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THE INFLUENCE OF SEASONALITY AND QUALITY OF DIET ON THE METABOLISM OF THE AARDWOLF, *PROTELES CRISTATUS* (SPARRMAN 1783)

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The influence of seasonality and quality of diet on the metabolism of the aardwolf, *Proteles cristatus* (Sparrman 1783)

by

Mark David Anderson

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"Dedicated to Tania, my wife and best friend"

The influence of seasonality and quality of diet on the metabolism of the aardwolf, *Proteles cristatus* (Sparrman 1783)

by

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ABSTRACT

The aardwolf *Proteles cristatus* was studied for two years from December 1988 to January 1991 on Benfontein Game Farm, in the northern Cape Province, South Africa. The aardwolf's principle food source in this area, snouted-harvester termites *Trinervitermes trinervoides*, are largely inactive and hence unavailable during winter. Consequently, this seasonal food restriction imposes severe nutritional stresses on *P. cristatus*.

Unlike the other typical "anteaters", aardwolves do not dig for their prey but lick foraging termites off the soil surface. Consequently, aardwolves do not possess the physical features which are characteristic of typical ant- and termite-eating mammals. Nevertheless, aardwolves do have a number of anatomical features which are clearly adaptations to their diet and feeding style. The most obvious of these are a broad spatulate tongue covered with large, hardened papillae, a broad palate, large

mandibular salivary glands, and a muscular pyloric region in the stomach. The aardwolf is committed to a diet of surface foraging termites and due to reduced dentition is unable to feed on alternative, larger prey items.

The nutritional quality of *T. trinervoides*, like other invertebrates, is poor. Aardwolves compensate for this by consuming vast quantities of termites. As many as 300 000 may be consumed per night during the warm summer months, thus enabling subcutaneous fat to be deposited. The body masses of aardwolves decreased by 25% from approximately 10 kg to 7,5 kg during the winter months (April - August). Subcutaneous fat reserves (measured at six body localities) showed a significant decline during winter. Blood samples analyzed during summer and winter for 16 blood chemistry and eight blood hematology parameters also showed significant sex, age-class and seasonal differences. Triglyceride and cholesterol values were the most reliable indicators of nutritional status.

When inactive, aardwolves sought refuge in underground dens, which were usually modified springhare *Pedetes capensis* burrows. Daily denning times during winter were approximately 20 h in comparison to a shorter 15 h 20 min during summer. The den environment is thermally stable, representing a favourable micro-habitat to escape the thermal extremes of the northern Cape. In comparison to the extreme variation in ambient temperatures on the soil surface outside the dens, the den temperatures were constant, with temperatures of approximately $12^{O}C$ and $27^{O}C$ during winter and summer, respectively.

In the den body posture and social huddling are hypothesized to be important energy saving mechanisms. A significant increase in insulation, with a concomitant decrease in thermal conductance, during winter were important in limiting heat loss. Water conservation through a limited use of evaporative cooling is important in maintaining body water homeostasis during winter.

Active aardwolves maintained relatively constant body temperatures (T_b) of 37,0-37,5^{o}C. While inactive, however, and particularly during winter, significant decreases in T_b were observed. T_bs as low as 31,2^{o}C were recorded during the middle of the inactive period during winter. The observed drop in T_b results in energy savings of up to 17,7%, and contributes to the aardwolf's ability to cope with the periodic limitations in energy supplies during winter.

The basal metabolic rate (BMR) of captive aardwolves averaged 1869,5 ml O_2 h^{-1} and 2194,3 ml O_2 h^{-1} during winter and summer, respectively. These BMRs are significantly lower (58,9% - winter; 67,1% - summer) than is predicted by allometric equations. A low BMR, which is further reduced during winter, decreases the overall energy requirements of the aardwolf.

The aardwolf feeds on a food source which is largely avoided by other mammals. *T. trinervoides* are unavailable during winter and due to a number of physical specializations the aardwolf is unable to exploit alternative food sources. Survival during winter, however, is achieved through a combination of behavioural and physiological adaptations. As a consequence of the aardwolf's specialization on this unique diet, and the ability to cope with the absence of termites during winter, it has invaded a trophic niche which is almost entirely devoid of competitors.

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GLOSSARY OF TERMS

BMR: basal metabolic rate (ml O_2 g^{-1} h^{-1} or ml O_2 h^{-1})

C: conductance (ml O_2 g^{-1} h^{-1} $^oC^{-1}$)

EWL: evaporative water loss (g H_2O h^{-1})

m: body mass (g)

M: metabolism (ml O_2 g^{-1} h^{-1} or ml O_2 h^{-1})

MR: metabolic rate (ml O_2 g^{-1} h^{-1} or ml O_2 h^{-1})

T_a: ambient temperature (^oC)

T_b: body temperature (^oC)

T_d: den temperature (^oC)

TNZ: thermal neutral zone

W: body mass (g)

CHAPTER 1. GENERAL INTRODUCTION

Aardwolves *Proteles cristatus* (Protelidae; *ca* 9 kg) (Sparrman 1783) occur within two discrete distributional areas on the African continent, one in east and north-eastern Africa and the other in southern Africa (Figure 1.1) (Smithers 1983; Koehler & Richardson 1990). Within this range aardwolves occur in a wide range of habitat types, with the exception of forests and pure deserts (Smithers 1983). In these habitats climatic variability is marked, especially in the distribution and abundance of rainfall and in the daily and seasonal variation in ambient temperature (Tyson 1986).

The aardwolf's occurrence anywhere is dependent on the availability of *Trinervitermes* termites, which constitute its principle food source (Kruuk & Sands 1972; Cooper & Skinner 1979; Richardson 1987a). The aardwolf (Figure 1.2) is thus a highly specialized mammal (Richardson 1987b); it eats only termites, a diet that makes it one of the few true mammalian myrmecophages (Redford 1987). This obligate myrmecophagous diet contrasts to the aardwolf's external characteristics (Anderson, Richardson & Woodall 1992). It does not possess the specialized morphological traits which characterize typical myrmecophages (Griffiths 1968) and in contrast has a "progressive" body plan, similar to that of its relatives, the hyaenids (Smithers 1983; Redford 1987; Koehler & Richardson 1990).

In South Africa the aardwolf feeds primarily on *T. trinervoides* (Termitidae; Nasutitermitinae) (Cooper & Skinner 1979; Richardson 1987a). *T. trinervoides* live in dome-shaped mounds (Figure 1.3), and are common throughout the grassland areas of South Africa (Figure 1.4 & 1.5) (Skaife 1953). These termites lack cuticular pigmentation and consequently are not active during the day (Hewitt, Nel & Schoeman 1972). At night they move through foraging tunnels to areas away from the mound, where they forage in dense aggregations exposed on the soil surface (Figure 1.6).

