per min., the hyrax lay prostrate in the cage, but neither sweat droplets on the feet nor a nasal secretion were observed and muscle tonus was still maintained. The animal was then placed in a cool environment (T_A 19°C). Hyraces A, B and D tended to avoid intense solar radiation, particularly after midday, remaining in the shelter or in the shade (Fig. 6.5, 12h00 - 15h00). Maintenance of the fairly constant body temperatures during the day was achieved by alternately basking in the sun and then retreating to the shade or the cooler shelter when T_B approached 2°C above the minimum recorded for each particular animal.

Control of T_B by behavioural means, however, is clearly dependent on the complex interrelations between the various meteorological parameters and cannot be elucidated further from these results.

6.3.4.3 *Activity*

Activity, such as running (which took place as a result of intraspecific aggression) and rolling, caused an increase in body temperature. This was particularly apparent before feeding periods (Fig. 6.4, 17h00 to 19h30). The body temperature of one experimental animal that was chased by another rose to 39,4°C despite the decreasing ambient temperature and solar radiation and the high wind speed (10,0 - 19,0 $m.sec^{-1}$). A similar increase in body temperature, while ambient temperature dropped and solar radiation was minimal, was recorded in the early morning (04h00 - 07h00, Fig. 6.4) after approximately four hours of

lowered body temperature during the night. The body temperatures of animals A and B began to rise while still in the shelter and rose to a maximum between 06h00 and 07h00. All animals briefly emerged with the first light at 06h00 and feeding began at approximately 08h00. Increased activity on waking and emerging may have caused this rise in temperature.

6.3.4.4 *Huddling*

For differing periods during the night, body temperatures of all the experimental animals dropped approximately 1°C, the decline beginning after the evening feed at around sunset. The advantage of huddling and interacting with other hyraces in a sheltered crevice became apparent when examining body temperatures first in the early hours of the morning while still dark and later in the day under cloudy conditions. Between 04h00 and 10h00 (Fig. 6.5, day 2) when ambient temperature began to rise, crevice temperature remained stable and the sun was obscured by cloud, the body temperatures of hyraces A and B (in the colony) rose and from 05h30 on were maintained between 1 - 2°C above the minimum nocturnal body temperature. During this period both animals emerged from the shelter for only approximately 5 minutes. Despite the rising ambient temperature and low wind speed the body temperature of the solitary animal (C) dropped below the previously recorded minimum, thereafter rising slightly, but reached 1°C above the minimum only when the sun emerged and air temperature rose rapidly at 10h00 (Fig. 6.5, Day 2).

6.4 DISCUSSION AND CONCLUSIONS

6.4.1 Metabolic rate of various species of hyrax

The highly inactive nature of the rock hyrax behaviour has prompted the curiosity of several scientists over the past decade into examining the energy metabolism and thermoregulation of this animal (Taylor & Sale, 1969; Sale, 1970a; Bartholomew & Rainy, 1971; Meltzer, 1971; Louw *et al.*, 1973; Rubsamen *et al.*, 1979; McNairn & Fairall, 1979; Rubsamen & Kettembeil, 1980). These studies, however, have been of several different species of hyrax living in different climates and often no mention of the season is made in which the animals were studied. Moreover, the different methods of study have led to an array of conflicting results, summarized in Table 6.1 with respect to temperatures and metabolic rates. One physiological feature that appears to be true for all species is that of a lower metabolic rate than predicted according to body size (Schmidt-Nielsen, 1975). It has been shown that some arid-adapted animals have lower metabolic rates than the more temperate counterparts (Hart, 1971; Hudson *et al.*, 1972; Borut & Shkolnik, 1974; Shkolnik & Schmidt-Nielsen, 1976). In an arid region where both water and food may be scarce, annually or seasonally, a low metabolic rate reduces evaporative water loss as well as reducing the need for food.

In the present study, the basal metabolic rate (BMR) of *P. capensis* was 40 per cent lower than predicted for eutherian mammals (MacMillen &

TABLE 6.1 Comparison of data on temperature, oxygen consumption and thermal conductance for different species of hyrax

Species	Climate and distribution	Mass	T_B at thermoneutrality ±SD	T_B range at (T_A Range)	Oxygen consumption (VO_s ±SD) Observed	Predicted[1]	Lower Critical T_A	Thermal conductance (C ±SD) Observed	Predicted[2]	Reference
		kg	°C	°C	$ml O_2.g^{-1}.h^{-1}$		°C	$ml O_2.g^{-1}.h^{-1}.\ °C^{-1}$		
Procavia capensis	Temperate to arid	2,94	37,23 ±0,12	36,8-39,75* (4,0-39,0)♀	0,27 ±0,03	0,458	19,7	0,0137 ±0,0019 (0,0169-0,0176 at 22°C)	0,0173	Present study
	South Africa to Zimbabwe	2,63	38,0	38,0-41,0 (5-40)	0,417	0,472	15	-		Taylor & Sale, 1969
		-	34,6	33,2-38,2 (15-40)	-	-	-	-		Louw *et al.*, 1973
		2,5	37,0	-	0,649	0,478	-	-		McNairn & Fairall, 1979
Procavia syriacus	Arid? Syria & Israel Arabian Peninsula	-	-	32,8-37,8 (5 - 35)♂ 34,6-38,6 (10 - 35)♀	Lower than predicted		28	Higher than predicted		Meltzer, 1971
Procavia Johnstoni	Alpine Mt Kenya Tanzania	2,75	38,7	38,5-41,0 (5 - 40)	0,479	0,466	10	-		Taylor & Sale, 1969
Procavia habessinica	Tropical to warm temperate	2,25	37,8	36,6-41,0 (10 - 40)	0,408	0,491	30	-		Taylor & Sale, 1969
		2,4	-	-	0,27 ±0,03	0,483	27	0,018	0,0192	Rubsamen *et al.*, 1979
	Equatorial E. Africa to Middle east	2,1	37,2	36,6-39,6* (12 - 38)	0,34 ±0,04	0,500	28	0,0359	0,0206	Rubsamen & Kettembeil, 1980a
		-	-	36 - 42 (10 - 40)	-		-	-		Sale, 1970
Heterohyrax brucei	Tropical to warm temperate	1,31	36,4	34 - 41 (0 - 42)	0,52	0,567	25	0,0392	0,0262	Bartholomew & Rainy, 1971
	Equatorial E. Africa Red Sea - Maputo	2,0	37	36,2-41,0 (5 - 40)	0,354	0,507	23	-		Taylor & Sale, 1969

* Measured telemetrically in hydrated hyraces

1. $VO_2 = 3,8 \times Mass(g)^{-0,265}$ (MacMillen & Nelson, 1969)
2. $C = 1,098\ Mass\ (g)^{-0,52}$ (Herreid & Kessel, 1967; MacMillen & Nelson, 1969)

Nelson, 1969) and lower than found in all other studies on hyraces except that of Rubsamen *et al.* (1979) on *P. habessinica*. The metabolic rate of *P. syriacus* has been reported to be lower than predicted but no actual figures were quoted (Meltzer, 1971). It may be suggested that the lower metabolic rate of *P. capensis* is an adaptation to the arid areas in which they live, typified by hot dry summers and cold winters, often with the occurrence of snow. This statement is suspect, however, since *P. habessinica*, which does not experience the same extremes has as low a metabolic rate (Table 6.1). Furthermore, the comparative study of Taylor and Sale (1969) showed *H. brucei* a more tropical species, to have a lower metabolic rate than *P. capensis* and *P. habessinica*, with the alpine species *P. johnstoni* having the highest metabolic rate. In their study, and as can be seen from Table 6.1, the lower critical temperature of the different species can be correlated with their different habitats.

As there is no clear correlation between habitat and the metabolic rates of the various species from the literature published after Taylor and Sale's (1969) study, the validity of the apparent differences in metabolic rates in reflecting the habitat of each particular species, must be questioned. It is unlikely that the large discrepancies shown in the various studies are due solely to differences in the technical methods employed in the measurement of the metabolic rates. They may also be due to differences in the animals themselves at the particular time of measurement. Factors such as seasonal differences, whether the animals were under basal or resting conditions, the illumination during measurements, the activity or quiescence of the sexual organs

and whether males or females were used, could have had marked effects on the metabolic rates at the time of measurement. If more than one of these factors were operative and if they all had an additive effect on metabolism, then disparate results would be expected. Unfortunately many of these factors were not noted in the several studies quoted in Table 6.1 and it is therefore difficult to draw a final conclusion. Some of the above-mentioned factors, however, are discussed below in relation to the disparate results of oxygen consumption presented in Table 6.1

1. In the present study and those of Rubsamen *et al.* (1979), Rubsamen & Kettembeil (1980) on *P. habessinica* and Bartholomew and Rainy (1971) on *H. brucei*, basal metabolic rates were recorded. Taylor and Sale (1969) did not specify the nutritional state of the various species used. The figures of the latter authors may have been resting metabolic rates and therefore would have been higher. This is not applicable to *H. brucei* as the value found by Taylor and Sale (1969) was lower than that of Bartholomew and Rainy (1971) and other factors (outlined below) may have caused this discrepancy.

2. The marked variations in body temperature between individual animals have been shown in the present study and the general thermolability of the hyrax has been described by several of the afore-mentioned authors. Since a correlation between body temperature and metabolic rate in *P. habessinica* has been shown by Rubsamen and Kettembeil (1980), it is highly likely that the metabolic rate also shows intra-specific variations. With this in view, it is essential that many animals are

used to assess the BMR for it to be representative of the species. Some of the studies in Table 6.1 used only two or three animals and therefore may not be representative. This factor may apply particularly to *P. habessinica*, *H. brucei* and possibly *P. syriacus*, species which seem to be more thermolabile than *P. capensis* or *P. johnstoni* (Table 6.1). Furthermore, the diurnal cycle in body temperature described for *Procavia* (species uncertain - Sale, 1970a) may also mean that a similar cycle exists for the metabolic rate. Although a diurnal cycle in body temperature was not well defined in *P. capensis*, it may exist in the other species and should have been considered when measurements of oxygen consumption were taken.

3. Seasonal fluctuations in either metabolic rate or body temperature have not yet been investigated in any species of hyrax. However, some small mammals increase their basal metabolism as a response to cold winter temperatures or on exposure to continuous cold in the laboratory (Hart, 1957; Wunder *et al.*, 1977). Other seasonal increases in metabolic rate may be associated with the seasonal growth of the testes in the male hyrax or during the mating season. It would be preferable therefore, to measure metabolic rates in sexually quiescent male hyraces. Pregnant or lactating females must obviously be excluded for this type of measurement. As it is sometimes difficult to assess the sexual condition of both male and female hyraces, other than from the knowledge of seasonal sexual activity reported in the literature, some of the animals used in the various studies may have been sexually active which would have given erroneous evaluations of BMR. Those males used in the present study were in a quiescent

state as the experiments were performed after the mating season and at the end of summer into the beginning of winter. Neither were the females pregnant as no young were produced later in the year.

4. Meltzer (1971) has reported a difference in body temperatures of male and female *P. syriacus*, with those of the latter being significantly higher. If this difference is due to a higher metabolic rate in the females, then sexual differences in other studies may have caused some of the variability. A higher body temperature may also be due to better insulation, however.

6.4.2 Body temperature

6.4.2.1 *Laboratory*

Among the various species of rock hyrax studied, only *P. johnstoni* (Taylor & Sale, 1969) showed the same stability of body temperature found for *P. capensis* in the present study. Other reports on the physiological control of body temperature in *P. capensis* are conflicting. Both Louw *et al.* (1973) and McNairn and Fairall (1979) have described a decline in body temperature with decreasing ambient temperatures below thermoneutrality (though the range of body temperatures reported differ markedly), while Taylor and Sale (1969) found a remarkably stable body temperature (*ca.* 38°C) at ambient temperatures from 5 to 30°C. None of these studies are directly comparable to the present because of the different experimental conditions and methods of recording the body temperatures. Louw *et al.* (1973)

measured intra-abdominal temperatures, but these were recorded only five hours after recovering from an anaesthetic. Thus the extremely low temperatures they have reported were probably an after-effect of the anaesthetic which is known to inhibit thermoregulation. McNairn and Fairall (1979) measured rectal temperatures with a clinical thermometer in hyraces that had been acclimated to each ambient temperature for three weeks. Since the effect of acclimation on body temperature in these animals is not known, their results cannot be compared with the present. Furthermore, I have found that several consecutive measurements of rectal temperatures in individual hyraces to vary considerably depending on the depth of insertion of the recording device and on the excitability of the animals. Although the response of rectal temperature to ambient temperature in *P. capensis* from the results of Taylor and Sale (1969) was similar to the present findings, their values were higher. They used only two animals, however, and in view of the variation in body temperature from individual to individual, these authors may have biased results. Other species of hyrax, except *P. johnstoni*, showed decreasing body temperatures below thermoneutrality, though again, the ranges of body temperatures reported were sometimes conflicting (Table 6.1). At ambient temperatures above *ca.* 30°C, however, all species of rock hyrax showed an increase in body temperature (Taylor & Sale, 1969).

6.4.2.2 *Field*

In order to separate the influence of behavioural thermoregulation from physiological in the maintenance of body temperature, it is necessary

to compare laboratory data with those in the field. The deep body temperatures of 'free'-living *P. capensis* were maintained within the limits (38 ± 2°C) normally found in eutherian mammals (Schmidt-Nielsen, 1975). As for most diurnal mammals, highest temperatures were recorded during the day and lowest at night with a maximum range of 2°C. The limited field data in the present study showed that at night, with lower ambient temperatures (7,6°C), *P. capensis* was able to maintain body temperature at a constant though slightly lower level than in the day. The nocturnal drop in body temperature occurred in all experimental 'field' animals, irrespective of whether they were huddled or not. This does not appear to be part of the endogenous temperature cycle as has been described for *Procavia* sp. (Sale, 1970a) since a similar pattern was not shown in the laboratory. Rather, the decrease in temperature was due to a low ambient temperature or the absence of solar radiation as an external heat source which maintained the body temperature at a higher level during the day. Free-living *H. brucei* showed a similar diurnal fluctuation of body temperature (2°C) though over a lower range (35 - 37°C) with a small decline at night when huddled (Bartholomew & Rainy, 1971).

6.4.2.3 *Huddling and basking*

The interaction between hyraces in a shelter at night, whether in the form of huddling, low-key aggression or some form of activity, appeared to be important in stimulating an increase in body temperature prior to emergence with first light. Since the laboratory animals also showed a slight increase in body temperature prior to a change in lighting a part of the increase observed in the field may have been due to an

endogenous temperature cycle. However, without the social facilitation, body temperature rose only slightly as was seen in the solitary animal in the field. This animal relied on solar radiation and the rising ambient temperature for the increase in body temperature to *ca.* 38°C normally maintained during the day. Moreover, since the body temperatures of the individually caged 'field' animals, recorded indoors at approximately midday and at air temperatures within the thermoneutral zone, were near the lowest limits of the respective ranges recorded when the animals were free, it is clear that interaction between hyraces was important in increasing body temperature to the daytime range. Thereafter, however, the exploitation of external heat sources maintained the temperature at a relatively higher level and its stability (within 1°C) was achieved by shuttling between sun and shade.

6.4.3 Thermal conductance

6.4.3.1 *Single animals*

The thermal conductance of an animal is a measure of the balance between heat production and heat loss and is inversely related to the total insulation of the animal. At temperatures below thermoneutrality the lower than predicted thermal conductance of *P. capensis* indicates that these animals were relatively well insulated. Besides the insulative properties of fur and subcutaneous fat in reducing heat loss, various other factors have been observed in single animals which would have a similar effect. In the cold these include piloerection and the

assumption of a rounded posture, particularly obvicus when the animals first emerge from the crevice in the morning. Further, peripheral cooling, particularly in the feet, which has been described in *H. brucei* (Bartholomew & Rainy, 1971) also occurs in *P. capensis*, the temperature of the feet being approximately 11°C lower than the rectal temperature at low ambient temperatures (personal observations). This is brought about by the existence of alternative routes of venous flow; a deeper system of closely applied parallel bundles of arteries and veins in the limbs and an alternative superficial system of veins lying just beneath the skin (Leon, 1972; King, 1973). In addition an arterio-venous shunt exists in the proximal part of the hind-limb which would reduce blood flow to the extremities, therefore reducing heat loss from the body (Leon, 1972). The low conductance found in this study is supported by the comparative data of Taylor and Sale (1969) which, although not quantified showed that both *P. capensis* and *P. johnstoni* had lower conductances than the more tropical species *P. habessinica* and *H. brucei*. Bartholomew and Rainy (1971) found the latter species to have a conductance value 39 per cent higher than predicted. Meltzer (1971) has recorded that conductance in *P. syriacus* rose as ambient temperatures dropped below thermoneutrality. He concluded that the thermal insulation of this animal was poorly developed to the extent that endogenous heat production could not compensate for the heat losses at low ambient temperatures and resulted in a drop in rectal temperature. The opposite seems to be true of *P. capensis* as the calculated conductance at the lower critical temperature was higher than at lower ambient temperatures. Thus the mechanisms used by *P. capensis* to reduce heat losses must have been well developed and

allowed this species to maintain a constant body temperature even at low ambient temperatures. The differences in conductance between both *P. capensis* and *P. johnstoni*, and *P. habessinica* and *H. brucei* would be expected as the former two experience lower temperatures in the field and therefore it is clearly advantageous to be better insulated, at least in the cold season. Judging from the high conductance and the high lower critical temperature (28°C) *P. syriacus* does not experience the same low temperatures as *P. capensis* or *P. johnstoni* and should therefore be similar to *P. habessinica* and *H. brucei* in respect to other physiological responses.

6.4.3.2 *Huddling*

Most authors have described mass-specific thermal conductance in huddled animals to be consistently lower than in single animals (Withers & Jarvis, 1980; Glaser & Lustik, 1975; Baudinette, 1972). It was unexpected, therefore, to find similar slopes for the regression lines in single and huddled *P. capensis*. However, the effect of huddling in a crevice may merely affect the ambient temperature of the micro-environment, thereby delaying the onset of shivering below the thermo-neutral zone. A reduction in conductance would be expected because of the smaller surface area exposed to radiant and conductive heat loss. In the present experiment the former effect may have masked the latter effect. Also, the variations in oxygen consumption at low ambient temperatures without simultaneous measurements of body temperature may have led to erroneous values of conductance since the slope of the regression line does not make allowances for alterations in body

temperature. Thus further experimentation is necessary to clarify these results.

6.4.4 Energy considerations

Both basking and huddling or heaping behaviour in *P. capensis* are significant in terms of energy conservation. Using an external heat source as a means of increasing body temperature even 1°C, rather than increasing metabolic heat production has obvious advantages in energy conservation. Using the same method of calculation as Bartholomew and Rainy (1971), increasing the body temperature of a 2,94 kg animal by 1°C requires 11,7 kJ which is equivalent to 0,171 ml O_2 per gram of animal and *ca.* 63 per cent of the heat produced in one hour at the lowest metabolic rate of *P. capensis*. At ambient temperatures below thermoneutrality, basking would have the effect of raising the peripheral body temperature, reducing the temperature gradient between core and periphery, thereby minimising metabolic heat loss to the environment. An increase in heat production may therefore be avoided. This same principle explains the advantage of piloerection for heat and therefore energy conservation (Moen, 1973).