Aardwolves are solitary foragers and a monogamous pair with their most recent

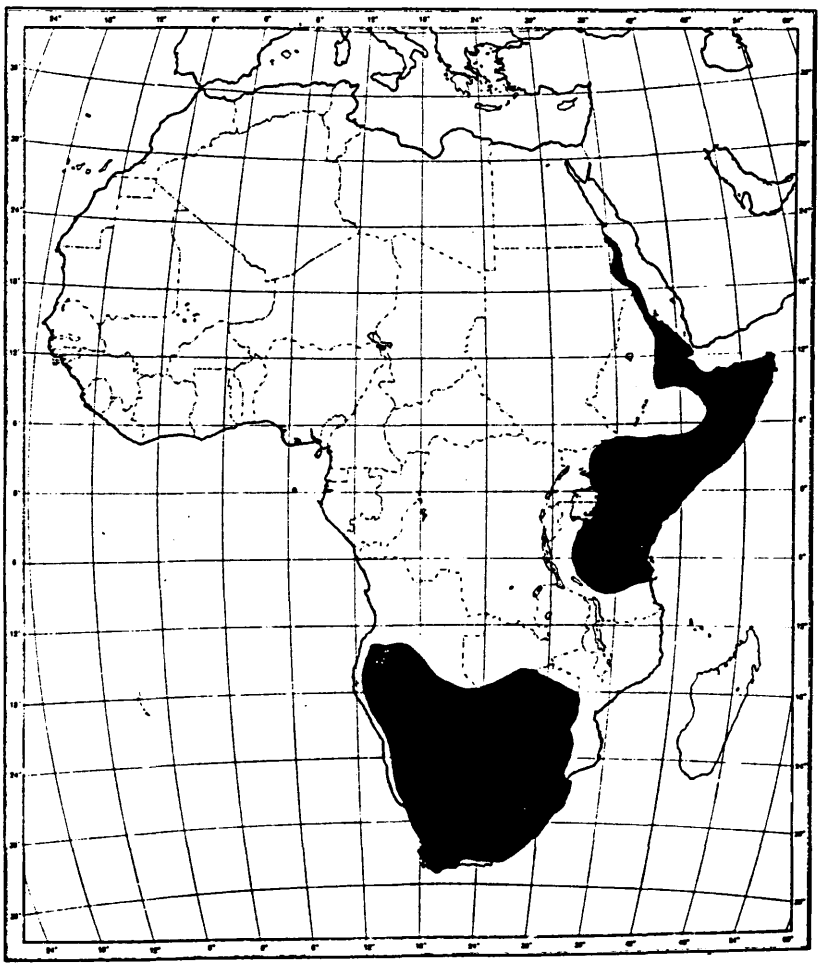


Figure 1.1 Distribution of the aardwolf in Africa (from Smithers (1983)).

Figure 1.2 The aardwolf *Proteles cristatus*: most highly specialized carnivore?

Figure 1.3 An example of the dome-shaped mound of the snouted-harvester termite, *Trinervitermes trinervoides*. The mound is approximately 50 cm high.

Figure 1.4 *Trinervitermes trinervoides* mounds are common throughout the grassland areas of South Africa.

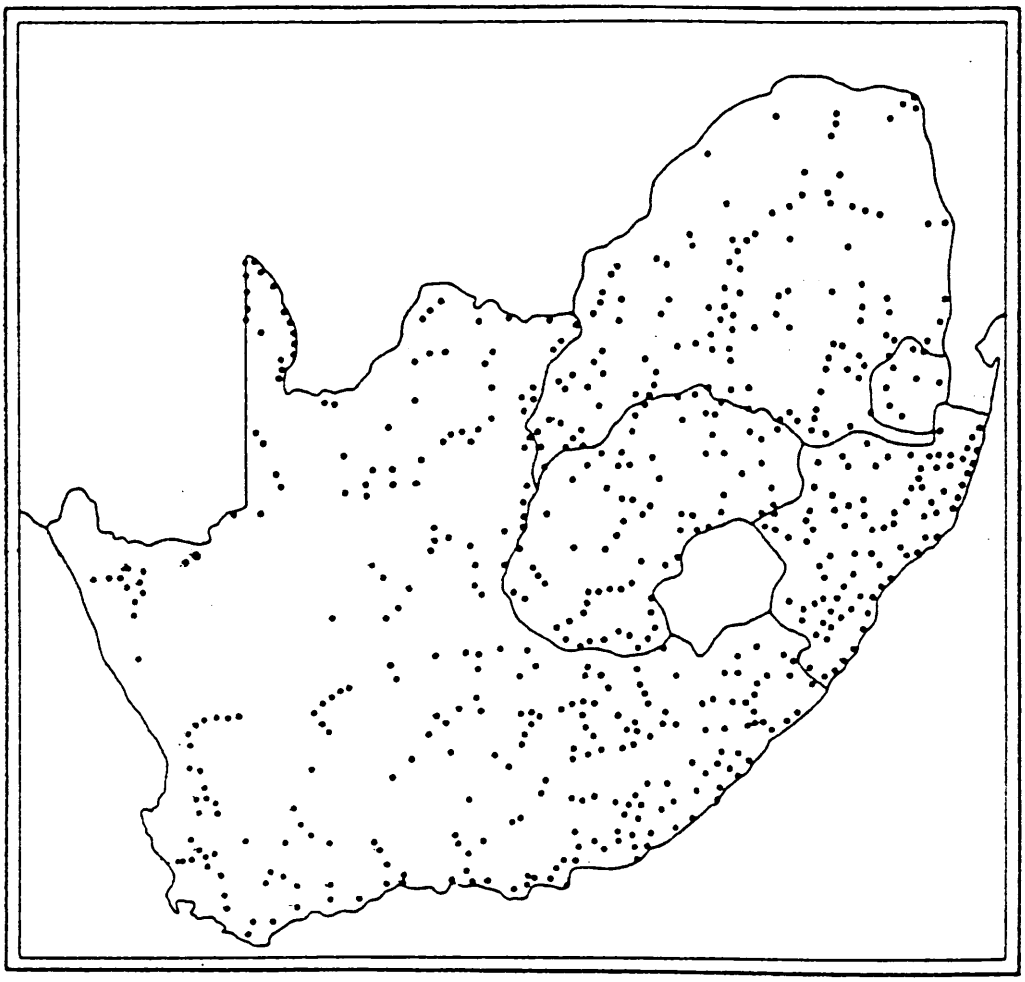


Figure 1.5 Distribution of *Trinervitermes* in southern Africa (after Coaton (1963)).