Huddling or heaping has advantages in the retention of body heat within the group, through the direct contact between animals. Further in an enclosed volume such as a crevice, transfer of heat from the animals to the air raises the air temperature, and providing that air currents through the crevice are minimal, the temperature of the crevice

is maintained at a stable level and higher than the external environment. Within this warmer environment, the necessity to increase the metabolic rate is obviated. In the present study the temperature within the metabolic chamber, when occupied by three animals, increased 2°C above that when occupied by a single hyrax and conferred an energy saving of 10 per cent on the huddled animals. Higher reductions in oxygen consumption of 18 to 28 per cent due to huddling have been recorded in several rodents, however (Withers & Jarvis, 1980; Baudinette, 1972; Glaser & Lustick, 1975; Pearson, 1960). In the natural environment, nevertheless, the extent to which air temperature in a crevice is increased and the consequent energy saving would be dependent on the crevice volume, the number of animals per unit volume, air flow through the crevice and the thermal conductivity of the rock.

In conclusion there appears to be a graded change in body temperature, lower critical temperature, thermal conductance and possibly metabolic rate in the several species of hyrax discussed above. These differences are associated with the environmental temperatures experienced and as such can be considered adaptations to the particular habitat of each species. At the one extreme, the alpine *P. johnstoni* has physiological features predominantly geared to allow this animal to tolerate cold conditions commensurate with its alpine habitat. These take the form of a comparatively high metabolic rate, low lower critical temperature, low thermal conductance or good insulation and a stable body temperature over a wide range of ambient temperatures. *P. capensis* must tolerate a wider range of ambient temperatures as well as an arid

environment. Thus, in a similar fashion to *P. johnstoni*, the lower critical temperature is relatively low, body temperature is stable over a wide range of ambient temperatures and thermal conductance is low. In the hot, dry summers, however, the low BMR would be advantageous when water must be conserved. Thus, relatively less water would be required to dissipate the metabolic heat produced.

The heat gained from the environment would be regulated by behavioural thermoregulation demanding less water to be used than by the more expensive physiological method of evaporative cooling. This latter statement applies to the rest of the species of hyrax, mentioned below. The differences between *P. habessinica* and *H. brucei* are not easily explained since they are sympatric over parts of their distribution and the animals used in the studies described above all came from Kenya. Neither of these two species appears to have any marked physiological adaptation to low ambient temperatures in keeping with the fairly moderate climate they experience. Both do show features which can be considered as adaptations to high ambient temperatures, however, assuming the lowest values recorded to be valid. Thus a low BMR is common to both, but while *P. habessinica* has a relatively high lower critical temperature with a normal thermal conductance, the lower critical temperature of *H. brucei* is lower but thermal conductance is higher. The thermolability and range of body temperatures are similar, however. Although the data for *P. syriacus* are not complete, this species appears to be at the opposite extreme to *P. johnstoni*, with adaptations for a hot, dry climate. These include the lowest range of body temperatures of all the species described, a low

BMR and high lower critical temperature and thermal conductance or poor insulation.

In all species of hyrax, however, the behavioural use of solar energy to maintain a eutherian level of body temperature, huddling in the cold and overall selection of a favourable thermal environment are indicative of a life geared towards the conservation of energy. This is manifested further in the short feeding periods which allow the hyraces to spend most of the day in a state of relative inactivity or rest.

SECTION 7

THE EFFECT OF NOR-ADRENALINE (NON-SHIVERING THERMOGENESIS) ON THE ROCK HYRAX *PROCAVIA CAPENSIS* AND THE ELEPHANT SHREW *ELEPHANTULUS EDWARDI*

7.1 INTRODUCTION

Seasonal changes in climate and temperature place stresses on free living animals; the more extreme the changes, the greater are the physiological adjustments required by an animal to tolerate and survive them. Adaptation to cold in endotherms involves both behavioural and physiological adjustments which decrease heat loss and/or increase heat production. Physiologically, decreased heat loss can be achieved through vasomotor changes, peripheral heterothermy and lowering of the body temperature, and morphologically by increased fat and fur insulation. Behavioural adjustments include postural changes, huddling or selection of a favourable microclimate. Exercise, shivering and non-shivering thermogenesis are mechanisms by which heat is produced. Most mammals use some or all of these mechanisms when cold stressed, but the size of the animal has an important influence on the extent to which any of these can be employed. The greater surface area to volume ratio in small mammals results in a relatively faster rate of heat loss compared to large mammals. Moreover, in small mammals there is a physical limitation to which fur insulation can be increased, without augmenting heat production, in order to maintain a constant body temperature. The same is not true of larger mammals where, due to the relatively small surface area to volume ratio, small increases in heat production or insulation are sufficient to maintain homeothermy in the cold. Thus smaller mammals have to increase heat production to a greater extent than large mammals.

It has been found that cold-adapted small mammals (< 2 kg) increase

heat production mainly by non-shivering thermogenesis (NST) at ambient temperatures below thermoneutrality (Heldmaier, 1971). Shivering contributes a smaller amount to the total heat production but at much lower temperatures the heat produced by both mechanisms summate (Jansky, 1973). NST is defined as "a heat producing mechanism liberating chemical energy dueto processes which do not involve muscular contraction" (Jansky, 1973). Although several chemicals are known to have thermogenic properties, e.g. thyroxine, ACTH, corticosterone, glucagon and insulin, heat production by NST has been attributed primarily to the action of catecholamines and in particular noradrenaline (NA) from the sympathetic nervous system (Jansky, 1973). Some of the recorded effects of NA-mediated NST are an increase in oxygen consumption, deep body and interscapular temperatures, heart rate and respiratory frequency. The magnitude of these effects in cold-adapted animals, however, decreases with increasing body size and are negligible in mammals over 10 kg (Heldmaier, 1971).

Since cold adaptation facilitates the onset of NST, it can be assumed that the cold air temperatures during winter months act as an environmental stimulus for the development of NST in small mammals. Recently, physiological effects similar to those induced by NA administration to cold-adapted animals, have been observed in rodents and birds adapted to a long scotophase without a previous period of cold-adaptation (West, 1972; Haim *et al.*, 1979a & b; Haim & Fourie, 1980). These dark-adapted rodents also responded to NA administration showing an increased oxygen consumption, rectal and interscapular temperatures (Haim & Fourie, 1980), implying that cold-adaptation and dark-adaptation

have similar effects on the thermoregulatory system. Melatonin has also been shown to have a thermogenic effect on rodents (Lynch & Epstein, 1976; Haim & Borut, 1978; Haim & Fourie, 1981) and in view of the known influence of photoperiod on the production of melatonin by the pineal (Fiske *et al.*, 1960; Wurtman *et al.*, 1968), the thermogenic effects of a long scotophase and melatonin may be connected.

The hyrax *P. capensis* and the elephant shrew *E. edwardi* are similar in several respects. Within the Cape Province, both inhabit mountainous regions and utilize rock crevices for shelter and protection. Both also bask in the sun for some part of the day and show peaks of activity in the evening and early morning, though the latter has not been firmly established for the elephant shrew (see section 1) They differ, however, in their social organisation and food habits, the hyrax being gregarious and herbivorous while the elephant shrew is solitary and primarily insectivorous though they have been known to eat fruit and seeds (J. Breytenbach, personal communication). Within the southernmost ranges of both of their distributions, seasonal changes are marked by hot dry summers and cold wet winters. In certain areas, winter temperatures drop to freezing at night, often with the occurrence of snow. In the Cape Province, the cold season lasts for five to six months and it would seem reasonable to assume that during this time both the hyraces and elephant shrews would adapt to the cold. One possible way would be to develop NST. As in all mammals, both these mammals increase their oxygen consumption and therefore heat production, at temperatures below thermoneutrality (sections 6 and 8). The mechanism of increased heat production is not known, however, and may be due to

NST. The hyrax is of particular interest in this respect as, in many ways, its physiology is similar to that of a larger mammal, e.g. low metabolic rate, heart rate, relative food consumption (shown in previous sections of this thesis). Also, the fossil evidence suggests that the small size of the hyrax is a relatively recent evolutionary development (Kitching, 1966). It is therefore possible that the hyrax may not react to NA administration. However, no information on the metabolism and temperature regulation of *E. edwardi* has been published and only that presented in section 8 is known. Thus apart from contributing further to the knowledge of the physiology of this insectivorous mammal, it was of interest to examine whether elephant shrews showed the same response to NA as other cold-adapted small mammals. Furthermore, although the habitats and climate experienced by *P. capensis* and *E. edwardi* are so similar, their sizes are very different and a comparison of their responses to NA should be of interest.

The purpose of the present investigation therefore, was to establish whether the capacity for NST was present in *P. capensis*, a medium-sized mammal, and *E. edwardi*, a small mammal. The effect of NA administration on the oxygen consumption, rectal and interscapular temperatures and heart rate were recorded in cold-adapted *P. capensis* and compared to the effect of NA on the rectal and interscapular temperatures in the cold-adapted elephant shrew.

7.2 METHODS

7.2.1 The hyrax

Eleven hyraces (6 females, 5 males, mean mass 2,54 ± S.D. 0,57 kg) which had been in captivity for at least six months were used in the experiments. Nine were acclimated to 6°C for at least four weeks after being exposed to a gradual decline in temperature for two weeks. A constant photoperiod of 12 hours light : 12 hours dark was maintained throughout the acclimation period. The animals were kept in large cages, with two or three animals per cage, in a temperature controlled room. As only two large cages were available, the experiments were not concurrent, and four animals were used in the first experiment, five in the second. During acclimation commercial rabbit pellets, lucerne hay and occasionally fresh green leaves were provided as food on an *ad lib.* basis. Water was always available. Two animals were not acclimated and were kept in an outdoor run with food and water always available.

7.2.1.1 *Non-shivering thermogenesis*

Each animal was anaesthetised with 40 mg/kg sodium pentobarbitone (Nembutal, Abbott Laboratories) at the start of the experiment. Rectal (TREC., 11 cm deep) and interscapular (TISC) temperatures were then recorded using calibrated, copper-constantan thermocouples. Oxygen consumption ($\dot{V}O_2$) was measured using a flow-through system. Air was drawn through a tightly fitting mask around the animal's head, a tube

containing silica gel, a calibrated flowmeter (Rotameter) and again through water and carbon dioxide absorbants (silica gel and carbosorb, respectively) before passing through the oxygen analyser (either Beckman, OM14 or Applied Electrochemistry, S-3A). The oxygen analysers were calibrated at the beginning and end of each experiment. The thermocouples and oxygen analyser were connected to a data-logger (Esterline Angus PD2064) which recorded respective measurements every two minutes. Heart rate (HR) was monitored in some animals, at two minute intervals, using an ECG transducer and Gilson polygraph. ECG leads were connected to gold safety pins attached to three points on the animal's thorax. The occurrence of any movement or shivering was noted from the ECG recording as electronic noise.

Initial baseline levels of VO_2, TREC., TISC and HR were recorded for approximately 10 min and thereafter the hyrax was injected with pyrogen-free saline solution (amount as for the noradrenaline injection) and the same parameters recorded for 10 to 15 min. Finally noradrenaline hydrochloride (NA), dissolved in pyrogen-free saline, was injected intramuscularly (dose equivalent to 200 µg NA/kg). The dose used was calculated from the following equation:

$$\log \text{NA dose} = 0{,}82 - 0{,}458 \log W \quad \text{(Heldmaier, 1971)}$$

where NA dose is in mg/kg and W = body mass in grams.

The above measurements were recorded again until the animal recovered from anaesthesia.

7.2.1.1.1 *Experiment 1*

For four cold-adapted hyraces (3 females, 1 male, mean mass 2,85 ± 0,33 kg), VO_2, TISC, TREC and HR were recorded at an ambient temperature of 6°C, and the effects of NA on these parameters recorded. During the course of the experiment, one animal died an hour after the administration of NA, apparently from respiratory arrest. The results from this animal were therefore excluded.

7.2.1.1.2 *Experiment 2*

Five cold-adapted hyraces (3 females, 2 males) with a mean mass of 2,10 ± 0,50 kg were used. The effect of NA on VO_2, TREC and TISC was recorded as described above at an ambient temperature of 22°C, which is within the thermoneutral zone.

7.2.1.1.3 *Experiment 3*

The effect of NA on TISC, TREC and HR on the two non-acclimated hyraces (males, mean mass 3,05 kg) was recorded at thermoneutrality (22°C).

7.2.2 The elephant shrew

Six adult elephant shrews (3 females, 3 males, mean mass 51,7 ± 3,3 g) were trapped at the beginning of October near Ceres, in the Cape Province. They were brought to the University of Cape Town and housed in individual cages in the laboratory for two months prior to the experiment. During this time, all were fed daily with Pronutro (see section 7) mixed with water, as well as meal worms once a week. For six

weeks thereafter the elephant shrews were acclimated to 6°C in a temperature controlled room with a 12 hour light : 12 hour dark photoperiod. Additional food was provided at this low temperature.

7.2.2.1 *Non-shivering thermogenesis*

Each animal was anaesthetised with 1,2 mg pentobarbitone sodium (Nembutal, Abbott Laboratories) at the start of the experiment. Rectal (TREC, 2,5 cm deep) and interscapular (TISC) temperatures were recorded using calibrated copper-constantan thermocouples, attached to a data logger (Esterline Angus PD2064). After approximately ten minutes the elephant shrews were injected with pyrogen-free saline solution (amount as for NA injection) and TREC and TISC recorded for a further 15 minutes. Noradrenaline hydrochloride dissolved in pyrogen-free saline was then administered subcutaneously (dose 1,3 µg/g body mass calculated according to Heldmaier, 1971) and the above parameters recorded until the animals awoke from anaesthesia. The experiments were run at an ambient temperature of 12°C and three animals were run concurrently. As some of the animals awoke before the full effect of the NA was seen, it was thought that the increase in temperatures may not have been due to the NA but to recovery from the anaesthetic. Therefore, the effect of the anaesthetic alone on the two temperatures was recorded in one animal.

7.3 RESULTS

7.3.1 Cold-adapted hyraces

7.3.1.1 *Experiment 1 : Ta = 6°C*

During the acclimation period this group of animals lost on average 15 per cent of the initial body mass, despite food and water being provided *ad lib.* They also moulted and exhibited piloerection whenever observed.

7.3.1.1.1 *Rectal and interscupular temperatures*

In the three animals, TREC declined when the anaesthetised animals were exposed to 6°C and continued to decrease after the saline injection. Administration of NA apparently induced or coincided with the onset of shivering in two animals and consequently, TREC and TISC stabilised or decreased at a slower rate than previously. No increase in either of these temperatures was apparent (Fig. 7.1). In all three animals TISC followed changes in TREC almost identically though TISC was always lower than TREC. Shivering began in the two animals when TREC was 33,5°C. The animal that died during the experiment did not shiver and showed respiratory distress after the NA injection with a fall in TREC below 30°C.

7.3.1.1.2 *Oxygen consumption*

In three animals, administration of saline caused a slight rise in VO_2 of roughly four minutes duration, but had no effect in one. With the onset of shivering after the NA injection in two animals, VO_2 increased

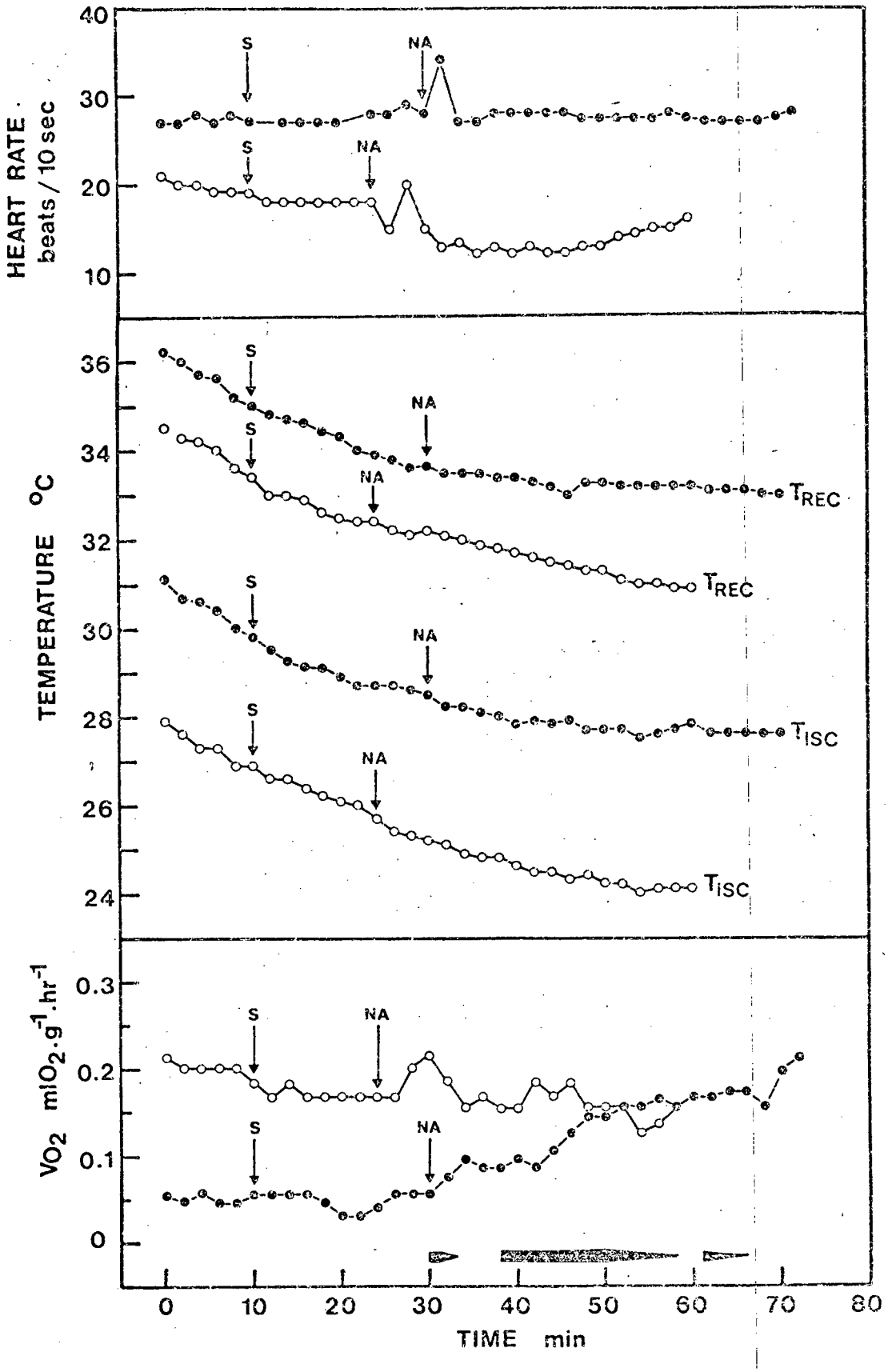


Fig. 7.1 Effects of saline (S) and noradrenaline (NA) on the heart rate, rectal (TREC) and interscapular (TISC) temperatures and oxygen consumption (VO_2) of two cold-adapted *P. capensis* measured at 6°C.

(●) Hyrax shivered for periods marked ▬

(○) Hyrax did not shiver

continually until the animals recovered from the anaesthetic (Fig. 7.1). The one animal that survived without shivering showed an increase in VO_2 of 0,033 $ml O_2.g^{-1}.h^{-1}$ after NA administration which is 19,6 per cent above the increased level recorded after the saline injection (Fig. 7.1). The rise in VO_2 lasted for a total of seven minutes and thereafter fell below the previously recorded level with occasional smaller increases until the animal awoke.