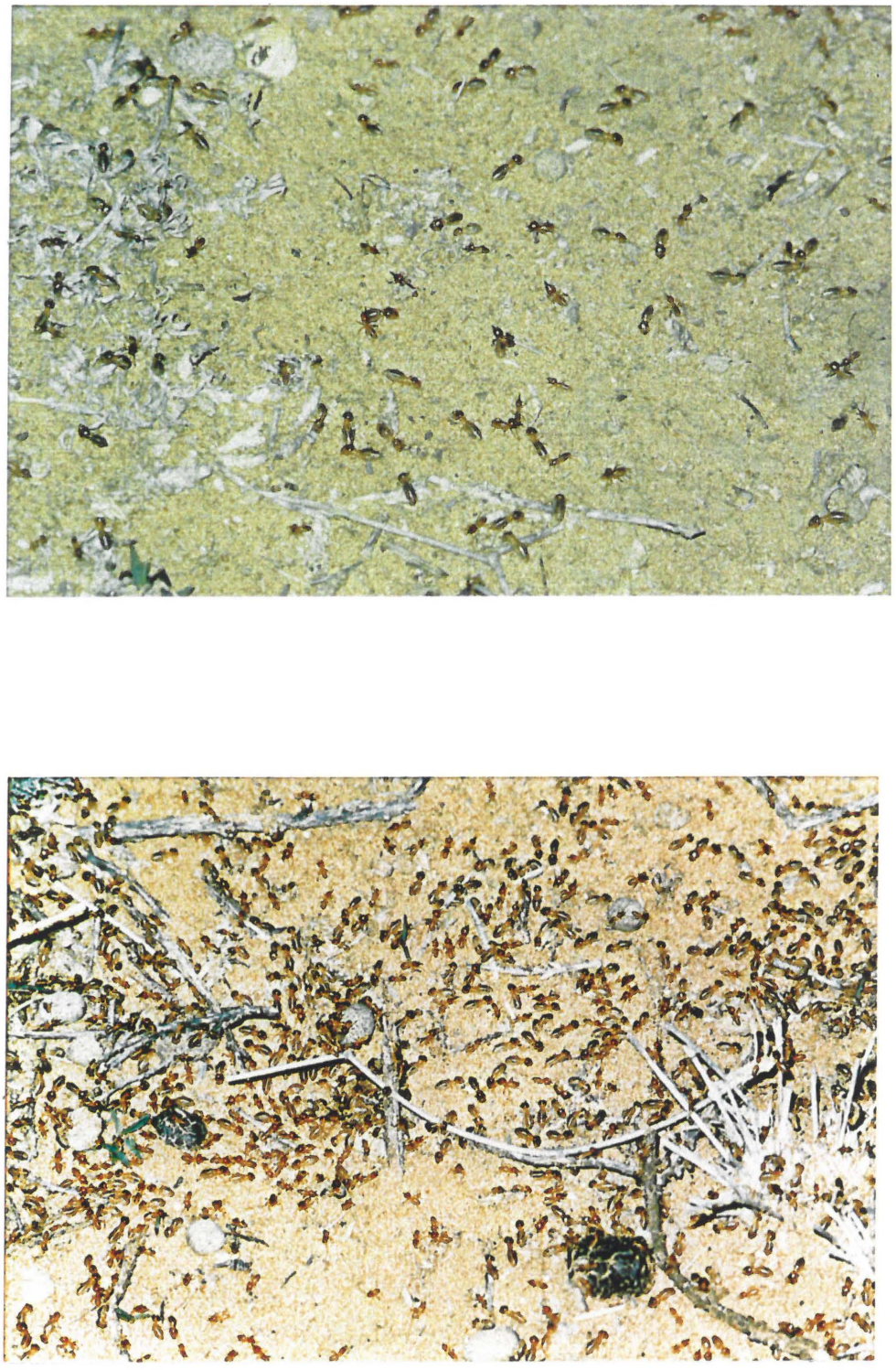


Figure 1.6 *Trinervitermes trinervoides* forage in dense aggregations on the soil surface.

offspring live in a territory of 1-4 km^2 (Skinner & van Aarde 1985; Richardson 1991a,b). Territory size varies with the density of *Trinervitermes* mounds, with each territory having approximately 3 000 mounds, with an average of 55 000 termites per mound (Richardson 1985, 1987a).

Most African termites forage under the protection of mud galleries. *T. trinervoides*, however, can afford to forage openly on the soil surface as they have a chemical defence system of noxious terpene-based secretions which are sprayed at predators (Figures 1.7 & 1.8) (Prestwich 1983). This defence system has been effective in limiting predation from most mammals and other termite-predators (Longhurst, Johnson & Wood 1978, 1979; Lubin & Montgomery 1981; Redford 1985). The aardwolf locates foraging termites using its acute senses of smell and hearing (Kruuk & Sands 1972; Richardson 1987b), and once a termite patch is located they are rapidly licked off the soil surface. Feeding in this manner, an aardwolf can consume as many as 300 000 termites per night during summer (Richardson 1987b).

During winter when the temperature at night falls below $9^{o}C$ it is generally too cold for *T. trinervoides* and they are inactive and hence unavailable for the aardwolf (Richardson 1987a). The aardwolf, however, feeds on an alternative food source during winter, albeit to a much less extent (Figure 1.9) (Richardson 1987a). This species, the common-harvester termite *Hodotermes mossambicus*, is darkly pigmented and hence active by day, and this explains the aardwolf's diurnal activity (during the late afternoon) during this season. This seasonal food unavailability is reminiscent of the ecological problems which are imposed on mammalian species of the temperate latitudes during winter (Lyman 1963), and unusual for a carnivore which occurs in Africa. Winter is a period of great stress for the aardwolf (Richardson 1985, 1987a,b).

Two questions arise specifically regarding the aardwolf's specialization on a diet of *Trinervitermes*. Firstly, why and how did the aardwolf specialize on a diet of termites which are noxious and generally avoided by other mammals? Secondly,

Figure 1.7 The soldier caste of *Trinervitermes trinervoides* have a well developed chemical defence system. The soldiers protect the workers while they harvest grass on the soil surface.

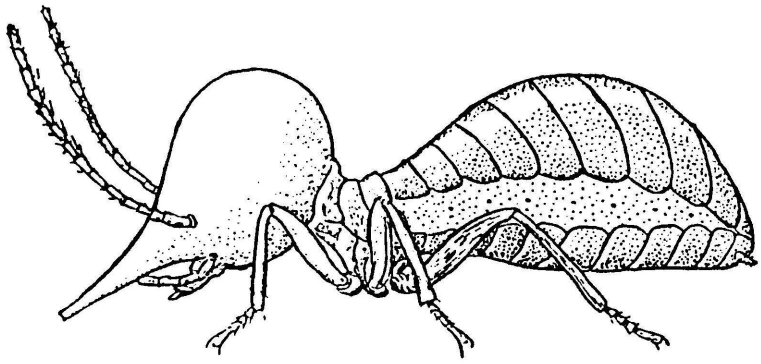


Figure 1.8 The head or frontal gland of the soldier termite is large and contains noxious terpene-secretions. The chemical secretions are sprayed through an opening at the tip of the snout at predators, such as ants.

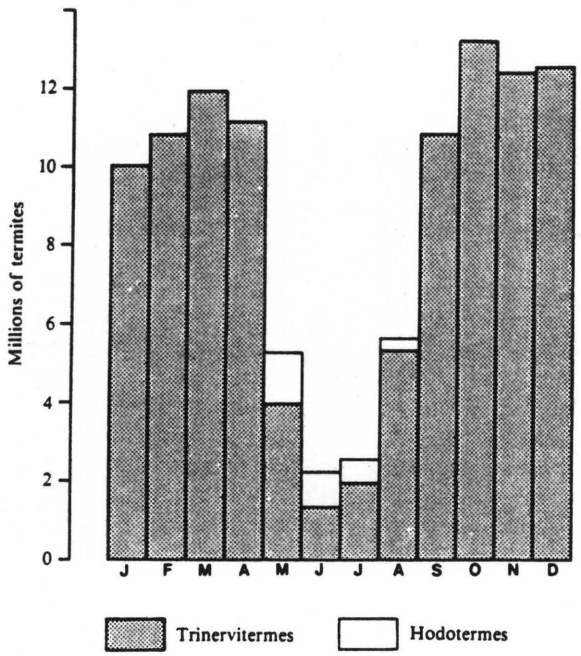


Figure 1.9 The aardwolf's annual consumption of *Trinervitermes trinervoides* and *Hodotermes mossambicus* in the northern Cape Province of South Africa. Numbers of termites refer to *Trinervitermes*, whereas the values for *Hodotermes* are a relative measure (from Richardson (1987b)).

why does the aardwolf not feed on an alternative food source during winter when *T. trinervoides* are unavailable?