7.3.1.1.3 *Heart rate*

NA administration caused an increase in heart rate of 20 to 25 per cent above the resting level in all three animals. The onset of this rise, after the NA injection, varied from one to twelve minutes and the duration of the increased heart rate was only four minutes. In the animals that shivered, HR either returned to basal level or stabilised at a rate higher than recorded before the NA injection. A lower heart rate was recorded, after the NA peak, in the animal that did not shiver (Fig. 7.1).

7.3.1.2 *Experiment 2: Ta = 22°c*

This group of five cold-adapted hyraces maintained a steady body mass throughout the acclimation period, unlike those in experiment 1. Although they did appear to shed some fur over the acclimation period, there was no obvious change in their coats as there was in experiment 1.

7.3.1.2.1 *Rectal and interscapular temperatures*

Both these temperatures decreased when the animals were under anaesthetic

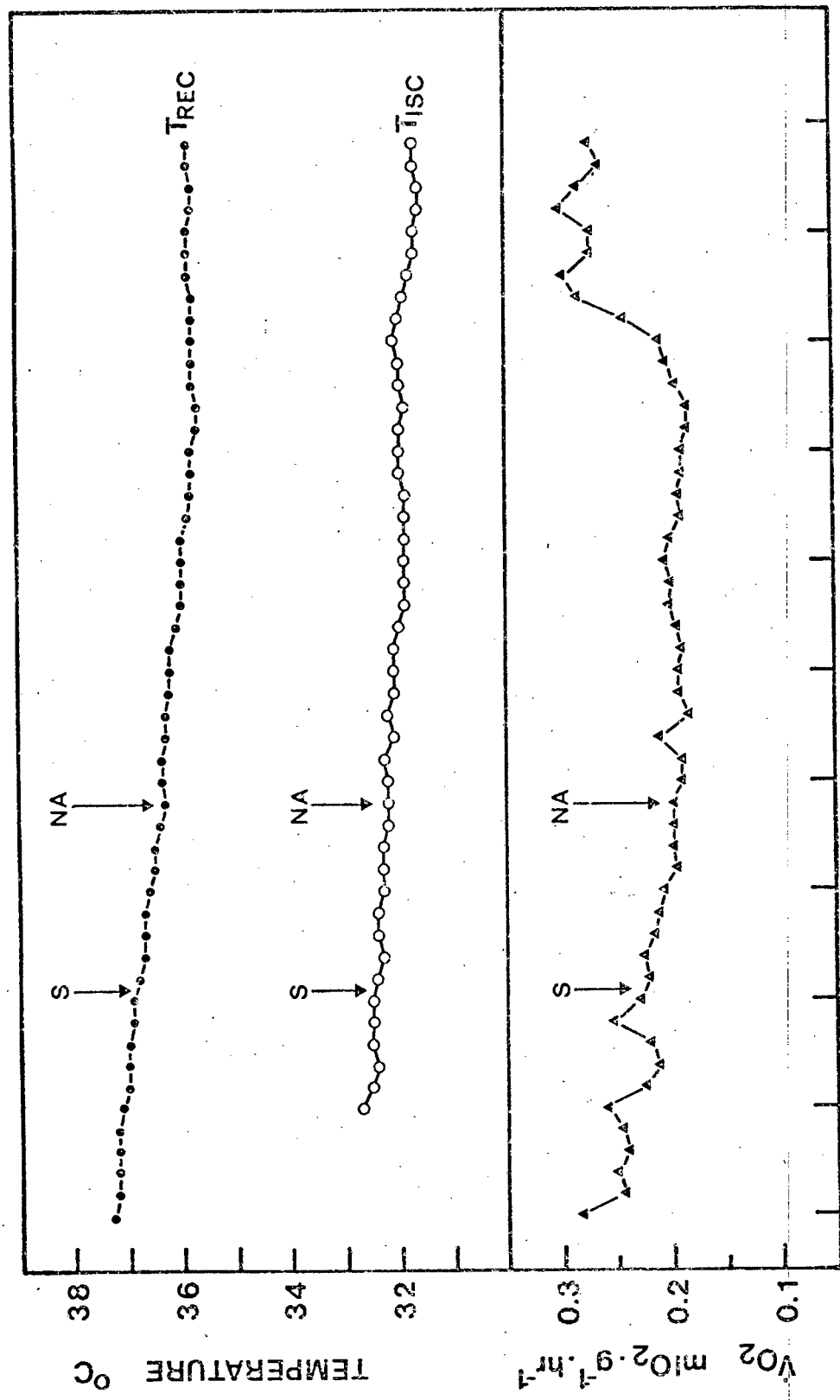


Fig. 7.2 Effects of saline (S) and noradrenaline (NA) on oxygen consumption ($\dot{V}O_2$), rectal (T_{REC}) and interscapular (T_{ISC}) temperatures in a cold-adapted hyrax, measured at 22°C

but never fell to the low levels recorded in experiment 1. This was undoubtedly a function of the different ambient temperatures. The administration of saline had no marked effect on either temperatures, and any small rise was within the variation recorded before the administration of the saline (Fig. 7.2). NA affected TREC in two of the five animals causing it to increase maximally by 0,05°C above the rise caused by the saline injection. The significance of this was doubtful since the normal variation recorded in TREC was of the same order. TISC increased in two animals after NA administration with a maximum rise of 0,1°C above the saline effect. Again the significance of this is doubtful.

7.3.1.2.2 *Oxygen consumption*

The saline injection had a small but unimportant augmentative effect on the VO_2 of three of the five hyraces. This occurred from two to five minutes after the injection and lasted for roughly four minutes. In three animals NA administration also increased the VO_2 but only one of these rises appeared to be noteworthy in view of the normal variation (Fig. 7.2). This increase was approximately 5 per cent of the base-line level taking the saline rise into account. In each animal, just prior to waking, VO_2 increased erratically, but this was probably due to the increased oxygen required for the limb movement as the animals came out of anaesthesia and the greater heat production necessary to re-establish the normal body temperature (Fig. 7.2).

7.3.2 Non-acclimated hyraces

7.3.2.1 *Experiment 3: Ta = 22°C*

These two animals maintained a steady body mass while in captivity. The response in TREC, TISC and HR to NA administration was similar to that following the saline injection (Fig. 7.3) in both animals. Nevertheless, some differences were apparent. In one animal, both the saline and NA injection caused an increase in TREC and TISC of 0,2°C and 0,4°C, respectively, with a decrease in HR after NA administration (Fig. 7.3). The other animal responded to both saline and NA injections with a small increase in HR and no obvious change in TREC or TISC. None of these changes were of any importance.

7.3.3 Elephant shrews

The elephant shrews remained healthy during the period of acclimation at Ta = 6°C and their body masses remained fairly stable. The mean change in mass was a gain of 2,3 per cent with ranges for individuals of -12,3 to +11,8 per cent. No changes in the fur were apparent. When anaesthetised, and at an ambient temperature of 12°C, TREC was higher than TISC in all six animals and both temperatures declined steadily with time (Fig. 7.4). The saline injection had no effect on these temperatures unlike the NA injection. With the latter, a dramatic rise was recorded and a typical example of this response is shown in Fig. 7.4. In all cases, TISC responded to the NA before TREC and superseded the rectal temperature initially. The time taken for the onset of the NA effect, the maximum increase in temperatures and

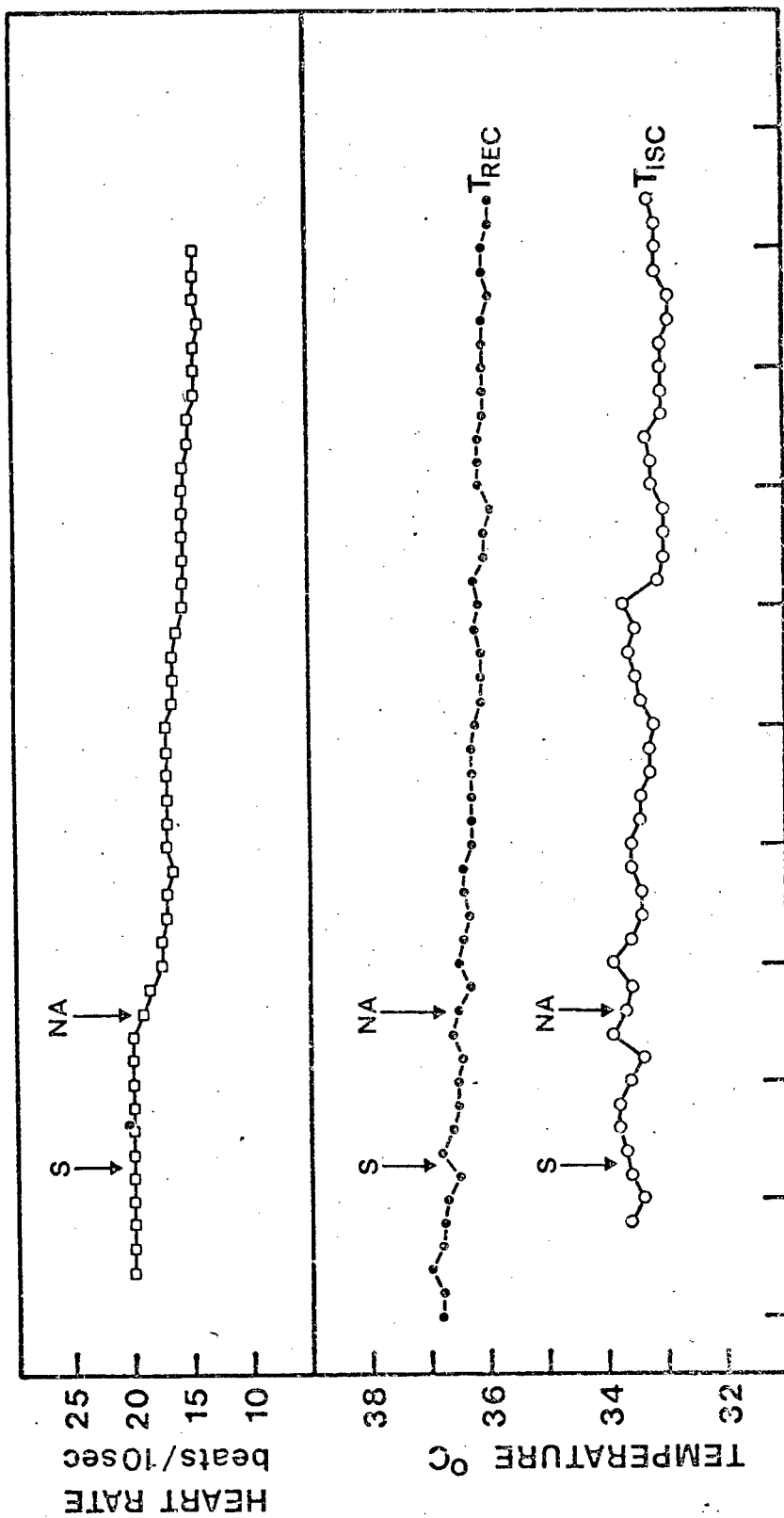


Fig. 7.3 Effects of saline (S) and noradrenaline (NA) on heart rate, rectal (TREC) and interscapular (TISC) temperatures in a non-acclimated hyrax measured at 22°C

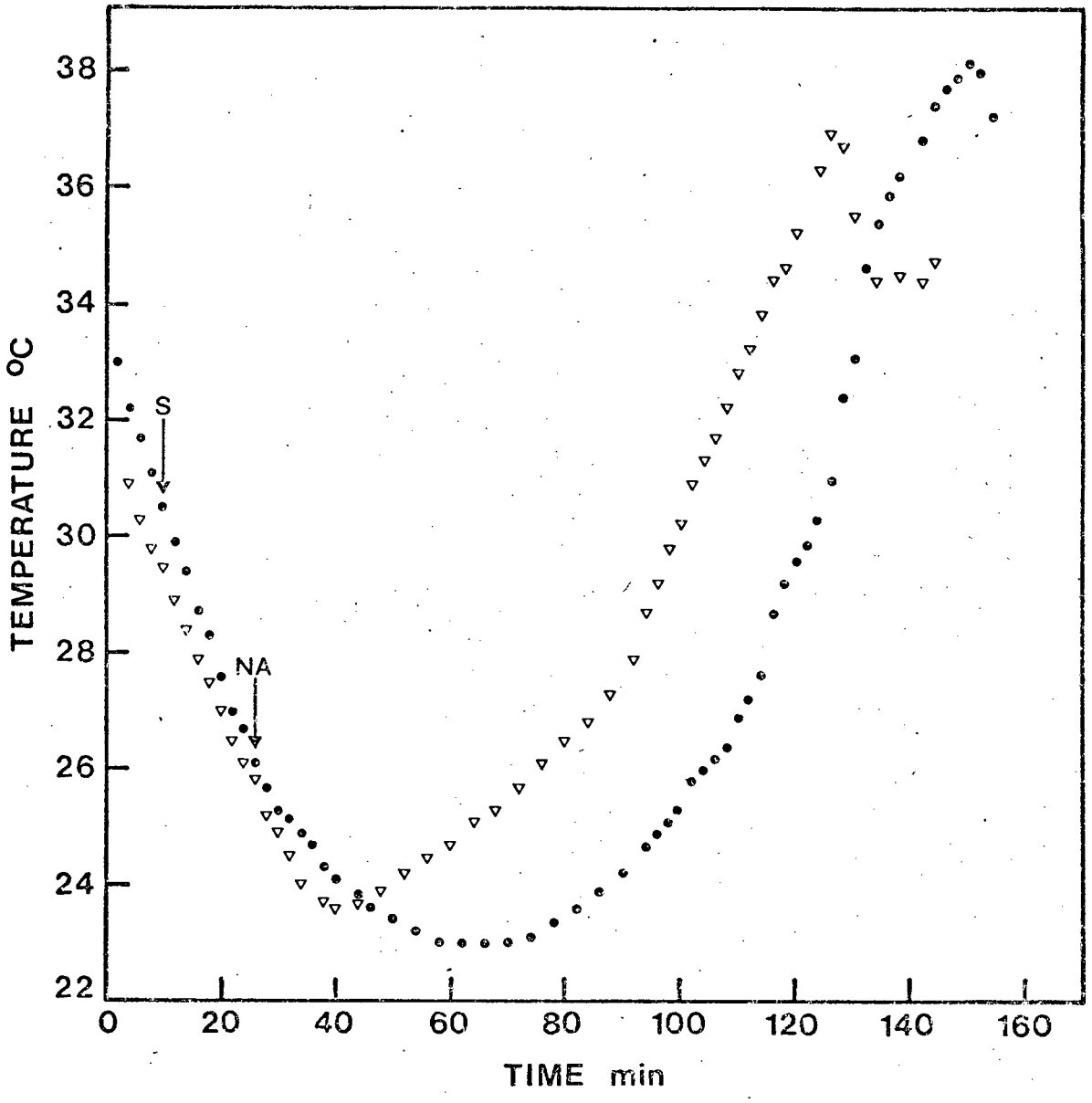


Fig. 7.4 The effect of saline (S) and noradrenaline (NA) on rectal (•) and interscapular (▽) temperatures on the cold-adapted elephant shrew *E. edwardi* measured at 12°C

the time from the onset of the temperature increase to the peak, were variable and the respective ranges are shown in Table 7.1. The maximum temperature increase was 15,8°C in TREC. The rectal temperature of the anaesthetised animal that was not given NA, continued to drop and after 100 minutes reached a low level of 19°C. The experiment was then terminated since it was clear from these results that the increased temperatures in the other animals were caused by the NA injection.

7.4 DISCUSSION AND CONCLUSIONS

Prolonged exposure to low temperatures was apparently stressful for the one group of hyraces and resulted in a significant loss in mass. It is difficult to understand why the second group (experiment 2) did not show the same response under the conditions of cold-adaptation. The only difference between the two groups was the season in which the experiments were conducted. The first experiment was done at the end of June while the second was performed at the beginning of December. Possibly the first group was not in as good a nutritional condition as the second, having been exposed to cold, wet conditions prior to the experiment, while the second group had been exposed to the warmer and drier climate of spring and summer. That winter conditions are stressful to hyraces has been noted by Mendelssohn (1965) and Millar (1972) since in captivity under natural climatic conditions, most deaths occur during this season. Considering that the two environmental factors

TABLE 7.1 The effect of noradrenaline (NA) administration on rectal (TREC) and interscapular (TISC) temperatures in six elephant shrews, *E. edwardi*. (Mean mass 52,5 ± 2,3 g)

	n	TREC range	TISC range
Time for onset of NST after NA injection (min)	6	9-31	3-19
Maximum increase in temperature (°C)	4	11,9-15,8	13,3-15,0
Duration of NST effect from onset to peak (min)	4	52-86	58-86

which are known to induce the development of NST are cold temperatures and a long scotophase (Haim & Fourie, 1980), it would be expected that the first group of animals, exposed to winter conditions prior to the experiment, would have developed NST with possible changes in the pelage and consequent increased resistance to cold. It may be argued that in the field, cold-acclimation in winter is a slow process since air temperatures are not consistently low. If, however,a long scotophase induced NST in the hyraces, it would be expected that the first group of animals would have developed a greater resistance to cold than the second group. This was not apparent in the present experiments, since the first group lost weight during cold-acclimation and the pelages of all the animals appeared to be in a similar condition prior to the experiments. Conditions of acclimation in the laboratory were more severe than would be encountered in the field, as the animals in the laboratory had no respite from the consistently low temperature. The initial responses to cold in both experimental groups were pilo-erection, visible shivering, later accompanied by loss of fur or moulting. The latter may eventually have increased the insulation of the animals by the growth of new fur of different texture and length. It is unlikely that a marked decrease in body mass would also occur in the wild, considering that the animals would have an opportunity to sunbask, even in winter, thus giving intermittent relief from the cold.

Physiologically, cold-adaptation resulted in an increased sensitivity to NA in the hyraces exposed to a Ta of 6°C since an increase in heart rate was observed, contrary to the pattern shown in the non-acclimated animals. This β-adrenergic response did not appear to have a thermo-

genic effect however. Unfortunately heart rate could not be recorded in the cold-adapted animals measured at Ta of 22°C and therefore, it is not known whether the increase in heart rate, in the group measured at Ta of 6°C, was due to the NA injection alone or to both a low temperature and NA. By comparing the VO_2, TREC and TISC in the cold-adapted hyraces which shivered at Ta of 6°C, with the same parameters in the hyrax that did not shiver, it is clear that shivering and not NA, caused the rise in VO_2 and stabilized TREC and TISC in the former group. The increase in VO_2 in the single, non-shivering animal probably occurred as a result of the increased contraction of the heart muscle after the NA injection. Nevertheless this had no pronounced thermogenic effect on the overall body temperature. A similar increase in heart rate with a slight but insignificant rise in VO_2 and TREC has also been found in neonatal calves (Jenkinson *et al.*, 1968) and these authors have concluded that NA-induced NST does not occur.

In contrast, there can be no doubt as to the thermogenic effect of NA in the cold-adapted elephant shrew and the implication of NA-mediated NST in the tolerance to cold stress is therefore evident. As the elephant shrews were not tested in the thermoneutral zone the maximal thermogenic effect of NA cannot be established with any certainty from this experiment. Jansky (1973) has shown that the thermogenic significance of NA can be demonstrated by comparison of the increase in metabolism of cold-adapted mammals, after NA administration in the thermoneutral zone and at lower ambient temperatures. Significance is shown by a higher response at the thermoneutral temperature than at the lower temperature. A difference in response arises because there is a maximum ceiling for

heat production in a mammal and therefore a similar maximum for the effect of NA-induced NST. Thus the augmentation of metabolism due to endogenous and exogenous NA are additive only until this maximum level of metabolism is reached. Since the increased metabolism at low ambient temperatures is near the maximum level and is probably due to endogenous NA secretion, the effect of exogenous NA administration will be small. At thermoneutrality, however, administration of an optimal dose of exogenous NA should cause metabolism to rise to the maximum level and a large increase will be observed, unmasked by the effect of endogenous NA secretion. This has been graphically illustrated by Jansky (1973) and is repeated here in Fig. 7.5. Therefore, if a difference in response to NA at the two temperatures is shown, the mechanism of thermogenesis in the cold and that due to exogenous NA application can be considered to be interchangeable and NA-induced thermogenesis has significance. If the responses are similar, the same conclusion would not be true and may indicate the presence of an alternative thermogenic mechanism (Jansky, 1973). However, with anaesthesia, the mechanisms of heat production are partially inhibited. This was shown in the anaesthetised hyraces where the lowest metabolic rates recorded were ($0,17\ ml O_2.g^{-1}.h^{-1} \pm 0,07$) lower than the basal metabolic rate in unanaesthesised hyraces ($0,27\ ml O_2.g^{-1}.h^{-1}$, section 6). Thus in the experiments with the cold adapted hyraces, the lack of a well-defined thermogenic response at exposure to both 22°C and 6°C, despite the anaesthesia and according to Jansky's (1973) rationale, indicates that NA-induced NST was of no significance.

In the case of the elephant shrews, the anaesthetic would have the same effect as in the hyraces and therefore one can assume that the metabolic

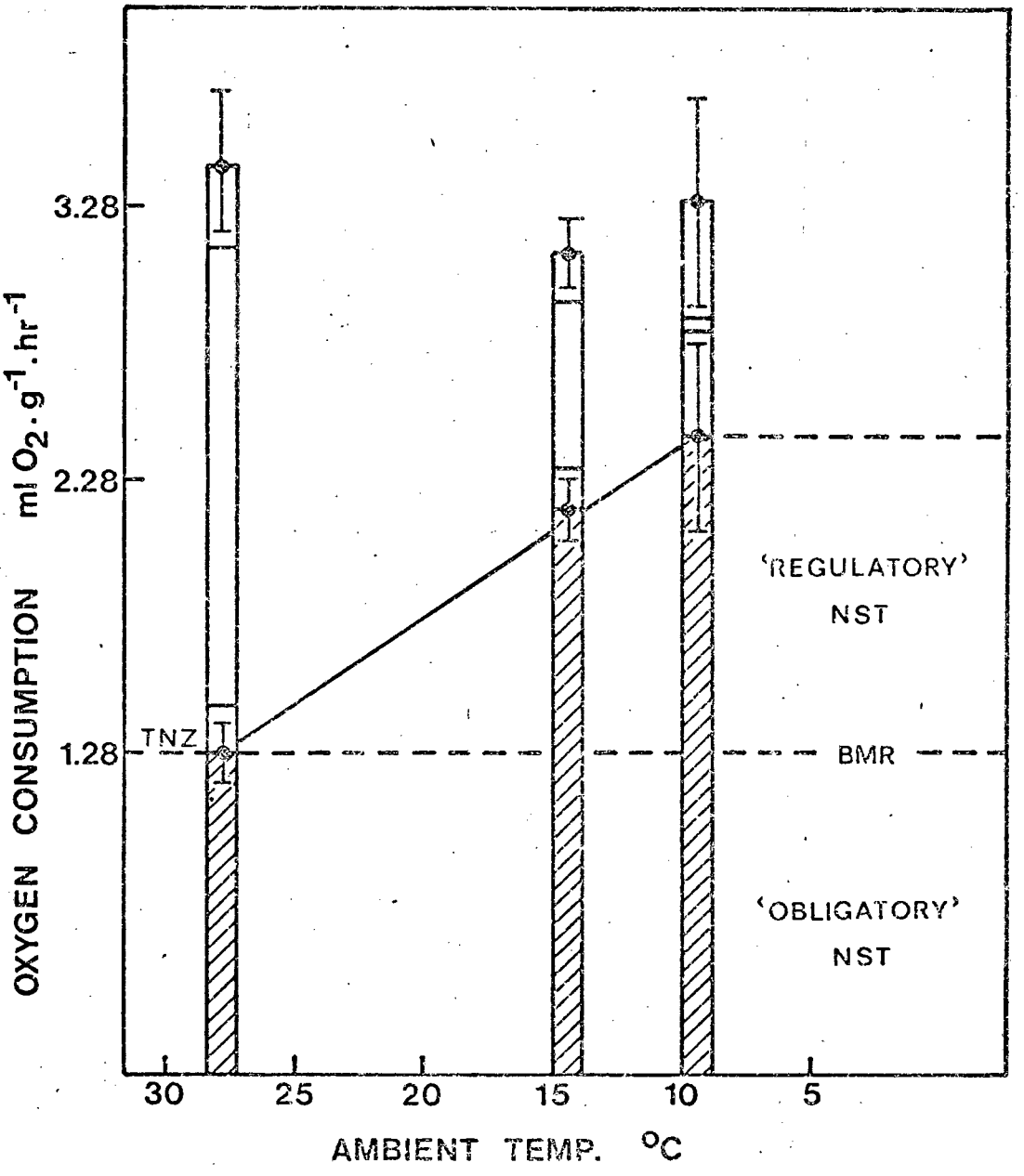


Fig. 7.5 The substitution of the calorigenic effect due to exogenous and endogenous noradrenaline, shown by the metabolic response of cold-adapted rats to noradrenaline administration at different ambient temperatures. White columns indicate metabolic increase after the infusion of noradrenaline; cross-hatched columns indicate resting metabolism in the cold due to endogenous noradrenaline. (From Jansky, 1973)

rate, prior to the NA injection was near the basal level and similar to that at thermoneutrality. Thus, with the partial suppression of the normal mechanisms of heat production at low ambient temperatures, the increase in metabolism which caused TREC to rise *ca.* 15°C, can be considered to be near the maximal rate attainable, and generated by the NA. A rough estimate of the heat required to increase the body temperature of a 52 g elephant shrew by 15,8°C in 74 minutes (actual figures for one animal in the present experiment) can be calculated assuming the specific heat of protoplasm to be 3,43 $J.g^{-1}.°C^{-1}$ (from Schmidt-Nielsen, 1975). This amounts to a heat production of 2,818 kJ in 74 minutes or an increment in metabolic rate of 2,19 $ml O_2.g^{-1}.h^{-1}$, assuming near perfect insulation. When the latter figure is added to an assumed basal metabolic rate of 1,09 $ml O_2.g^{-1}.h^{-1}$ (section 8), the metabolic rate of the elephant shrew at 12°C at the peak of the NA effect would be roughly 3,28 $ml O_2.g^{-1}.h^{-1}$. Applying the same calculation to the results from the other elephant shrews, the range of metabolic rates would be 2,99 to 3,44 $ml O_2.g^{-1}.h^{-1}$. The actual metabolic rate at 12°C found in section 8 was 3,17 $ml O_2.g^{-1}.h^{-1}$. The similarity of the calculated and actual figures indicates that in the elephant shrew the increase in metabolism and maintenance of homeothermy at low ambient temperatures is probably due, almost entirely to NA-mediated NST, rather than a decrease in conductance.

In the elephant shrew, the time lag between the responses of TISC and TREC to NA can be explained in terms of the location of the interscapular area and the rectum in relation to the major tissues involved in heat production during NST. Situated in the interscapular area is a large

proportion of the brown adipose tissue of the body. This tissue has a large thermogenic potential and is probably a major source of heat for animals acutely exposed to cold (Smith, 1961; Smith & Horwitz, 1969). Thus, in the present experiment the temperature probe in the interscapular position would have recorded the heat generated by the brown fat in response to NA. Since the rectal probe was distal to any site of thermogenesis, a temperature rise in this area would occur only after the distribution of heat from the thermogenic tissues; hence the time lag in the temperature increases between the two areas.

The extent of the contribution of heat by brown adipose tissue to the total heat generated during NST has not been firmly established. Values of 6 to 15 per cent have been given by Jansky (1973), while Foster (1976) estimated the contribution to be approximately 60 per cent. Nevertheless, with cold acclimation brown fat in the rat undergoes changes such as hyperplasia, hypertrophy, an increase in metabolic activity and vascularisation (Horwitz & Smith, 1971). These changes together with its rich supply of sympathetic nerves and high concentrations of catecholamines, suggest an important involvement of this tissue in NST (Flattery & Sellers, 1971). Although brown adipose tissue may not contribute extensively to the total heat produced in NST it influences the thermosensitive area in the cervical spinal cord, a part of the nervous system network which induces either shivering or non-shivering thermogenesis (Bruck & Wunnenberg, 1966). Other areas which form part of this network are sensors in the skin, anterior hypothalamus and a controller in the posterior hypothalamus (Bruck *et al.*, 1971). Since the interscapular brown fat adjoins the cervical

spinal cord and vascular connections exist between the two areas, the heat produced by this tissue, in response to acute cold, is distributed to the adjoining thermosensitive area. The stimulus for shivering is suppressed, in part at least, by warming this area, therefore allowing for non-shivering heat production. Only at very low temperatures when the heat from the brown fat is insufficient to warm the cervical spinal cord, does shivering begin (Jansky, 1973).

Although NA does not induce the same thermogenic response in large mammals as in small mammals, clearly seen in the present study, the increased metabolism at low ambient temperatures in the former cannot be assumed to be due to shivering alone. The ability of sheep to increase their basal metabolic rate after cold acclimation, without shivering (Webster *et al.*, 1969 from Chaffee & Roberts, 1971) and without showing a thermogenic response to NA (Webster *et al.*, 1969) indicates that other mechanisms are involved in cold-adaptation. The same may be true of the hyrax and other mammals such as miniature pigs (Bruck *et al.*, 1969) that do not show NA-mediated NST. With the data available at present, however, it may be concluded that although some β-adrenergic response was evident, NA-mediated NST was insignificant in the adult, cold-adapted hyrax, *P. capensis*. Shivering appeared to be a more important form of heat production at low ambient temperatures. The possibility, however, that NST occurs in neo-natal hyraces or in hyraces with reduced insulation, as has been found in rabbits shaved of their fur (Heroux, 1967), cannot be excluded. In its response to cold, *P. capensis* behaves as a large mammal, relying on increased fur

insulation, piloerection, shivering and behavioural mechanisms such as huddling and the selection of a favourable microclimate for the maintenance of homeothermy. Thus in the evolution of the hyrax from a large size some 30 million years ago (Bond, 1964; Brain & Meester, 1964; Cooke, 1964) to the smaller present day form, it is apparent that amongst other physiological factors, the response to cold, characteristic of a larger size, has been retained. The elephant shrew *E. edwardi* on the other hand responds to cold adaptation in a way that is typical of small mammals. With the restrictions imposed on insulation by its small size and its solitary existence, the elephant shrew has recourse to few other means by which heat losses or energy expenditure can be minimised. One such avenue is the exploitation of the microhabitat afforded by the rock crevices and another, common to many small mammals, is hibernation. While the former is definitely used, the latter has not yet been recorded in the elephant shrew. Thus it has to rely almost totally on increasing its metabolism by NA-mediated NST and probably shivering at lower ambient temperatures for the maintenance of homeothermy.

SECTION 8

TEMPERATURE REGULATION AND WATER METABOLISM IN THE ELEPHANT SHREW *ELEPHANTULUS EDWARDI*

8.1 INTRODUCTION

Despite the common occurrence of the genus *Elephantulus* in southern Africa and the general interest in an animal of unusual lineage and affinities, the physiology of any species within the genus, with respect to energy, water metabolism and temperature regulation, are unknown. Systematically, the traditional placement of the family of elephant shrews, Macroscelididae, within the Insectivora and its controversial association with the Tupaiidae gives rise to speculation about the above physiological parameters. Does the elephant shrew have the high metabolic rate and high body temperatures characteristic of shrews of the family Soricidae (Morrison & Pearson, 1946; Pearson, 1947, 1948; Morrison, 1948; Gebczynski, 1965; Platt, 1974)? Does it have a low body temperature and low metabolic rate as do hedgehogs of the family Erinaceidae (Shkolnik & Schmidt-Nielsen, 1976; Hildwein & Malan, 1970; McNab, 1978) or is the body temperature low and labile with metabolic rates near or slightly lower than predicted for eutherian mammals, as is shown by the Tupaiidae or tree shrews (Nelson & Asling, 1962; Yousef *et al.*, 1971; Bradley & Hudson, 1974; Whittow & Gould, 1976)? Furthermore, in view of the semi-arid to arid distribution of the species *Elephantulus edwardi*, what physiological adaptations exist to enable it to tolerate these conditions? The general pattern of adaptation to arid environments as seen, for example, in hedgehogs and heteromyid rodents is a low metabolic rate and high renal efficiency (Shkolnik & Schmidt-Nielsen, 1976; McNab, 1979a). Does the elephant shrew follow this trend?

In the present study, I have examined the temperature regulation, energy and water metabolism of *Elephantulus edwardi*, the Cape elephant shrew, in an attempt to answer some of the questions posed above and to give further information which may help to clarify the systematic position of the Macroscelididae.

8.2 METHODS AND MATERIALS

Seven adult *Elephantulus edwardi** (four females, three males, mean mass 49,8 ± 3,1 g) trapped in the Clanwilliam district (32°11'S, 18°52'E) and the Rooiberg Mountains (33°28'S, 21°15'E) of the Cape Province, South Africa, were used in this study. Animals were housed individually in glass tanks in a temperature-controlled room at 27°C with a 12-hour light period. They were fed *ad lib.* on a commercially manufactured cereal mixture (Pronutro), mixed with water (59% carbohydrate, 22% protein, 6% fat on a dry basis - manufacturer's analysis). Vitamins and minerals were added to provide a balanced diet for human nutrition and this ration was fed every evening while mealworms were provided once a week. Drinking water was always available. At least three weeks were allowed for the animals to become accustomed to captivity before any experiments were initiated. The four animals from Clanwilliam had been in captivity for three months.

* Animals were identified according to the criteria given by Corbet & Hanks (1968).

8.2.1 Body temperature

Deep body temperature (T_B) was measured at ambient temperatures (T_A) ranging from 10°C to 40°C using a copper-constantan thermocouple inserted 2,5 cm into the rectum. At each new T_A the animals were allowed four hours (except at T_A of 40°C, when three hours were allowed) to become thermally equilibrated before T_B was recorded.

8.2.2 Oxygen consumption

Non-fasting, resting metabolic rate was measured at ambient temperatures ranging from 10 - 39°C using a flow-through system. During oxygen consumption measurements the animal was housed in a water-tight perspex chamber. This was fitted with a grid, on which the animal rested, above a container of liquid paraffin to cover any faeces or urine voided during the experiment. Chamber temperature (T_A) was recorded by means of a thermocouple sealed into the chamber. The housing was submerged into a temperature-controlled water bath and dry air at the same temperature as the bath passed through the chamber at a flow rate of 300 $ml.min^{-1}$. Air leaving the chamber passed through a tube of fine silica gel and soda asbestos to remove moisture and carbon dioxide before entering the oxygen analyser (Beckman, model OM14). The analyser was calibrated at the beginning and end of each experiment. Both the chamber thermocouple and oxygen analyser were connected to a data logger (Esterline Angus PD 2064) which automatically recorded the chamber temperature and oxygen concentration

of the outflowing air every two minutes. At each new T_A, an hour was allowed for equilibration of the system before any measurements were taken and thereafter oxygen consumption was recorded for at least one hour. The mean oxygen consumption at each T_A was calculated and corrected to standard temperature and pressure. Readings taken while the animal was active were discarded. On completion of measurements at a particular T_A the animal was removed from the chamber and rectal temperature (2,5 cm deep) was recorded immediately.

8.2.3 Evaporative water loss

Evaporative water loss (EWL) was measured while measuring oxygen consumption. A preweighed capsule containing fine silica gel was incorporated into the air flow system immediately after the metabolic chamber. It was removed after half an hour and reweighed. The increase in mass was assumed to represent EWL. Two measurements were taken at each temperature. Recovery was tested and found to be 90%.

8.2.4 Thermal conductance

Thermal conductance at each T_A was calculated using the formula

$$C = \frac{HP - EHL}{T \times S}$$ (Dawson and Schmidt-Nielsen, 1966)

Where C = conductance, J/cm².hr. °C

HP = metabolic heat production, J/hr (assuming 1 ml O_2 = 20,1J)

EHL = evaporative heat loss, J/hr (assuming 1 mg H_2O = 2,34 J)

T = temperature difference between ambient and body, °C

S = surface area, cm², where S = 10 x Mass $(g)^{0,67}$.

8.2.5 Water turnover rate

Water turnover rate (WTR) was measured using the isotopic dilution technique (Richmond *et al.*, 1962; Holleman & Dieterich, 1973; Yousef *et al.*, 1974). Six animals of mean mass 48,9 ± 5,7 g were kept individually in stainless steel cages at 25°C with 12 hours light. They were fed on Pronutro which initially contained 80% water but after 24 hours under experimental conditions this evaporated to 45%. No free water was provided. Body mass was recorded daily.

Each animal was injected intraperitoneally with 25 µCi tritiated water (TOH) made up in saline. 25 µCi TOH were also added to a flask containing 50 ml water. The flask was sealed until the end of the experiment when the radioactivity of the solution was measured, and the value obtained used as a standard to calculate the total body water of the animals. WTR was calculated from changes in TOH concentration in consecutive urine samples. When urine was voided, it was collected immediately from the surface of a sheet of parafilm beneath each cage, the time of urination noted and the urine stored frozen in sealed capillary tubes for analysis at the end of the experiment. One

sample of urine was collected each day for at least four days. At the end of the experiment 20 µl urine were added to 5 ml Packard insta Gel scintillation cocktail and the radioactivity measured using a Packard liquid scintillation counter (Model 3385). A Wang 700 bench top computer, programmed to correct for quenching, was used to convert CPM to DPM. The DPM values for the urine of all animals were plotted as a function of time on a single graph using semilogarithmic paper. A least squares regression analysis was used to determine the equation which best described the data. Total body water (TBW) was calculated using the prepared standard as follows:

$$TBW = \frac{V_b \times DPM_b}{DPM_{ao}}$$

where V_b = volume of standard
DPM_b = radioactivity of standard
DPM_{ao} = intercept value of the regression equation.

Absolute water turnover rate and biological half-time were calculated using the method of Yousef *et al.* (1974).

After this initial experiment two animals were placed on the same cereal diet, but with less water (70% initially which was reduced to 43% after 24 hours at 25°C), for an additional five days. Urine was collected as above and body mass recorded daily. WTR was calculated assuming TBW to be the same as in the first experiment.