The first question can be adequately answered by looking at the aardwolf's ancestry (Richardson 1987b). It is generally accepted that hyaenids (including the aardwolf) were derived from civet-like viverrids (Ewer 1973; Savage 1978), but it is uncertain at what stage the aardwolf diverged from this lineage (Thenius 1966; Ewer 1973). Viverrids, and in particular the African civet *Viverra viverra*, have the remarkable ability of being able to tolerate poisonous and distasteful foodstuffs (Kingdon 1977). Therefore, as the aardwolf evolved from ancient civets it may have been pre-adapted to tolerate the terpene secretions of *Trinervitermes* (Richardson 1987b). According to Richardson (1987b) the aardwolf's specialization towards feeding primarily on this diet would have proceeded simultaneously with selection for the ability to tolerate the terpenes. This specialization enabled the aardwolf to invade a trophic niche which was almost entirely devoid of competitors.

Until today the aardwolf feeds on a food source which is not exploited by other myrmecophagous animals. Certain species such as the aardvark *Orycteropus afer* occasionally dig into *T. trinervoides* mounds and feed on the more palatable larvae and worker termites (Melton 1976). Other animals such as the Whitebrowed Sparrow-weaver *Plocepasser mahali* (Ferguson 1988), the Ant-eating Chat *Myrmecocichla formicivora* (Anderson 1992) and a beetle *Triaenogenius corpulentus* (Carabidae) (pers. obs.) carefully select the worker termites, thus avoiding the noxious secretions of the soldier caste.

During summer *T. trinervoides* are an abundant food supply which are exploited by the aardwolf without competition from other mammals. During winter, however, these termites are generally unavailable. Why then does the aardwolf not switch to an alternative (and possibly larger) food source during winter? The answer to this question is explained if one looks at the aardwolf's anatomy. The aardwolf is morphologically and anatomically adapted to its manner of feeding on surface foraging termites (Flower 1869; Richardson 1987b; Anderson, Richardson &

Woodall 1992) and unable to feed on alternative, larger prey items. Unconfirmed reports of aardwolves eating lambs, carrion, eggs, small rodents and reptiles (Shortridge 1934; Maberly 1962; Bothma 1965) are not substantiated by any studies of gut or faecal contents and probably result from mistaken identity (i.e. striped hyaenas *Hyaena hyaena* or jackals) (Kruuk & Sands 1972). This mistaken belief has lead to the persecution of many aardwolves (Anderson 1988; Anderson & Jordaan 1991) and contributed to their present status of rare in the South African Red Data Book - Terrestrial Mammals (Smithers 1986).

The nutritional quality of ants and termites is low (Redford & Dorea 1984) and this, therefore, places further stress on the aardwolf. During winter there is a 20% decrease in the body mass of aardwolves and an increased cub mortality (Richardson 1985, 1987a). According to Richardson (1985), survival during winter is attributed to their use of subcutaneous fat reserves which are deposited during the summer months, and an increased period of inactivity in the den. Thus far no studies on aardwolves have been undertaken to determine whether any physiological mechanisms, such as hypothermy or metabolic adaptations, are associated with the observed seasonal unavailability of food.

McNab (1984) measured the metabolism of a single captive aardwolf and found this animal's basal metabolic rate (BMR) to be approximately 70% of that predicted from Kleiber's (1961) allometric equation. An important advantage of a low BMR is that it lowers energy demand and, thus, facilitates survival during periods of food stress. McNab (1984) has attributed various factors to the low BMR of all myrmecophagous mammals. He suggested that mammals which feed on a food source of ants and termites, which is (1) nutritionally poor, (2) seasonally unavailable, (3) filled with chemical poisons and (4) ingested with grass and sand, have low BMRs.

This study was undertaken in order to, firstly, substantiate McNab's (1984) single measurement and, secondly, to attempt to understand some of the eco-physiological adaptations of the aardwolf to a seasonally unavailable food source.

Key questions

(1) What are the anatomical and morphological features (adaptations) of the aardwolf which (a) are specifically related to a myrmecophagous diet and facilitate specialization on this diet, and (b) inhibit their ability to utilize alternative and larger food sources?

(2) What is the nutritional quality of *Trinervitermes trinervoides* and how does it compare with the nutritional quality of other food items?

(3) What happens to the body condition of the aardwolf during winter? Does the aardwolf deposit fat reserves during summer? Are there sexual, age class and seasonal differences in the blood chemistry and blood hematology of free-ranging aardwolves which are indicative of the nutritional status of individuals?

(4) Does the den environment function in facilitating the aardwolf's survival during winter?

(5) What behavioural (e.g. reduced activity, social thermoregulation) and morphological (e.g. increased insulation) adaptations facilitate the aardwolf's survival during winter?

(6) Are there any seasonal and daily fluctuations in body temperature (hypothermy, torpor) and if so what are the implications for energy and water conservation?

(7) What are the evaporative water loss rates of the aardwolf?

(9) Does the aardwolf, like other myrmecophagous mammals, have a low basal metabolic rate and does it vary seasonally?

CHAPTER 2. MATERIALS AND METHODS

2.1 STUDY AREA

Location and general description

The study was conducted on Benfontein Game Farm (28°50'S; 24°50'E), situated approximately 6 km south-east of Kimberley in the northern Cape Province, South Africa (Figure 2.1). Benfontein is 11 300 ha in extent, and the main study site is a 2 500 ha portion in the east. The vegetation consists of semi-arid open savanna (Figures 2.2a & b), and elements of three major biomes that converge in the Kimberley area (Acocks 1975) are present in the study area. The Kalahari biome lies to the north-west, the grassveld biome to the east and the Karoo biome to the south. A large pan (Figure 2.2c) is situated in the north-west of the study area, around which occur more specialized plant communities.

Climate

(1) **Rainfall** The northern Cape has a "semi-arid continental climate" (Schulze & McGee 1978). There is a distinct "arid" period during the winter months and a "humid" period during the summer months (Figure 2.3). In a semi-arid area, rainfall is the most important factor influencing changes in the vegetation and therefore in the animal communities (for example, termites) (Louw & Seely 1982). Rainfall in the northern Cape is extremely variable, both in time and in spatial distribution (Tyson 1986).