8.2.6 Renal function

Each animal was housed in a metabolism cage placed over a sheet of parafilm and constant conditions of 25°C and 12 hours lighting maintained. In order to assess the maximum concentrating capacity of the kidneys, the animals were initially fed *ad lib.* cereal containing 80% water which was reduced to 45% water content after 24 hours in the temperature chamber. After four days on this regime the water content of the food was gradually reduced over a further seven days, the diet on the last day consisting of air-dried cereal only. Body mass was recorded daily. After feeding, the first urine voided by each animal was immediately collected from the parafilm and the osmolality determined. The rest was stored frozen in sealed vials for later analysis.

8.2.7 Urine analyses

Osmolality was determined using a vapour pressure micro-osmometer (Wescor, model 5100B) and urea concentration using the spectrophotometric method of Chaney and Marbach (1962). Chloride concentration was determined by a modification of Asper and Shales titration with mercuric nitrate for micro-amounts (Smith, 1956) and sodium and potassium concentration using a flame photometer (Instrumentation Laboratory, model 243).

8.2.8 Relative medullary thickness of the kidneys

At the end of the above experiments all animals were killed with pento-

barbitone sodium (Nembutal, Abbot Laboratories). The kidneys were removed, weighed and the length, width and depth measured. The thickness of the medullary region was measured on the medially bisected kidneys. Relative medullary thickness was calculated according to Sperber (1944).

8.3. RESULTS

8.3.1 Body temperature

The elephant shrews were able to maintain a stable body temperature at T_A between 10 - 35°C (Fig. 8.1). Below 35°C a mean T_B of 37,6 ± 0,38°C was recorded. At T_A above 36°C the animals became hyperthermic, T_B rising with T_A, but T_B remaining above T_A even at 40°C. At the highest experimental temperature (40°C), the shrews lay prostrate with bellies against the ground and exhibited open-mouthed panting. No fur-licking behaviour took place, but the animals occasionally licked their noses which twitched excessively. Blood vessels in the ears appeared more prominant. No fluid loss through the nose or mouth was observed. The lowest experimental temperature (10°C) did not induce hypothermia.

8.3.2 Oxygen consumption

During measurements of oxygen consumption (VO_2) the elephant shrews were inactive for long periods, thus facilitating measurement of resting

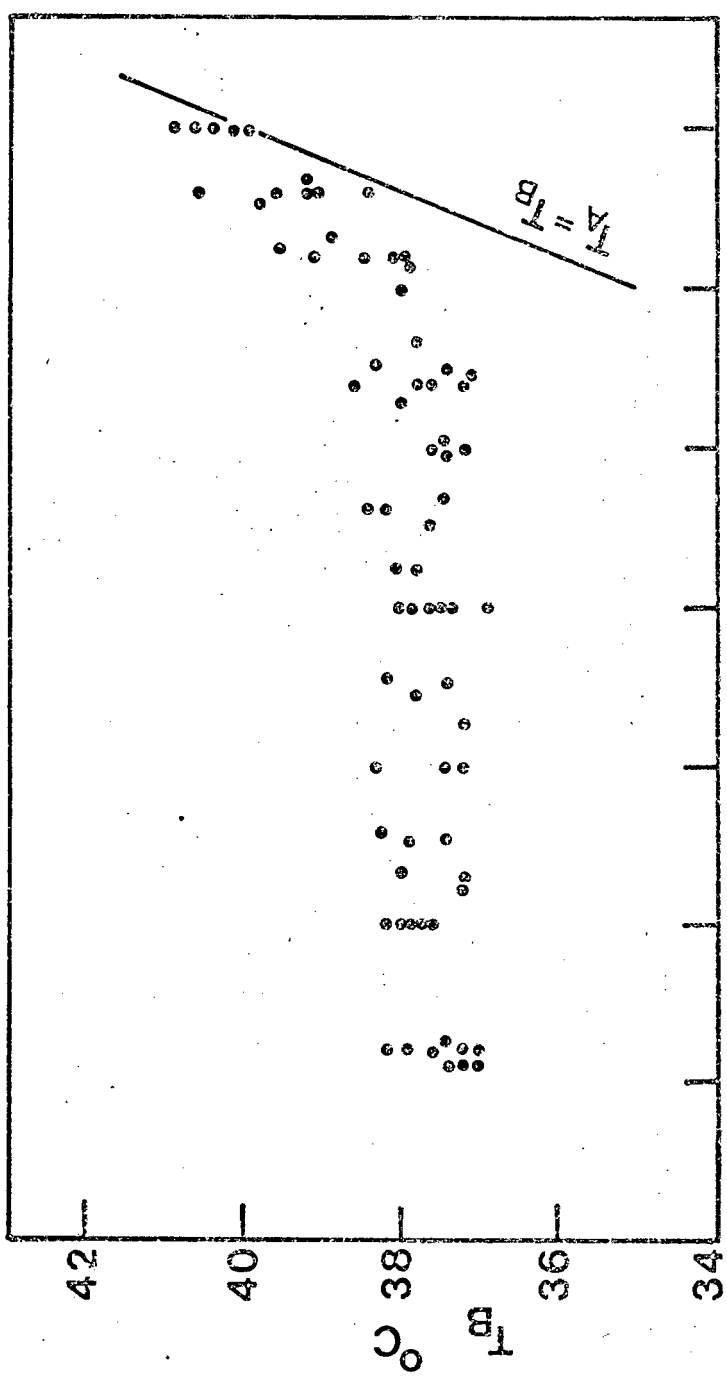


Fig. 8.1 Body temperature (T_B) of *E. edwardi* at various ambient temperatures (T_A)

metabolic rates. At the thermoneutral zone between about 32,5°C and 36,0°C (Fig. 8.2) the lowest mean metabolic rate of 1,09 ± 0,13 ml O_2 $g^{-1}.hr^{-1}$ was recorded. This is 76% of the predicted eutherian rate according to Kleiber's (1961) equation. As T_A decreased below the lower critical temperature, metabolic rate increased. The regression equation which described this relationship was VO_2 ($ml.g^{-1}.hr^{-1}$) = 4,330 - 0,097 T_A (°C) (r^2 = 0,825). Extrapolation of this line intercepts the x-axis at a T_A of 44,6°C which is much higher than the normal T_B of *E. edwardi*. The intercept value of 4,330 $ml.g^{-1}.hr^{-1}$ at T_A = 0°C is approximately four times as high as the minimum metabolic rate. Metabolic rate also increased above 36°C.

8.3.3 Evaporative water loss

At T_A between 10 and 30°C, the rate of evaporative water loss (EWL) remained fairly stable at a mean value of 2,02 ± 0,35 mg $H_2O.g^{-1}.hr^{-1}$ (Fig. 8.3). Within the thermoneutral zone, EWL began to increase and reached a maximum of 5,89 mg $H_2O.g^{-1}.hr^{-1}$ at 38,3°C the highest experimental temperature. EWL per unit of oxygen consumed (VO_2) and the proportion of metabolic heat lost through evaporation as functions of T_A are shown in Fig. 8.4. Values of 2,34 J/mg H_2O and 20,1 J/ml O_2 were used to convert EWL and oxygen consumption to thermal units. At T_A of 30°C, EWL per VO_2 was high (1,99 ± 0,48 mg H_2O/ml O_2) and the heat lost through evaporation at this temperature represented approximately 20% of the metabolic heat produced. The maximum amount of heat lost through evaporative cooling was 54% of the heat produced at 38,3°C.

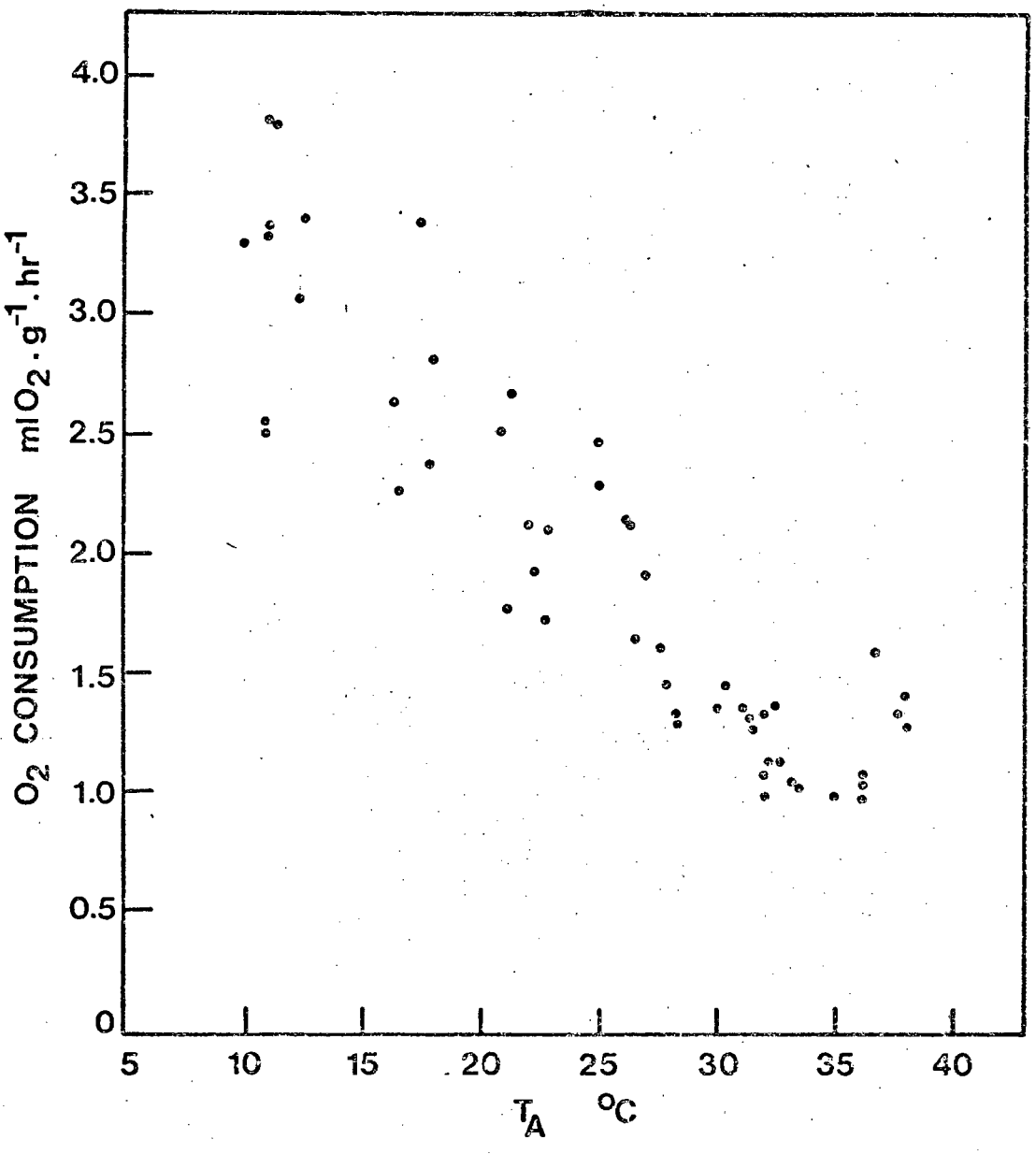


Fig. 8.2 Rate of resting oxygen consumption of *E. edwardi* at various ambient temperatures (T_A)

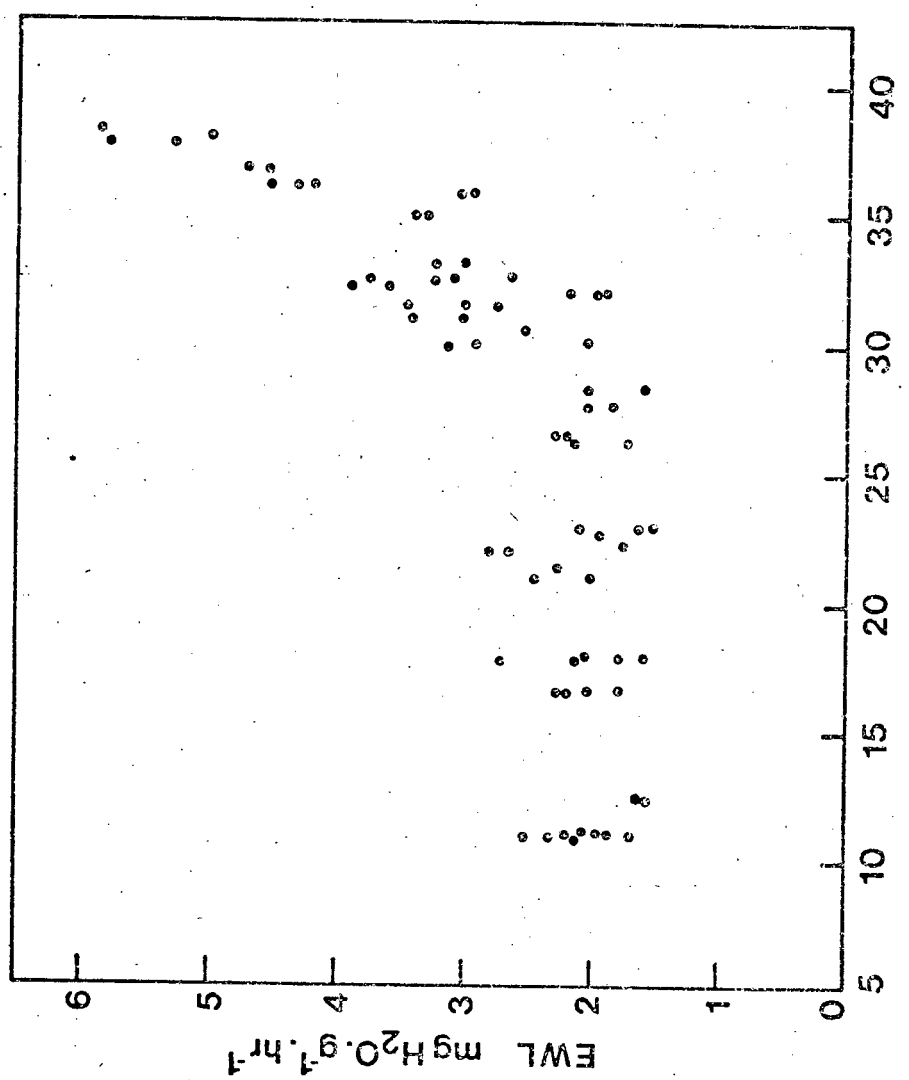


Fig. 8.3 Evaporative water loss (EWL) of *E. edwardi* at various ambient temperatures (T_A)

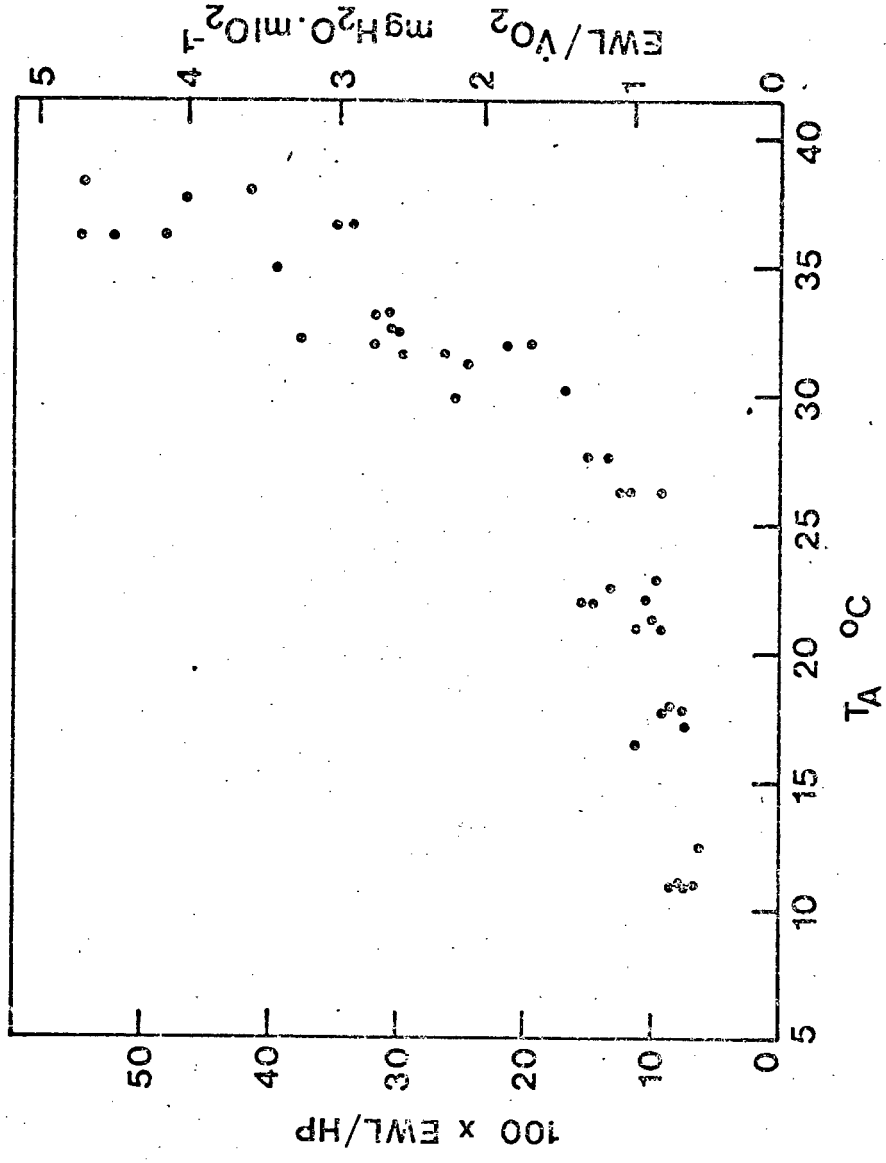


Fig. 8.4 Ratios of evaporative water loss (EWL) to simultaneous oxygen consumption ($\dot{V}O_2$) (right-hand ordinate) and evaporative heat loss as a percentage of metabolic heat production (HP) (left-hand ordinate) in *E. edwardi* at various ambient temperatures (T_A). Values of 2,34 J/mg H_2O and 20,1 J/mlO_2 were used to convert EWL and $\dot{V}O_2$ to thermal units.

8.3.4 Sensible thermal conductance

With a rise in T_A of 10°C to 35°C surface-specific, sensible thermal conductance increased from approximately 0,84 to 1,13 J/cm².hr.°C (Fig. 8.5). At higher T_A, a more marked increase was shown, conductance reaching a maximum of 4,64 J/cm².hr.°C at 38,3°C. Thus effective vasomotor control is indicated by the increased conductance (reduction in total insultation) above the thermoneutral zone and the small decrease below the lower critical temperature.