Rainfall in Kimberley usually peaks in the late summer months with March being the wettest month (Figure 2.4). Precipitation is usually in the form of late afternoon thundershowers. The mean annual rainfall for Kimberley is 431 ± 127 mm (Weather Bureau, Pretoria). The mean monthly rainfall for the study period (January 1989 -

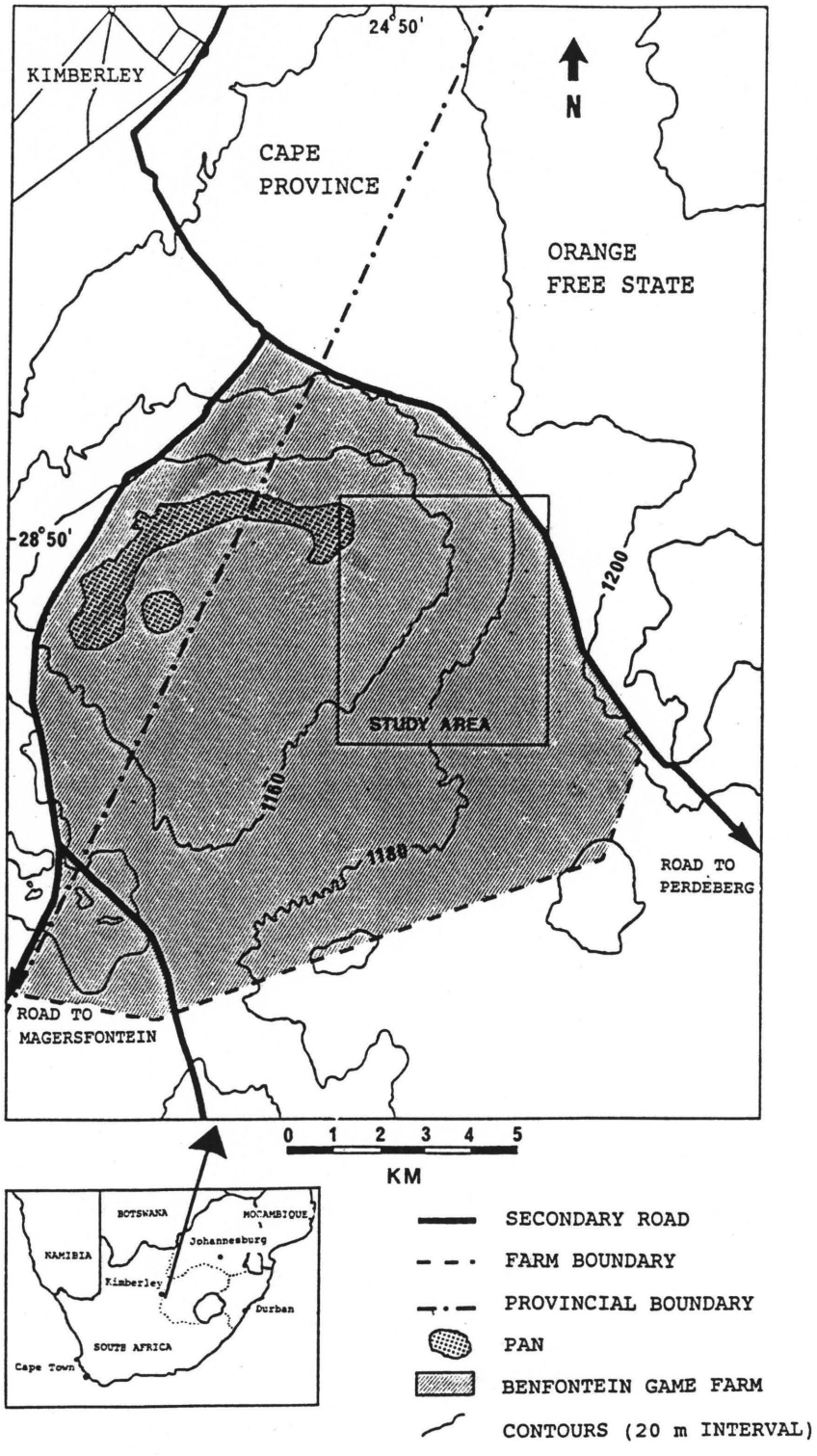


Figure 2.1 Benfontein Game Farm indicating the study area, the most important geographical features and the position of the study area relative to Kimberley (adapted from Richardson (1985)).

(a)

(b)

(c)

Figure 2.2 The three major vegetation communities in the study area: (a) sandveld communities, (b) the pan slope communities and (c) pan communities (situated in the north-west of the study area).

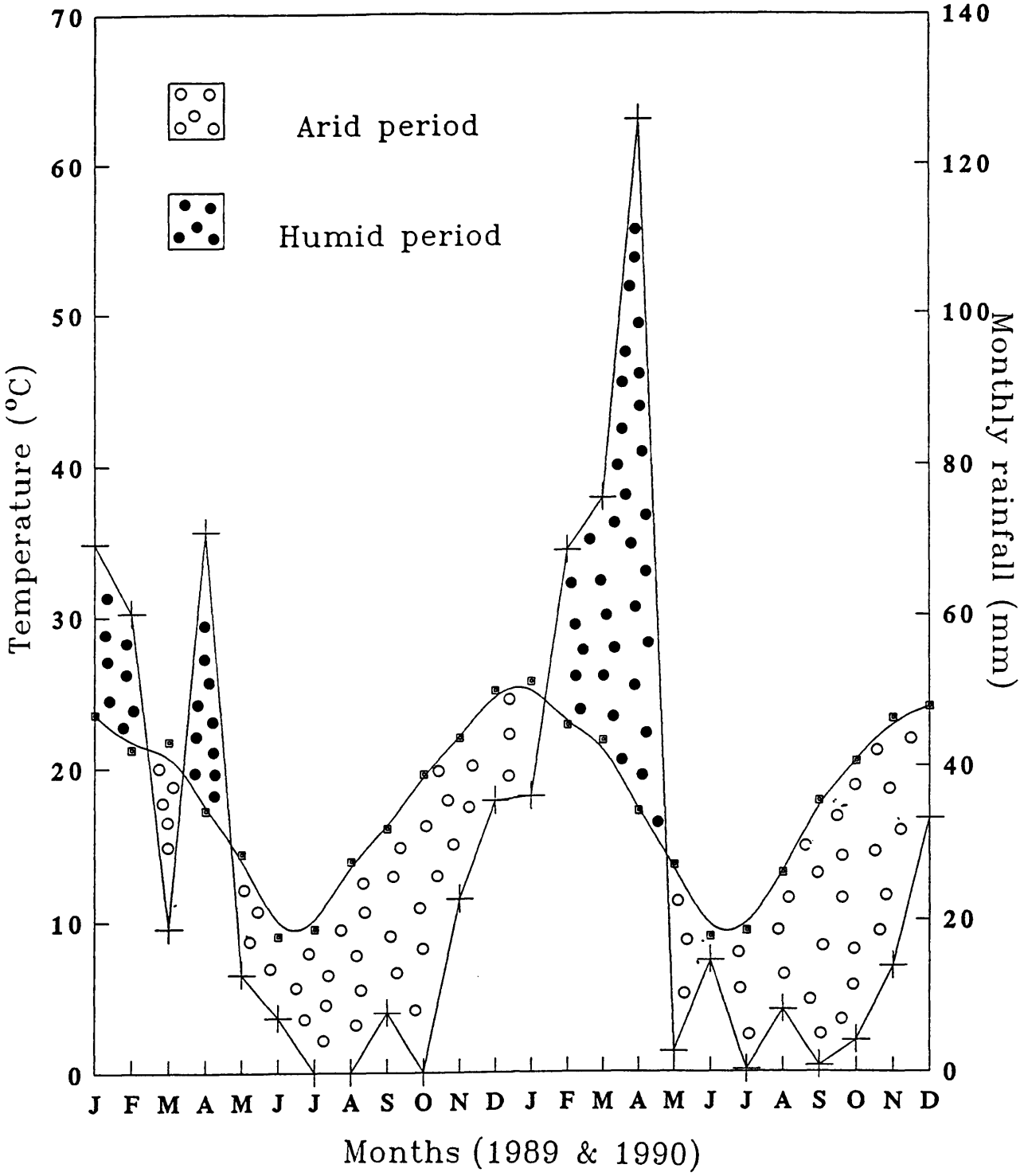


Figure 2.3 Climate diagram (Walther 1963) for Kimberley for the study period, January 1989 - December 1990.