For comparative purposes, the minimal thermal conductance was calculated using the slope of the line relating metabolism to air temperature at T_A below thermoneutrality (0,097 ml O_2 /g.hr.°C). Since the line did not extrapolate to a temperature, on the abscissa, equal to the body temperature, and therefore the value of the slope is an underestimate of minimal thermal conductance (McNab, 1980), the correction equation below was applied:

$$C_m/C_f = 0{,}060\ (\delta T) + 1{,}0 \qquad \text{(McNab, 1980)}$$

where C_m = corrected minimal conductance

C_f = fitted slope using the least squares method

δT = overestimate of T_b

Thus the corrected minimal conductance was 0,138 ml O_2/g.hr.°C which is as predicted (97,2%) by the equation relating minimal conductance to body mass:

$$C_m \text{ (ml } O_2\text{/g.hr.°C)} = 1{,}0 \times \text{mass (g)}^{-0{,}50} \qquad \text{(McNab \& Morrison, 1963).}$$

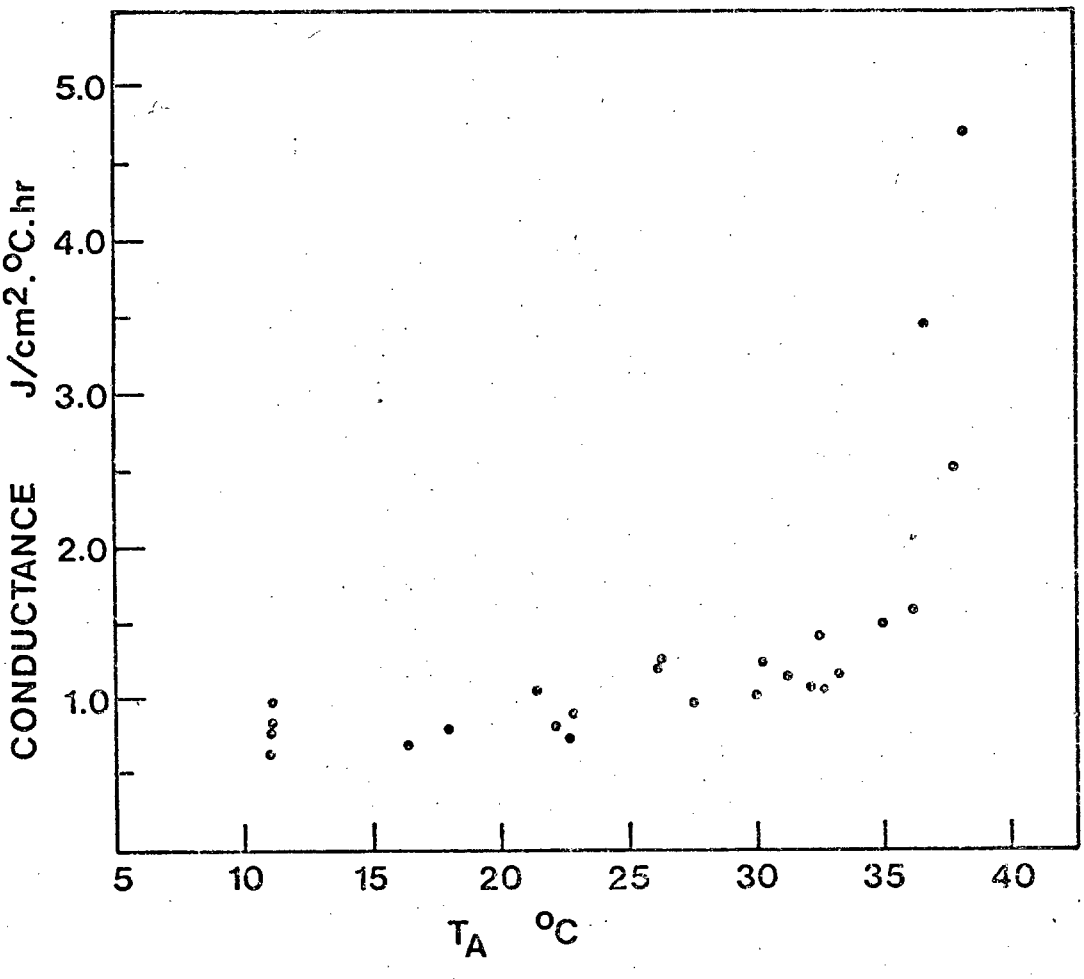


Fig. 8.5 Sensible thermal conductance of *E. edwardi* at various ambient temperatures (T_A)

8.3.5 Water turnover rate

On the diet initially containing 80 per cent water, the regression equation which described the TOH activity in the urine of *E. edwardi* as a function of time was TOH (DPM) = 41454 $t^{-0,0204e}$ (hr) (r^2 = 0,9265). The total body water (TBW), biological half time ($t_{\frac{1}{2}}$) and daily water turnover rates of the animals, calculated from the equation, are shown in Table 8.1, as well as the same parameters for the two animals on the diet with the lower water content.

In the first experiment, the animals showed a slightly positive water balance, gaining approximately 3 per cent of the initial body mass after four days. In the second experiment, on a lower water intake both animals lost weight (approximately 3 per cent and 8 per cent) (Table 8.1). A 3 per cent gain or loss in mass may be considered negligible as WTR is affected by only about 0,3 ml/day. The WTR of the two animals on the lower water intake, when corrected for loss in mass were 7,51 and 6,35 ml/day. The WTR of the animals on the higher water intake was double that on the lower and therefore the diet initially containing 80 per cent water must have provided water in excess of that required by the animals, resulting in water diuresis and consequent elevation of WTR. Thus the diet initially containing 70 per cent water would seem to be nearer the actual water requirement of *E. edwardi* with a WTR of approximately 7 ml/day. From the equation relating WTR to lean body mass (LBM) (Holleman & Dieterich, 1973) the predicted WTR of approximately 9 ml/day is slightly higher than the actual rate of *E. edwardi* at moderate ambient temperatures.

TABLE 8.1 Total body water (TBW) and water turnover rates (WTR) of *E. edwardi* on two diets of different water content

Water content of diet		n	Mean Mass		Gain or loss in mass	TBW	$^{x}k \times 100$	$^{+}t_{\frac{1}{2}}$	Water Turnover Rate		*Predicted WTR
Initial	After 24 hr at 25°C										
%	%		g	±SD	% of initial Body Mass	g/100g	hr	days	ml/day	$ml/kg^{0,82}$ day^{-1}	ml/day
80	45	6	46,4	7,1	+3,4	65,6	2,04	1,42	14,85	184,2	8,81
70	43	1	48,6	-	-3,3	65,6	0,94	3,07	7,19	85,8	9,14
70	43	1	49,3	-	-8,5	65,6	0,71	4,07	5,51	71,0	9,23

x k = Disappearance rate of tritiated water (Yousef *et al.*, 1974)

+ $t_{\frac{1}{2}}$ (Biological half-time) = $^{e}/k$ (Yousef *et al.*, 1974)

* WTR ml/day = 0,48 $(LBM)^{0,78}$ where lean body mass (LBM) g = TBW(g)/0,73 (Holleman & Dieterich, 1973).

8.3.6 Renal function

Although the initial cereal diet provided was different in composition from the natural insectivorous diet, the elephant shrews remained healthy with a mean change in mass of 1,9 per cent over the experimental period. Over the period of water restriction the mean loss in mass was 16,6 per cent, with only one death which occurred on the fifth day of this period, the animal having lost 22,5 per cent of its initial body mass.

On the initial diet a mean urine osmolality of 1265 ± 347 $mosm.kg^{-1}$ was recorded, but it cannot be assumed that this value reflects the normal hydrated condition since excessive water was contained in the food (see WTR). Osmolality, however, increased progressively over the period of water restriction reaching a mean maximum of 3118 ± 267 $mosm.kg^{-1}$ on the last day of the experiment when water was withheld (Fig. 8.6). The mean urine urea concentration which was initially 1024 ± 346 $mmol.l^{-1}$ rose concomitantly with increased osmolality and reached a mean maximum concentration of 2446 ± 211 $mmol.l^{-1}$ on the last day of water restriction (Fig. 8.6). Clearly urea exerts a major influence on the osmolality of the urine. The initial concentrations of urinary electrolytes, sodium (71 ± 31 $mmol.l^{-1}$), potassium (172 ± 32 $mmol.l^{-1}$ and chloride (103 ± 26 $mmol.l^{-1}$) increased when water was reduced, becoming approximately twice as high as the initial concentrations (Fig. 8.7). The mean maximum concentrations over the period of dehydration were sodium 150 ± 50 $mmol.l^{-1}$, potassium 337 ± 52 $mmol.l^{-1}$ and chloride 217 ± 24 $mmol.l^{-1}$ (Fig. 8.7). These electrolytes constituted

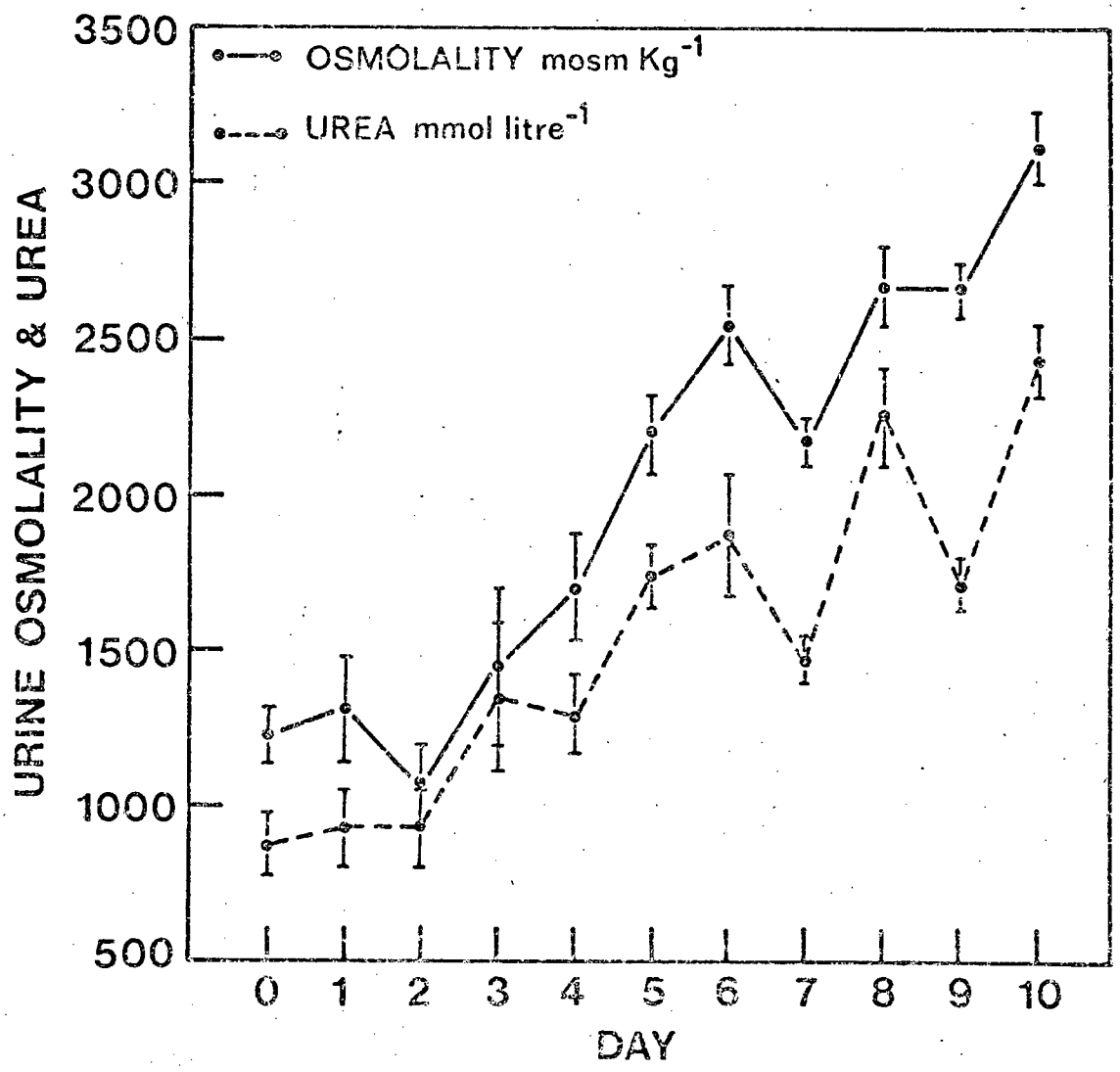


Fig. 8.6 The effect of dehydration on urine osmolality and urea concentration in *E. edwardi*. Water reduction began on day 4 and was withheld on day 10. Vertical lines represent ± 1S.E.

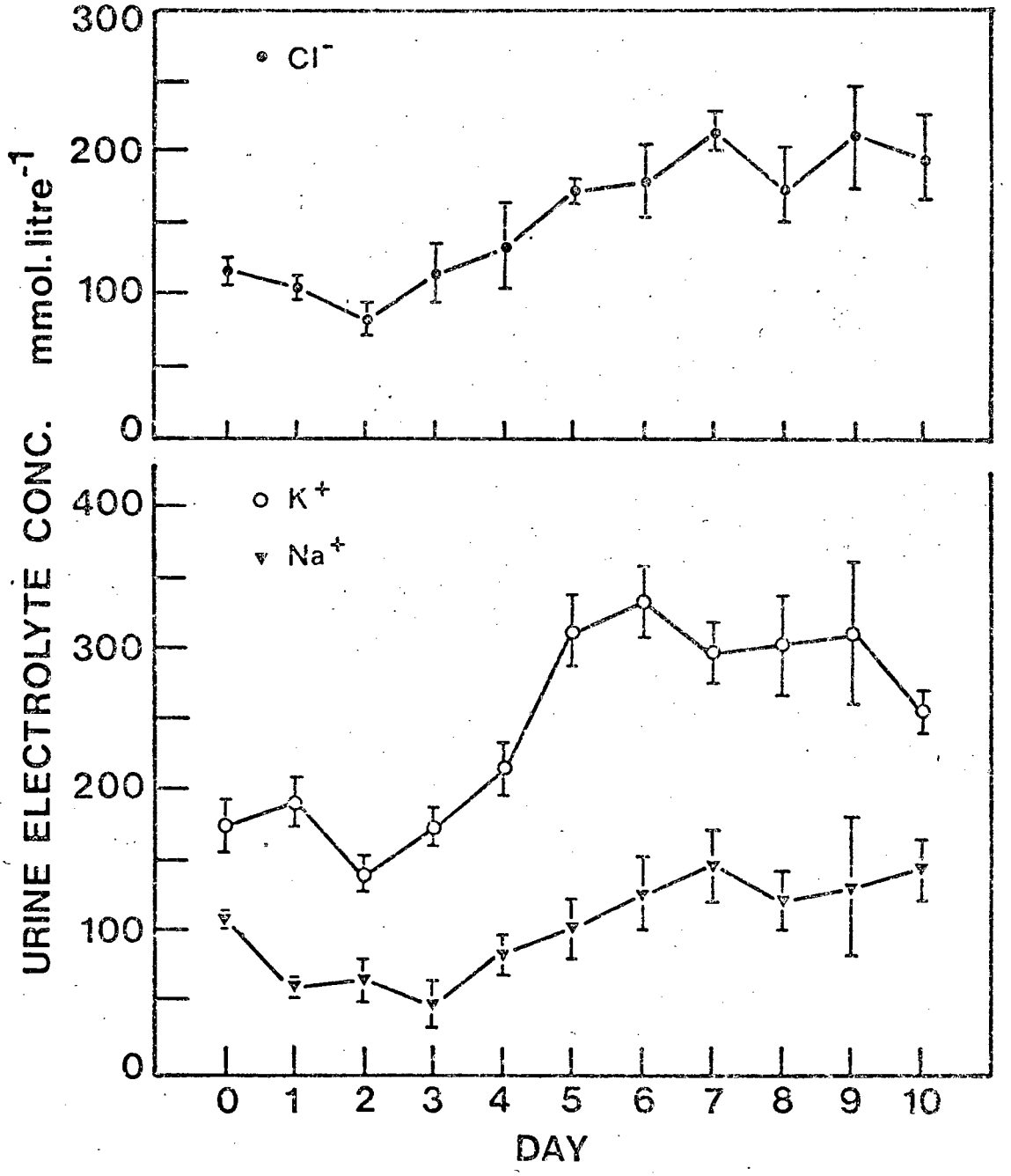


Fig. 8.7 The effect of dehydration on urinary electrolytes in *E. edwardi*. Water reduction began on day 4 and was withheld on day 10. Vertical lines represent ± 1S.E.

only 22,6 per cent of the maximum osmolality of the urine and the ratio of urea to total electrolyte concentrations remained the same throughout both experiments.

8.3.7 Relative medullary thickness of the kidney

In the freshly dissected kidney of *E. edwardi* a single renal papilla was present which extended into the ureter to the outer limits of the juxtaposed renal cortex. The mean kidney mass was 0,266 ± 0,033 g and relative medullary thickness inclusive of the papilla was 6,61 ± 0,84 (n = 14). From the relationship between relative medullary thickness and maximum urine concentration in other mammals reported by Yaakobi and Shkolnik (1974), the kidney of *E. edwardi* should be capable of producing a more concentrated urine than the maximum concentration actually found.

8.4 DISCUSSION

8.4.1 Body temperature and oxygen consumption

In the natural environment of *Elephantulus edwardi* the temperature conditions and water availability in summer are typical of semi-arid to arid areas. Climatological data from the Clanwilliam area show mean monthly maximum shade temperatures of 32,3 and 31,2°C for January and February, the hottest months, respectively and mean monthly rainfalls of

3,9 and 8,6 mm for these months. Whereas heat and aridity are the major climatological stresses during summer, in winter water may be abundant and daily temperatures more moderate. Nocturnal temperatures, however, fall from approximately 14°C in summer to around 5°C in winter with occasional freezing temperatures and snow. The thermal stability shown by *E. edwardi* in the laboratory implies a thermoregulatory capacity adequate for these conditions. However, 24 hourly measurements were not taken and it is not known if these animals show torpor. Nevertheless, the recorded stable body temperature of 37,6°C lies within the range of 36 - 38°C expected for typical eutherian mammals (Schmidt-Nielsen, 1975), morphologically "primitive" mammals usually having body temperatures that are labile or maintained at a lower level than that shown by *E. edwardi* (Dawson, 1973). Amongst the Insectivora there is a tendency towards low body temperatures as in the family Erinaceidae or hedgehogs with body temperatures of 34 to 35°C (Shkolnik & Schmidt-Nielsen, 1976) and the Tenrecidae or tenrecs with a body temperature of 33°C (Hildwein, 1970). The tree shrews (Tupaiidae), however, have low body temperatures during the day (*ca.* 35°C) but nocturnal temperatures, when active, around 37°C (Bradley & Hudson, 1974; Whittow & Gould, 1976). Shrews of the family Soricidae appear to be exceptions with high body temperatures, but measurement of resting or basal temperatures in these highly active animals is difficult and the validity of these data has been questioned (Dawson, 1973).