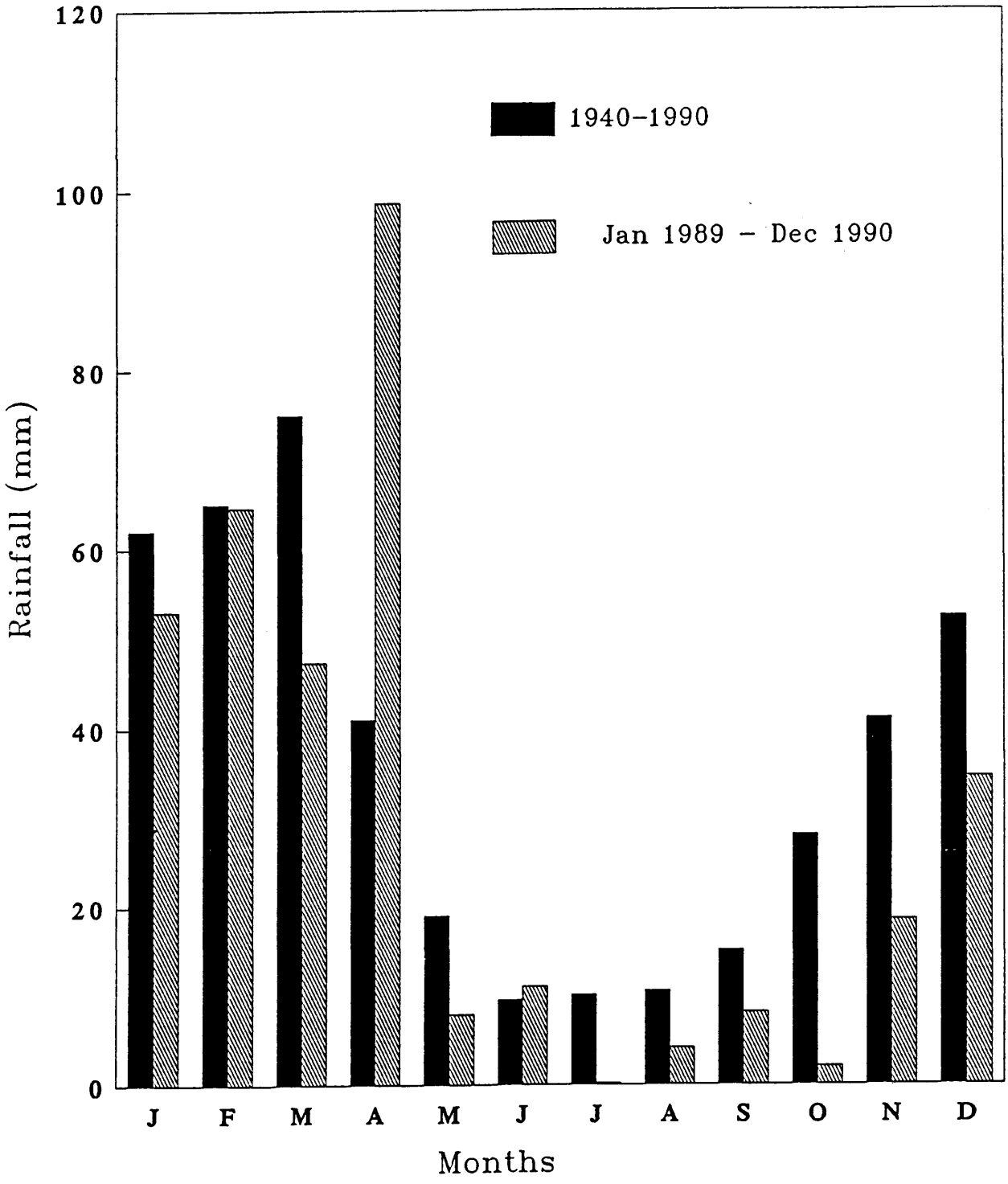


Figure 2.4 The mean monthly rainfall for Kimberley for the study period plotted against the mean monthly rainfall for the past 50 years (1940 - 1990).

January 1991) (Kimberley Weather Station, B.J. Vorster airport, Kimberley) compared to that for the last 50 years (Weather Bureau, Pretoria) is presented in Figure 2.4. The mean monthly rainfall recorded during the study period was generally lower than the long-term averages, except for exceptionally high rainfall recorded during April 1989 and April 1990.

(2) **Temperature** The mean minimum and maximum monthly temperatures for the study period (Kimberley Weather Station, B.J. Vorster Airport, Kimberley) are shown in Figure 2.5. The winters (May to August) are very cold and dry and the summers (October to March) are very hot. During winter there is usually very little cloud cover and the temperature at night often drops below freezing. During this period frost occurs relatively frequently.

Topography

Benfontein can be divided into five geographical regions. In the north-west is a large, closed depression or **pan** with a substrate consisting primarily of calcium carbonate (calcrete). A layer of calcrete also underlies all the soils surrounding the pan. Encircling the pan basin, and rising gradually in altitude, are the **pan slopes**. Further away from the pan the ground levels off and a belt of red **Kalahari sand** occurs to the south-east, which also has an underlying calcareous tufa. The sand gets increasingly deeper to the east and south, and trees (mainly *Acacia erioloba*) grow here. A few **dolerite koppies** occur along the southern and south-western boundaries of the farm, outside the limits of the study area. Two prominent **drainage lines** run down to the eastern sector of the pan. They are not deep but are rather shallow depressions, and their soils are periodically waterlogged.