Although *E. edwardi* has a high body temperature compared to other insectivores, resting metabolic rate is below that predicted for placental mammals of their body mass. In Table 8.2 the body tempera-

TABLE 8.2 Body temperatures (T_B) and oxygen consumption (VO_2 - resting: R basal: B) in some species of the Insectivora

Species	Mass g	T at TNZ+ °C	VO_2 $ml O_2 . g^{-1} . h^{-1}$	VO_2 as % of Predicted BMR[x] %	Reference
FAMILY ERINACEIDAE					
Erinaceus europaeus	2000	-	0,26 B	51	McNab (1978)
Erinaceus europaeus	749	34 - 35	0,45 B	71	Shkolnik & Schmidt-Nielsen (1976)
Hemiechinus auritus	397	34 - 35	0,38 B	52	
Paraechinus aethiopicus	453	34 - 35	0,25 B	37	
FAMILY TENRECIDAE					
Tenrec ecaudatus (summer)	790	33,0	0,330B	46	Hildwein (1970)
Tenrec ecaudatus (winter)	650	32,0	0,201B	27	
FAMILY TUPAIIDAE					
Ptilocercus lowii (day)	58	35,7	0,75 B	53	Whittow & Gould (1976)
Ptilocercus lowii (night)	58	37,4	0,80 B	58	
Tupia chinesis (male)	172	-	1,04 R	100	Yousef *et al.* (1971)
Tupaia chinesis female)	150	-	0,85 R	78	
Tupaia glis (day)	198	37,0	0,76 B	75	Bradley & Hudson (1974)
Tupaia glis (night)	198	35,0	0,93 B	92	
Urogale everetti			0,87		Nelson & Asling (1962)

- continued

Table 8.2 (continued)

Species	Mass g	T_B at TNZ$^+$ °C	VO_2 $ml O_2.g^{-1}.h^{-1}$	VO_2 as % of Predicted BMR^x %	Reference
FAMILY SORICIDAE					
Sorex cinereus	3,3	38,8	2,8 - 3,6 B	100 - 128	Morrison *et al.* (1959)
Sorex cinereus	3,3	38,8	9,0 R	327	Morrison *et al.* (1959)
Blarina brevicaudata	21	38,5	1,9 - 3,2 B	107 - 180	Platt (1974)
Scalopus aquaticus	48	36,0	1,41 B	98	McNab (1979)
Sorex palustris	12,3	39,7	-	-	Calder (1969)
Sorex vagrans	4,5	-	8,6 R	330	Pearson (1948)
Sorex trowbridgii	6,7	-	7,2 R	305	Pearson (1948)
Sorex vagrans	9,2	-	6,1 R	280	Pearson (1948)
Sorex araneus	7,1	-	5,6 R	241	Hawkins *et al.* (1960)
Crocidura cassiteridum	7,6	-	5,5 R	240	Hawkins *et al.* (1960)
FAMILY CHRYSOCHLORIDAE					
Amblysomus hottentotus	70	33,5	1,21B	92	Kuyper (1979)
FAMILY TALPIDAE					
Scalopus aquaticus	48	36,0	1,41B	109	McNab (1979)
FAMILY MACROSCELIDIDAE					
Elephantulus edwardii	49,8	37,6	1,09R	76	Present study

tures and metabolic rates of various species within the Insectivora are shown. Within each family there appears to be a large variation in the metabolic rate ranging from below the predicted to the predicted value, with only the Soricidae having higher metabolic rates. The value for the elephant shrew falls within the ranges shown for the Tupaiidae, but in view of the wide variation in metabolic rates shown for the latter family and the lack of further data for the Macroscelididae any conclusion made concerning the relationship between the two families would be premature. Although *E. edwardi* appears to be closer to the Tupaiidae in its metabolic rate and temperature regulation, it differs from the tree shrews in maintaining a stable, high body temperature at T_A below thermoneutrality. Nocturnal body temperatures were not recorded in the elephant shrews, but since they appeared active during part of the night it seems unlikely that body temperature would drop, as it does in the Tupaiidae during the day when the animals are inactive.

In fact, the values for body temperature and metabolic rate recorded in the elephant shrew should not be used to show taxonomic affinities since they are similar to many "normal" eutherian placentals. It is acknowledged that the lower than predicted metabolic rate of *E. edwardi* could be considered "abnormal" since a similar situation has been associated with "primitive" mammals such as the monotremes, marsupials, tenrecs and hedgehogs (Dawson, 1973). This is not necessarily a primitive condition, however, as it is well documented that resting or basal metabolism is correlated with the overall environmental conditions an animal experiences (Shkolnik & Borut, 1969; Hart, 1971;

Hudson *et al.*, 1972; Shkolnik & Schmidt-Nielsen, 1976). In particular a low metabolic rate is found in many 'advanced' mammals inhabiting areas with hot, dry climates, examples being several desert rodents (Shkolnik & Borut, 1969; Hart, 1971). Thus the low metabolic rate of *E. edwardi* can be considered as a possible adaptation to the arid conditions of its environment. However, similar data on elephant shrews from more tropical areas are needed before it can be concluded with certainty that the low metabolic rate is an adaptation to the environment.

E. edwardi employs the same physiological mechanisms normally used by mammals for the maintenance of homeothermy both at low and high ambient temperatures. At low ambient temperatures heat production is augmented and peripheral heat loss reduced. At 10°C the metabolic rate increased three-fold above minimal level and as ambient temperature decreased below the lower critical temperature, thermal conductance decreased slightly. As thermal conductance is inversely related to the total insulation of an animal, vasomotor control and fur insulation must have contributed to the maintenance of a constant body temperature. Total insulation is an important factor for a small animal with a large surface area exposed to even moderate cold, as the tendency to lose heat is great and increasing metabolic heat production to compensate for heat loss is energetically costly.

McNab (1980) has indicated that if the extrapolation of the metabolism on air temperature curve meets the abscissa at a value greater than the body temperature, then the response to a fall in ambient temperature

involves both physical and chemical thermoregulation. That is, the response is a combination of increased metabolism (chemical thermoregulation) and decreased conductance (physical thermoregulation). This appears to be the case for *E. edwardi*, the implication being that physical thermoregulation alone is inadequate for the maintenance of homeothermy. The same situation, however, is true for many small mammals (McNab, 1980) and in view of the tendency to lose heat rapidly due to the relatively large surface area, small mammals may be expected to rely, for some extent at least, on chemical thermoregulation in the cold. The fact that the minimal thermal conductance of *E. edwardi* was as predicted for its size, indicates that it is as efficient as other placental mammals in its physical thermoregulation in the cold.

At high ambient temperatures, evaporative cooling appears to be an important avenue of heat loss in elephant shrews. Even at 30°C evaporative water loss per unit oxygen consumed was higher than found in most desert rodents (MacMillen, 1972) exceptions being *Acomys caharinus* and *Acomys russatus* (Shkolnik & Borut, 1969) which have similar levels of evaporation as *E. edwardi*. With increasing heat load at ambient temperatures above thermoneutrality, evaporative water loss increased, the heat lost through this means amounting to 54 per cent of the metabolic heat produced at 38°C. It is possible that this percentage would have increased at 40°C as open-mouthed panting and nose-licking behaviour was observed. In red kangaroos, *Megaleia rufa* licking of the well-vascularized forelimbs has been shown to aid in heat dissipation (Needham *et al.*, 1974) and the licking behaviour of *E. edwardi* may have the same function if a superficial vascular

network was shown to exist in the nose. Vasodilation in the extremities as observed in the ears and postural changes are reflected in the increased conductance at the high ambient temperatures. Above thermoneutrality, however, the high heat load was not totally dissipated and an increased body temperature was tolerated.

8.4.2 Basking behaviour

At present the rôle of basking behaviour in *E. edwardi* remains speculative. Nevertheless, heat uptake through basking, at low and moderate ambient temperatures, reduces the need for metabolic heat production thereby reducing energy expenditure.

8.4.3 Water economy

Although the insectivorous elephant shrew is ensured of a constant supply of water by virtue of the high water content of its diet, the protein-rich nature of this diet demands a relatively high urinary water loss. Additional demands on the water stores of the animal occur in the hot, dry summers when water is necessary for evaporative cooling. Examination of the water turnover data for *E. edwardi* show that on a diet with 70 per cent water initially, the water turnover rate was lower than predicted for an eutherian of its mass. The low water turnover rate can be correlated with the semi-arid to arid environment inhabited where conservation of water is necessary. Water stress, however, would be somewhat ameliorated by the high water

content of the insectivorous diet. Assuming that an insectivorous diet contains approximately 70 per cent water, the results indicate that *E. edwardi* may be able to exist without free drinking water in moderate temperature conditions. At high ambient temperatures, however, the increased water loss for evaporative cooling would require physiological and behavioural adjustments to prevent dehydration. Physiological compensation for water loss through evaporation may be accomplished by the production of a concentrated urine. This is shown in *E. edwardi* with maximum urine concentration in the laboratory of 3118 mosm kg^{-1}. Although fairly high, this value is lower than maximum concentrations found in insectivores adapted to semi-arid or arid conditions. The hedgehogs *Erinaceous europaeus* (mesic), *Paraechinus aethiopicus* (desert) and *Hemiechinus auritus* (semi-arid) had maximum urine concentrations of 3062, 3634 and 4010 mosm kg^{-1} respectively when dehydrated on a high protein diet (Yaakobi & Shkolnik, 1974). A higher maximum concentration of 4250 mosm kg^{-1} has been recorded for the nocturnal, insectivorous desert rodent *Onychomys torridus* when dietary water was reduced and salt solution provided as drinking water (MacMillan, 1972). These results are not directly comparable to those for *E. edwardi* as salt and protein loading are known to increase the maximum concentration of the urine in several mammals (Schmidt-Nielsen *et al.*, 1961). The high relative medullary thickness of the elephant shrew's kidney is indicative of a greater concentrating ability than was shown in the laboratory and is similar to that of the semi-arid adapted hedgehog *H. auritus* (Yaakobi & Shkolnik, 1974). Although the maximal electrolyte concentration of *E. edwardi* urine was roughly in accordance with that expected on the

basis of relative medullary thickness, urea concentration was markedly lower (Schmidt-Nielsen & O'Dell, 1961). In view of the high protein content of an insectivorous diet a higher urinary urea concentration and osmolality would be expected under more natural conditions.

That *E. edwardi* is entirely insectivorous has been questioned earlier in this thesis, since in the laboratory, they will eat dry seeds and grain. The question then arises whether an omnivorous diet is the norm for this animal either throughout the year, or whether there is a seasonal preference for one type of food over another. The availability of grain and insects would probably determine the diet in the field and in this respect, insects tend to be less numerous in the winter season. Thus, during winter, seeds may form a larger component of the diet than in summer. In terms of the water economy of the elephant shrew, a granivorous diet would not provide as much water as an insectivorous diet. If, however, the reliance on seeds for food occurred in winter, water would probably be available and therefore not constitute a problem for the animal. The same water turnover in winter as in summer would still be possible. These ideas are speculative, however, but do provide some indication where further work is required.

8.5 CONCLUSIONS

It is evident that *Elephantulus edwardi* has physiological mechanisms,

comparable to the most 'advanced' eutherian mammals, which enable it to maintain homeothermy and to cope with harsh conditions encountered in its environment. The extent to which these mechanisms must be employed depends largely on the behaviour of the animal. In this respect crepuscular feeding would be advantageous since selection of moderate temperature conditions for activities requiring greater energy expenditure reduces heat stress and excessive water loss. Diurnal basking may be an additional energy-saving mechanism associated with crepuscular or nocturnal activity. However, until further information is available concerning the behaviour of *E. edwardi* in the field, the interplay and relative contribution of physiological and behavioural mechanisms towards its adaptation to the environment cannot be elucidated further.

SECTION 9

FINAL SUMMARY AND CONCLUSIONS

In any natural environment there are many factors which may limit the energy intake of an animal. These limitations are a function of the climatic conditions, the plants and also the behavioural, physiological and anatomical make-up of the animal itself. Some of these limitations are, however, partly offset by various behavioural, physiological and anatomical features of the animal - the adaptive mechanisms which enable the animal to make the best possible use of the resources available and therefore to survive the particular stresses associated with that environment.

The nutritional status of any herbivore is partly determined by the energetic and nutritive value of the food it eats and this in turn depends on the composition of the herbage and the effect composition has on the digestibility and quantity of food ingested. Since the composition and quality of forages are affected by the quality of the soil, seasonal variations in temperature, insolation and rainfall and the phenology of the plants, these are also pivotal factors which set the limits on energy and nutrients available to the animals.

Living in the semi-arid and arid areas of the Cape Province with frequent droughts and seasonal extremes of temperature, the hyrax must tolerate a harsh, unpredictable climatic environment. Morecver, the poor nutritive quality of the vegetation typical of Table Mountain Sandstone areas could exacerbate these harsh conditions. Although it is not possible to describe the precise nutritional environment which *Procavia capensis* must tolerate, owing to its wide distribution and the varying

vegetation types of the Cape Province, in the southern and western Cape this species tends to inhabit mountainous areas which are covered by two major veld types - the Mountain Rhenosterbosveld and the False Macchia or Fynbos (Acocks, 1953). The nutritive value of these vegetation types in the southern Cape has been studied by Joubert *et al.* (1969), Stindt and Joubert (1979) and Joubert and Stindt (1979) with the general finding that these two veld types are deficient, in terms of the standard requirements for ruminants, in protein and minerals, particularly phosphorus, calcium, manganese and zinc either throughout the year or in the dry season only. Crude fibre levels in the plants are often above 30 per cent (dry matter basis) with crude protein levels varying between 3 and 7 per cent in the dry season (Joubert & Stindt, 1979). Apart from the inherently poor nutritive quality of the herbage, the well-developed thorns on some of the plants and the reputedly high levels of secondary compounds, both repellant to browsing animals, are further stresses that the hyrax must tolerate or overcome.

The initial approach in this thesis was to examine the energetics of the hyrax by evaluating the food and energy intake and its subsequent assimilation. It was established in section 2 that relative to its size, the food and energy intake of the hyrax was low, both in the laboratory and in the field. The interrelationship between protein and crude fibre content of the food influenced the dry matter intake, with high crude fibre levels also diminishing the efficiency of digestion of other food components and consequently reducing the efficiency of energy assimilation. In general, however, the digestibility of crude

fibre was relatively high and comparable to ruminant-like herbivores, though the breakdown was not as effective as in ruminants. Thus the efficiency of energy assimilation in the hyrax was commensurate with that of other herbivorous mammals. Due to the low food intake, however, the metabolizable energy intake was lower than predicted for similar sized eutherian mammals.

The ability of the hyrax to digest cellulose was due to the unique structure of its digestive system with at least two but possibly three major areas of microbial fermentation, where high concentrations of volatile fatty acids were recorded (section 3). Fermentation in the most proximal section, the extensible cardiac sac of the stomach, was unusual and appeared to be similar to a silage fermentation system with acetic and lactic acids predominating. The more distal sites of fermentation in expanded regions of the large intestine showed concentrations and proportions of volatile fatty acids comparable to caecal and rumen fermentation in non-ruminants and ruminants respectively. It was established in section 3, however, that the metabolism of the hyrax differed from that of ruminants as it was dependent on glucose rather than volatile fatty acids as a precursor for energy production. Furthermore the depot fat of the hyrax contained high levels of unsaturated fatty acids characteristic of non-ruminant herbivores.

Considering that the major food competitors of the hyrax are the larger ruminants such as the klipspringer, which also occupy a mountainous habitat and in some areas, domestic sheep, it is essential that some separation in the nutritional niche exists to allow the ruminants and

the hyrax to coexist. Norton (1980) has suggested that the hyrax may be able to utilize lower quality vegetation than the ruminants. Also, some separation would be attributable to the range over which the animals browse. In this respect the necessity to remain close to the rock crevices as a predator evasion strategy restricts the range over which the hyrax can feed, therefore limiting the forage available to them. Although some overlap may exist, the ruminant has no such restriction over its browsing area. In view of the restricted feeding range, hyraces may have to tolerate lower quality vegetation. Some characteristics of the nutritional and digestive physiology of the hyrax would partly offset this disadvantage. The catholic dietary habits and the selection of young leaves and shoots with high protein and low fibre content, as well as the hyrax's ability to feed on some toxic plants would increase the opportunity of finding enough food to meet its nutrient requirements. In the face of a depleted browsing or grazing area, the small migratory movements of the colony would also allow exploitation of new, richer food resources.

Under drought conditions, however, the vegetation over large areas may be of poor nutritional quality, being high in fibre and low in moisture and protein. Food selection or migration may then be of limited value and the effective use of the available vegetation of critical importance, especially in the face of competition from other herbivores. In this respect the more rapid rate of passage of the digesta through the gut of the hyrax albeit with a less efficient breakdown (section 2) relative to the ruminant, may become an advantage. Since the food intake and rate of its passage through the ruminant digestive tract

is limited by the particle size of the digesta within the rumen, fibrous or lignified plants which take a long time to be broken down, even with rumination, restrict the food intake of the ruminant. The hyrax, however, not having the same limitations on particle size, may be able to process relatively more food allowing the coarse undigested structural material to be voided. Digestive efficiency may be low but nevertheless, the low energy requirements (sections 2 and 6) may still be fulfilled in this way. Furthermore, the low nitrogen requirements of the hyrax (Hume *et al.*, 1980) has obvious survival value in the face of poor quality vegetation.

Although the mineral metabolism of the hyrax was not examined in depth, the patterns of excretion of calcium, magnesium and phosphorus were established in section 4. The renal pathway was the major route of calcium excretion, appearing in the urine as a calcium carbonate precipitate and suggesting an efficient calcium absorption mechanism in the alimentary tract. Magnesium excretion tended to follow the same pattern as calcium, though the major pathway for magnesium excretion depended on the quantity ingested. Phosphorus, however, was excreted mainly through the gastrointestinal tract. The excretion of all three elements in the urine depended on the dietary intake and, despite the unusual pathway for calcium and possibly magnesium excretion, normal mammalian levels of the three elements occurred in the plasma, bone and soft tissues. In view of the deficit of calcium

and phosphorus in the vegetation of areas inhabited by the hyrax, an efficient calcium absorption mechanism in the gut would allow the hyrax to fulfil its requirements. The metabolism of these three elements in the hyrax remains relatively unknown, however, and since it appears to be rather exceptional, deserves further attention.

Compounding the stresses of poor quality vegetation, particularly in summer, is the lack of water. The hyrax, however, has a low water turnover rate even when drinking water is available, as well as a low water requirement, giving credence to the popularly held belief that the hyrax can exist without drinking water. In this respect, it was shown in section 5 that the plants available to the hyrax in the wet season could supply it with all its water requirements, though in the dry season, only plants with moisture levels higher than the average would suffice. Nevertheless the ability of the hyrax to reduce the water turnover rate and to tolerate a substantial decrease in body mass in response to dehydration (Rubsamen & Kettembeil, 1980) would favour survival during a dry season. Recycling of sodium and chloride in the renal counter-current system with the consequent reabsorption of water was undoubtedly part of the mechanism responsible for the low water turnover rate of the dehydrated hyrax (section 5), though faecal and evaporative water losses can also be reduced (Louw *et al.*, 1973; Rubsamen & Kettembeil, 1980). In view of the low sodium content of plants the efficient reabsorption of this ion into the body is clearly advantageous. The extent to which water expenditure can be minimised, however, depends to a large extent on the behaviour of the animal. Thus avoidance of high ambient temperatures

which promote evaporative water loss and the inactive life style of the hyrax both reduce the use of water for evaporative cooling and are conservative mechanisms in terms of water expenditure. Furthermore, the humidity of rock crevices is usually higher than the surrounding air at high temperatures (section 6) and would probably be augmented by the collective respiratory water loss of a group of hyraces huddled in the crevice. Water conservation of individuals in a group may therefore be enhanced by such behaviour, but careful field work is necessary to substantiate this suggestion.

The inactive life style and behavioural thermoregulation are also important aspects of the energetics of the hyrax. It was shown in section 2 that the low metabolizable energy intake in the laboratory was commensurate with the low basal metabolic rate shown in section 6 and that the increment of the energy cost of free existence over the basal metabolic rate was 1,83. It was deduced, however, that of this increment, that portion of energy required for activity, thermoregulation and production in the wild was low (section 2).