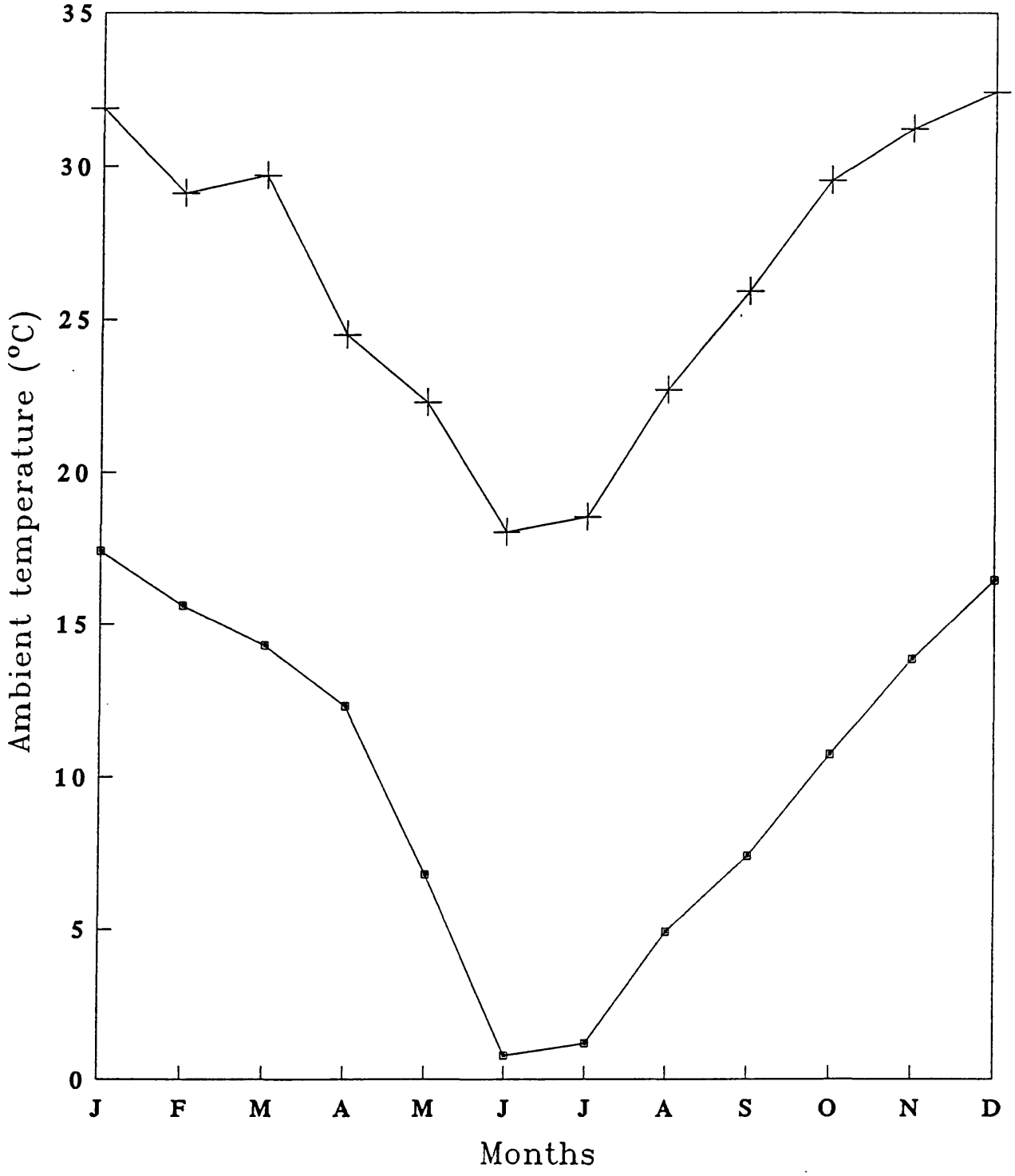


Figure 2.5 The mean maximum and minimum monthly temperatures for the duration of the study period (January 1989 - December 1990).

Water

Following good rains the pan (Figure 2.2c) fills with water creating a fertile, shallow wetland, occasionally with a length of up to 7 km. During the study period the pan was seldom dry. There is also a permanent spring in the north-east. During this study the aardwolves used the spring as a drinking point on a number of occasions. Following good rains, pools of water persist in the veld for a few days, and a small pan in the centre of the study area often holds water for up to 2-3 weeks following a thundershower.

Indigenous fauna

Between 1891 and 1970 Benfontein was run as a sheep/game farm (Richardson 1985). However, since the early seventies Benfontein has been run primarily as a game farm. A few thousand hectares in the southern part of the farm are, however, still used for domestic stock (cattle ranching).

A number of indigenous ungulates occur on Benfontein with springbok, *Antidorcas marsupialis*, being the most common (*ca* 4 000 individuals). Other ungulates occurring on Benfontein include blesbok, *Damaliscus dorcas phillipsi*, black wildebeest, *Connochaetus gnou*, steenbok, *Raphicerus campestris*, common duiker, *Sylvicapra grimmia*, and mountain reedbuck, *Redunca fulvorufula*.

There are no large carnivores on Benfontein but a number of smaller species occur in the area. These include the black-backed jackal, *Canis mesomelas* and the caracal *Felis caracal* (the aardwolf's only two potential predators on Benfontein), the bat-eared fox, *Otocyon megalotis*, Cape fox, *Vulpes chama*, small-spotted genet, *Genetta genetta*, and small-spotted cat, *Felis nigripes*.

Other potential predators of aardwolves in the study area and surrounding farmland include man (Anderson 1988) and two birds of prey, the martial eagle, *Polemaetus bellicosus*, and the giant eagle owl, *Bubo lacteus*.

Aardvark, *Orycteropus afer* (Melton 1976; Willis, Skinner & Robertson 1992), and bat-eared foxes (Nel 1978; Bothma, Nel & Macdonald 1984) are the two large mammalian species most likely to compete, to a very limited extent, with aardwolves for their food source. The springhare, *Pedetes capensis*, porcupine, *Hystrix africaeaustralis*, and aardvark are relevant to aardwolves in that they are avid diggers and their burrows are frequently used by aardwolves (Willis & Anderson 1990).

Vegetation

The vegetation of Benfontein consists of three major groups of communities namely pan communities, pan slope communities and sandveld communities (Figure 2.6). These are described in detail by Richardson (1985).

2.2 GENERAL METHODOLOGY

The field work for this study was conducted over a period of approximately two years, from December 1988 to January 1991. During this time I visited the study area on 305 occasions, amounting to over 1 800 hours of field work.

Observation of aardwolves

Aardwolves were followed in a vehicle from distances of 12-30 m. The first vehicle used was a 2x4 pick-up truck. This vehicle had the advantage of being extremely quiet, but the clearance was low and I sat fairly low above the ground making it difficult to observe aardwolves, particularly in long grass. In addition this vehicle was ineffective in driving out of aardvark holes.