The low energy cost of thermoregulation can be attributed to the extensive use of behavioural thermoregulation rather than a reliance on physiological regulation. Despite the fact that *P. capensis* is a good physiological thermoregulator maintaining a high stable body temperature of 37,2°C in the laboratory, in the field exploitation of solar radiation while basking, augments the body temperature during the day. Shuttling between the sun and shade keeps this temperature stable. Metabolic heat production to maintain the higher body temperature is

therefore obviated and in the absence of insolation a reduction of body temperature to the lower level recorded in the laboratory, again is a mechanism to avoid extra energy usage. Huddling within the crevices at low ambient temperatures does not have any profound effect on body temperature but reduces energy expenditure by virtue of the lowered metabolism at the higher ambient temperature of the enclosed area. It would not seem to be of any advantage for the crevice temperature to be increased beyond thermoneutral temperatures of the hyrax and possibly thermoneutral temperatures would set the limit on the number of animals that would huddle in a crevice of set volume. Further work in this respect, particularly in the field, would be of interest.

The physiological responses of *P. capensis* to low ambient temperatures (section 6) differed from those of several other species of hyrax in that a stable body temperature was maintained rather than the thermolability reported for all other species except the alpine hyrax *Procavia johnstoni* (Taylor & Sale, 1969). Effective vasomotor control and probably postural changes and piloerection which reduced thermal conductance at low ambient temperatures were responsible, in part at least, for the stability of body temperature in *P. capensis*. Since this species lives in a more extreme climatic environment than the more tropical species of hyraces, experiencing colder conditions as well as heat comparable to that in the tropics, the high stable body temperature and the relatively low lower critical temperature can perhaps be considered adaptations to a colder environment. It is possible, however, that at temperatures below 5°C, which were not tested in this

study, *P. capensis* may show some lability in body temperature, but in view of its huddling behaviour and the effect this has on the crevice temperature, it seems unlikely that hyraces in the wild would be exposed to such low temperatures for long periods of time.

It has been suggested that the low basal metabolic rate of the hyrax may be a vestige from the larger size of the ancestral hyraces and the same may be said of the absence of non-shivering thermogenesis in the hyrax (section 7). Evidence in support of this would be that the low basal metabolic rate appears to be a phylogenetic trait. However, ancestral hyracoids were both large and small in size and there is no evidence to suggest that the larger forms necessarily gave rise to the present-day hyraces. Secondly, it seems unlikely that such a fundamental characteristic would be retained as a physiological vestige with no adaptive advantage. Indeed, low basal metabolic rates have a positive value for animals living in arid environments and in the case of the hyrax may be the underlying factor responsible for the low water turn-over rate and the low food intake. The reason for the lack of non-shivering thermogenesis, nevertheless, remains unclear. It may be suggested that the koppie niche has such a favourable microclimate and that the behaviour of the hyrax is so well geared towards selection of favourable temperatures even to the extent of creating its own favourable microclimate within the crevices, that it seldom has to contend with extremely cold temperatures. Changes in thermal conductance by behavioural means may be sufficiently adequate to enable the animal to cope with moderately low temperatures, particularly if allowed to huddle with others of the colony. Shivering could then provide the

metabolic heat necessary at those infrequent times when the bounds of thermal conductance prove inadequate. Assuming the same huddling behaviour to be characteristic of the ancestral forms already living in rock crevices, there may have been no selection pressure for the development of non-shivering thermogenesis. Further long-term studies of the reactions of hyraces to the cold in the field are needed to provide conclusive evidence for the above suggestion, however.

In contrast, the elephant shrew, *Elephantulus edwardi*, relies heavily on non-shivering thermogenesis in the cold (section 7). Being a small animal it has relatively limited control over heat loss at low air temperatures in view of its large surface area. Furthermore, it has no recourse to behavioural thermoregulatory mechanisms such as huddling, being a solitary animal. While the microclimate in a crevice would provide some advantage in this respect, it is not as stable or effective as the microclimate in enclosed burrows which many small mammals utilize and which require adaptations in these burrowing animals to high temperatures (McNab, 1979). Thus, for the elephant shrew, effective physiological mechanisms of heat production and regulation, such as non-shivering thermogenesis and increased metabolism at low temperatures with a minimal thermal conductance as predicted for its size (section 8), are of critical importance. This is in contrast to the low minimal thermal conductance of the hyrax and high thermal conductances typical of fossorial rodents (McNab, 1979). In other respects, the elephant shrew is similar to the hyrax, having a low resting and therefore low basal metabolic rate and a high, stable body temperature

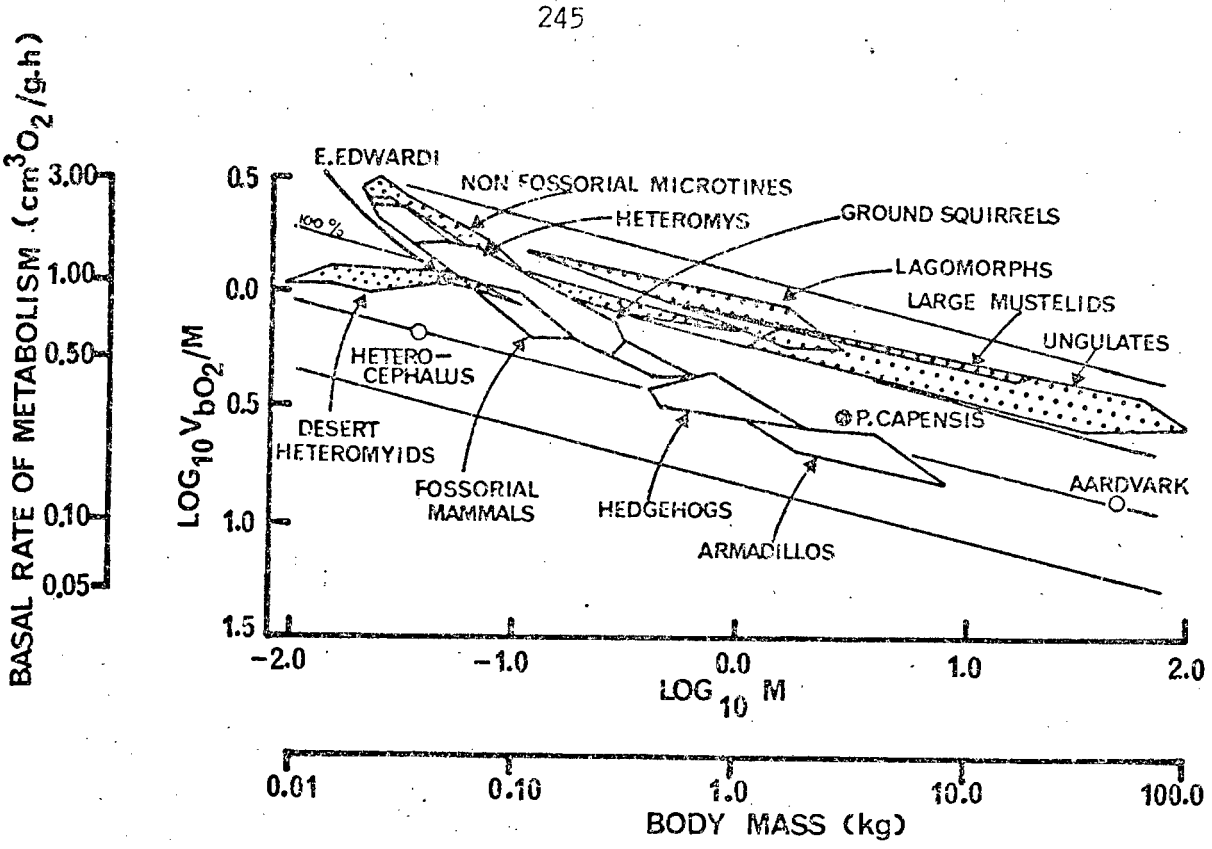
supporting the earlier suggestion that these are adaptations to the arid environment of both animals.

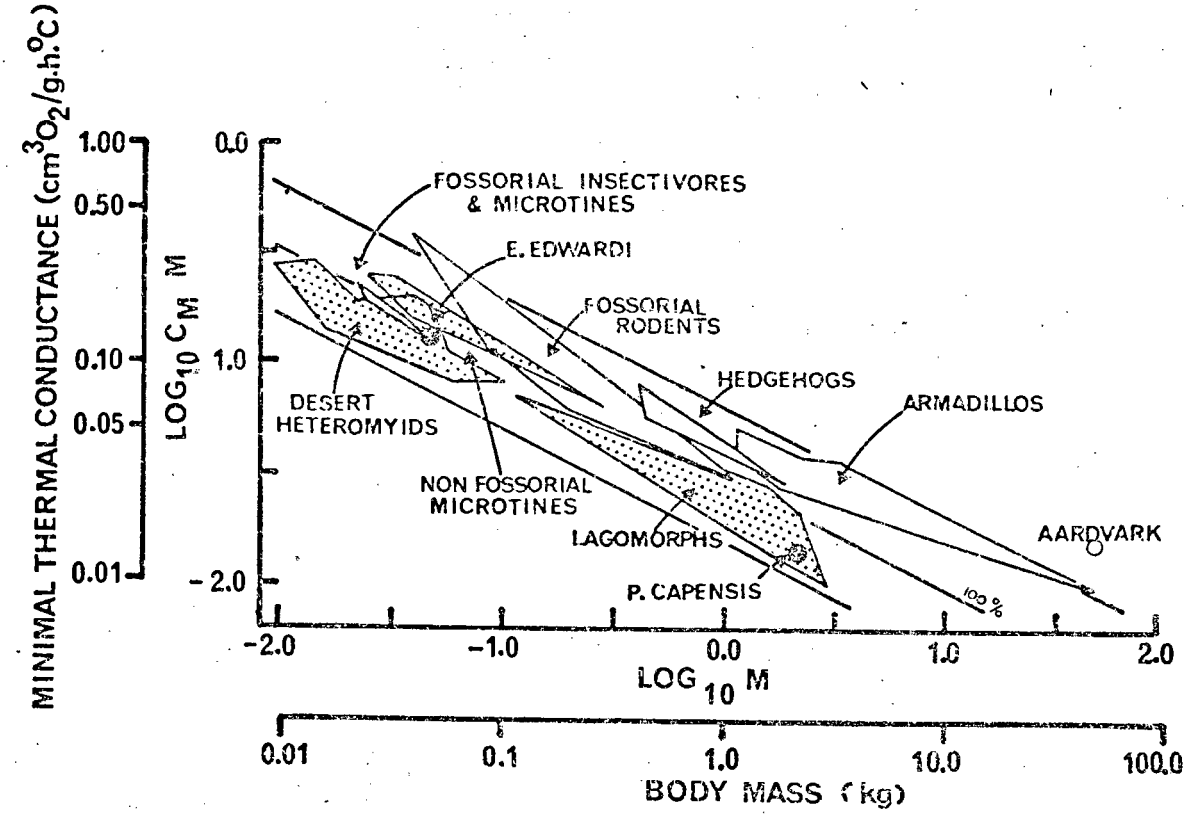
Although the water turnover rate of the elephant shrew is lower than predicted for its size (section 8), it is relatively higher than in the hyrax when the different sizes are taken into account. This may be attributed to the reliance by the elephant shrew on physiological mechanisms of heat regulation, although the different diets would seem to offer an equally acceptable explanation. An insectivorous diet has a high water content and despite the high protein content, does not demand as frugal a water expenditure as does an herbivorous diet. Like the hyrax, however, the elephant shrew avoids intense solar radiation by its inactivity at midday and its crepuscular habits, thus ameliorating excessive water expenditure for evaporative cooling. Furthermore, although the renal function of the elephant shrew is effective in producing urine with as high an osmolality as the hyrax, the elephant shrew does not conserve electrolytes when dehydrated, a possible reflection of the insectivorous diet where the availability of essential ions, such as sodium, is not a limiting factor.

It is interesting to compare the present findings of the basal metabolic rates and minimal thermal conductances of *Procavia capensis* and *Elephantulus edwardi* with those of McNab (1979) in fossorial and burrowing mammals. Neither of the two present species lives in enclosed burrows, but the crevices can be considered similar to cool open burrows. McNab (1979) has shown that fossorial rodents greater than 80 g in mass usually have low metabolic rates and high minimal thermal conductances,

while those less than 60 g have high basal metabolic rates but thermal conductance depends on whether they live in cool or warm burrows. He has also shown that burrowing mammals which spend appreciable periods out of the burrow have similar metabolic rates to fossorial mammals. The hyrax conforms to the pattern of a low metabolic rate of larger burrowing mammals such as hedgehogs, armadillos and ground squirrels (Fig. 9.1), but has a minimal thermal conductance lower than the hedgehog, aardvark and armadillo which have relatively high thermal conductances, apparently to reduce heat storage in their burrows (Fig. 9.2) (McNab, 1979). The hyrax may not conform to this pattern for three main reasons. Firstly, the crevices may be cooler than a deep burrow system, therefore requiring a low thermal conductance to minimise heat loss. Secondly, by virtue of its huddling behaviour which would provide good insulation for individual animals, a high minimal thermal conductance would be unnecessary. Thirdly, the hyrax is active during the day while the larger animals used in McNab's (1979) report were nocturnally active. Thus, the crevices are used by the hyrax predominantly at night when air temperatures even in the crevices are relatively cold so that a high minimal thermal conductance would be of no advantage.

The elephant shrew, however, has a metabolic rate (resting) intermediate between the high basal metabolic rate of burrowing mammals which live in cool burrows and the low basal metabolic rate of those living in warm burrows. That of *E. edwardi* appears to be similar to desert heteromyids which do not follow the usual pattern of fossorial or burrowing small mammals (Fig. 9.1). McNab (1979) suggests that the low


BASAL RATE OF METABOLISM (cm³O₂/g.h)
3.00
1.00
0.50
0.10
0.05
LOG10VbO2/M
0.5
0.0
0.5
1.0
1.5
E.EDWARDI
NON FOSSORIAL MICROTINES
HETEROMYS
GROUND SQUIRRELS
LAGOMORPHS
LARGE MUSTELIDS
UNGULATES
100 %
HETERO-CEPHALUS
DESERT HETEROMYIDS
FOSSORIAL MAMMALS
HEDGEHOGS
ARMADILLOS
P.CAPENSIS
AARDVARK
-2.0
-1.0
0.0
1.0
2.0
LOG 10 M
0.01
0.10
1.0
10.0
100.0
BODY MASS (kg)


MINIMAL THERMAL CONDUCTANCE (cm³O2/g.h.°C)
1.00
0.50
0.10
0.05
0.01
LOG10 CM M
0.0
1.0
-2.0
FOSSORIAL INSECTIVORES & MICROTINES
E.EDWARDI
FOSSORIAL RODENTS
HEDGEHOGS
ARMADILLOS
DESERT HETEROMYIDS
NON FOSSORIAL MICROTINES
LAGOMORPHS
AARDVARK
P. CAPENSIS
100 %
-2.0
-1.0
0.0
1.0
2.0
LOG 10 M
0.01
0.1
1.0
10.0
100.0
BODY MASS (kg)

metabolic rates of heteromyids are independent of their burrowing habits but may be an adaptation to the desert environment. The same may be true of the elephant shrew. Since this animal has a similar minimal thermal conductance to fossorial or burrowing mammals living in cool burrows and to desert heteromyids (Fig. 9.2), temperature regulation in the elephant shrew is typical of small mammals and the crevice can be considered similar to a cool burrow. In view of the lack of use of burrows or crevices by elephant shrews with a more tropical distribution, the exploitation of rock crevices by *E. edwardi* and probably *E. myurus* seems to be an adaptation to the climatic pressures of its more extreme environment.

This thesis was undertaken to investigate the energy and water metabolism of the herbivorous hyrax, *Procavia capensis* and the insectivorous elephant shrew, *Elephantulus edwardi* in relation to the environment in which they live. The hyrax has an extremely economical energy and water budget by virtue of its extensive use of behavioural thermoregulation, long periods of immobility and a gregarious life style. The availability of food, however, limits the number of animals that can live in a given area. Consequently, in view of the greater abundance of plants relative to insects, herbivores are more suited to gregarious living than insectivores. In contrast to the hyrax, the insectivorous elephant shrew is a solitary mammal and relies extensively on physiological mechanisms of thermoregulation. Water and energy are not conserved to the same extent as in the hyrax, but the necessity to do so is obviated by the high nutrient and water content of the

insectivorous diet. Thus, the work reported here has illustrated some of the mechanisms that can be used by animals living in an arid environment to exploit the different and limited resources available.

APPENDIX A MONTHLY BODY MASSES AND MASSES OF STOMACH CONTENTS OF *P. CAPENSIS* FROM TWO AREAS IN NAMIBIA

Area[a]	Month[a] & Season		Mean body[b] Mass g	Mean wet mass[a] of stomach contents g	(n)	Stomach Mass/ Animal Mass %	ME/BMR[c]
SANDMODDER (26°57'S,18°55'E)							
	1975						
	March	Wet	2226	109	10	4,90	1,87
	April		2038	116	9	5,69	2,17
	May		1967	83	6	4,22	1,61
	June	Cool	1425	50	6	3,51	1,34
	July	Dry	2535	111	10	4,38	1,67
	August		1960	82	10	4,18	1,59
	Sept	Trans-	1512	52	10	3,44	1,31
	Oct	ition[θ]	1417	93	4	6,56	2,50
	Nov		2050	121	5	5,90	2,25
	Dec	Hot	2733	174	3	6,37	2,43
	1976	Dry					
	Jan		2800	120	4	4,29	1,63
	Feb		3638	148	4	4,07	1,55
	March	Wet	2230	93	10	4,17	1,59
	April		2719	140	10	5,15	1,96
	May		3100	52	8	1,68	0,64
	June	Cool	2250	103	10	4,58	1,75
	July	Dry	1600	76	10	4,75	1,81

- continued

Appendix A - continued

Area	Month	Season	Mean body Mass g	Mean Wet Mass of stomach contents g	(n)	Stomach Mass/ Animal Mass %	MEI / BMR
WARMFONTEIN (27°7'S,19°15'E)							
	1975						
	March	Wet	1944	70	8	3,60	1,37
	April		2144	72	10	3,36	1,28
	May		2220	127	10	5,72	2,18
	June	Cool	2688	102	8	3,79	1,45
	July	Dry	2225	112	6	5,03	1,92
	August		1830	108	10	5,90	2,25
	Sept	Transition	2309	144	10	6,24	2,38
	Oct		1690	134	5	7,93	3,02
	Nov		2250	73	3	3,24	1,24
	Dec	Hot Dry	2592	158	6	6,10	2,32
	1976						
	Jan		2922	114	9	3,90	1,49
	Feb		2350	151	1	6,43	2,45
	March	Wet	2770	205	10	7,40	2,82
	April		2445	118	10	4,83	1,84

- continued

Appendix A - continued

Area	Month	Season	Mean body Mass	Mean Wet Mass of stomach contents		Stomach Mass/ Animal Mass	MEI / BMR
			g	g	(n)	%	
Warmfontein (contd)							
	May	Cool, dry	2340	92	10	3,93	1,50
	June		1615	74	10	4,58	1,75
	$\bar{x}$		2259	108,39	33	4,84	1,85
	± S.D.		505	35,99		1,33	0,51

9 Beginning of moderate rains

(a) Lensing (1978)

(b) Lensing (personal communication)

(c) MEI = metabolic energy intake;
BMR = basal metabolic rate.

See text, section 2, for methods of calculating MEI and BMR.

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