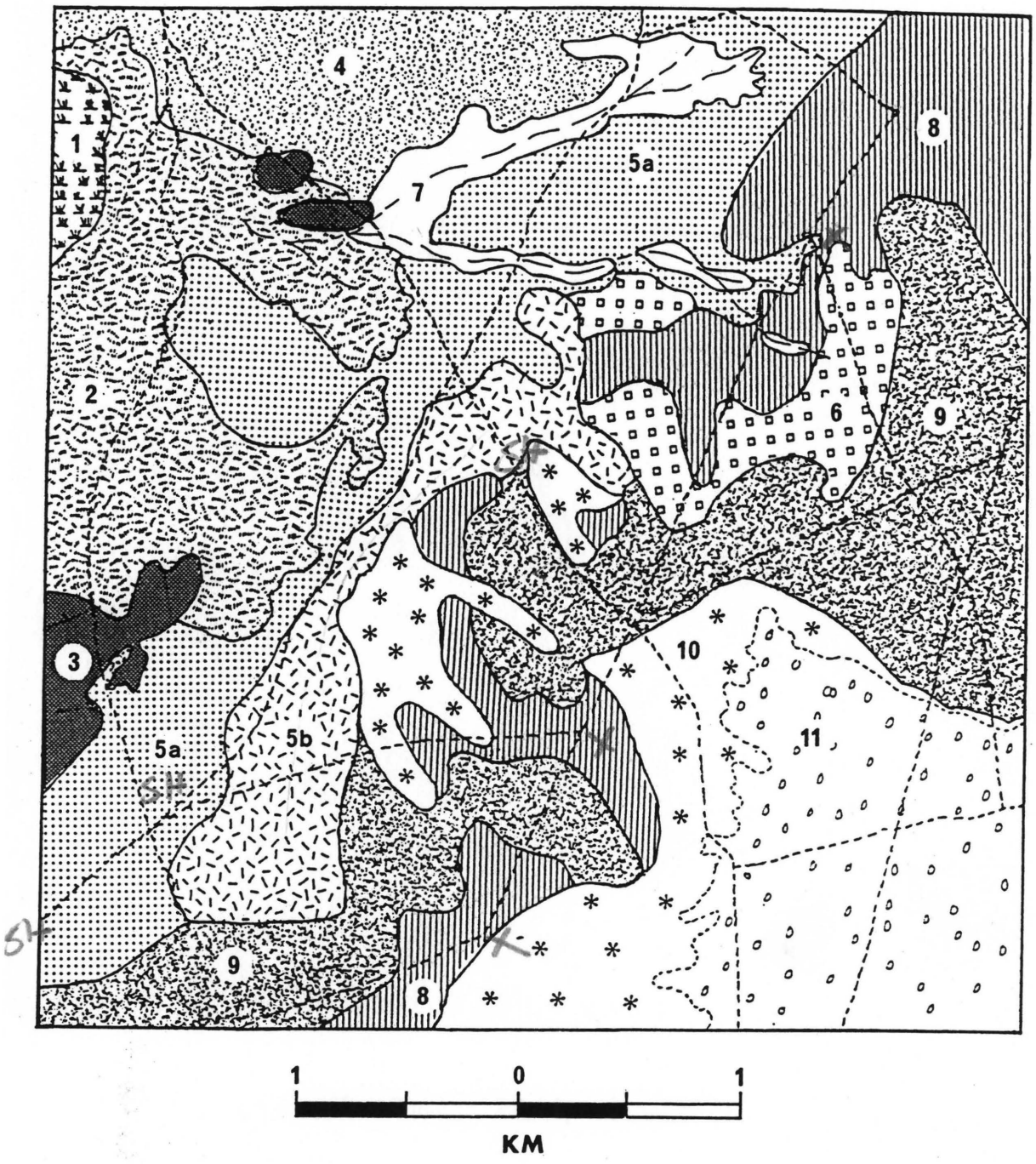


Figure 2.6 The study area illustrating the distribution of the major vegetation communities (adapted from Richardson (1985)).

Legend for Figure 2.6

1 - *Salsola exalata* - *Sueda fruticosa* community (pan floor)

2 - *Eragrostis bicolor* - *Lycidium horridum* community (pan border)

3 - *Psilocaulon articulatum* - *Lycium horridum* community (pan fringe or end of drainage lines)

4 - *Pentzia spinescens* - *Sporobolus ludwigii* community (pan slope)

5a - *Eragrostis truncata* - *Sporobolus ludwigii* subcommunity (higher pan slope)

5b - *Eragrostis lehmanniana* - *Pentzia calcarea* subcommunity (upper pan slope)

6 - *Enneapogon desvauxii* - *Tragus racemosus* community (upper pan slope, east)

7 - *Cymbopogon plurinoides* - *Panicum stapfianum* cmmunity (drainage lines)

8 - *Cymbopogon plurinoides* - *Aristida diffusa* community (north east corner)

9 - *Pentzia incana* - *Rosenia humilis* community

10 - *Stipagrostis uniplumis* - *Eragrostis lehmanniana* community (sandveld)

11 - *Acacia erioloba* - *Stipagrostis uniplumis* (sandveld community)

Later a 4x4 pick-up truck was used. This vehicle proved ideal. The vehicle had an excellent clearance and I sat fairly high thereby increasing the visibility in long grass. Aardwolves were followed with the vehicle in four-wheel drive and low range. Low range allowed the "revs" to remain fairly low without riding the clutch or creating too much noise and also reduced the chance of stalling. In addition, being in four-wheel drive, it was possible to drive out of an aardvark hole without unnecessarily disturbing and/or losing the study animal.

Observations were recorded on a Phillips pocket Dictaphone. This enabled detailed observations to be made while following the aardwolves. Aardwolves were observed with the aid of a pair of binoculars. Most of the aardwolves were accustomed to the presence of the vehicle and to the sound of a human voice. However, they were easily disturbed by the presence of a person standing outside the vehicle (particularly if standing in front of the spotlamp and head lights). To prevent unnecessary disturbance it was therefore necessary to switch off the headlights while climbing out of the vehicle in order to open a gate or recover a dart.

During winter, aardwolves were usually followed from the time they became active (15h00-17h00) until they retired to their dens (18h00-01h00). During summer aardwolves were followed from the time they became active (sunset and later) until an hour or two after midnight. On a number of occasions during summer aardwolves were followed for their entire active period in order to make more detailed behavioural observations. On other occasions, using radio telemetry, body temperature was determined at hourly (and/or half-hourly) intervals over 24 h periods.

During this study it was necessary to locate and immobilize aardwolves without radio-collars or internal radio-transmitters. These animals were located by parking the vehicle at a good vantage point and scanning the area through a pair of binoculars.

This was done during the late afternoon in winter and early evening in summer. At night aardwolves were searched for by driving along the roads, and through the veld, and then scanning the area with the aid of a handheld spotlamp. The spotlamp had a swivel mount and was attached to a roofrack directly above the driver's window. Attached to the lamp was an extended handle which I could hold while resting my arm on the window sill. The aardwolves were not disturbed by the light.

A detailed map (see Richardson 1985) with the position of the markers, fences and roads was used to record the movement of aardwolves. The position (distance and bearing) of aardwolves relative to these colour coded markers was determined when aardwolves changed direction or when there was a noticeable change in their behaviour.

Telemetry equipment used to locate aardwolves was a Yaesu FT29OR receiver (Yaesu Musen Co., Tokyo, Japan) and two 3-element Yagi type antennas mounted, facing forwards, but at 90^{o} to each other, to roof racks above the vehicle. A switch box inside the vehicle enabled the driver to switch from the one antennae to the other, and an equal signal strength from each side meant that the aardwolf was directly in front of, or behind, the vehicle.

Immobilization of aardwolves

During this study aardwolves were immobilized on 60 occasions using a combination of 12-20 mg/kg ketamine hydrochloride (Ketalar, Parke-Davis Laboratories (Pty) Ltd, Isando, RSA) and 0,15-0,40 mg/kg acetylpromazine (ACP, Centaur Labs (Pty) Ltd, Johannesburg, RSA) (Anderson & Richardson 1992). Immobilization of aardwolves was usually effective in inducing anaesthesia within five minutes. The aardwolves were darted from a vehicle during the late afternoon, or at night in the light of a spotlamp, when standing still while foraging or when lying down. Using a Telinject dartgun (Telinject SA, Randburg, RSA) aardwolves were darted from distances of 10,

12 or 15 m. The dartgun was calibrated using the minimum amount of pressure needed to dart at these three distances. All darts were marked with reflective tape to facilitate recovery at night (Richardson 1983; McKenzie 1989).

The aardwolves were immobilized for short periods (20-45 min) in order to fit radio collars, draw blood samples and earmark individuals; or for longer periods (up to 2,5 h) in order to implant temperature telemeters or to inject radio isotopes and draw equilibration blood samples.

During the latter part of the study 16 aardwolves were injected with intramuscular doses of 0,10-0,15 mg/kg diazepam (Valium, Roche Products (Pty) Ltd., Isando, RSA) in order to reduce the trauma of darting and in an attempt to reduce the shyness of aardwolves the night after immobilization (Anderson & Richardson 1992). This drug proved effective in reducing post-capture shyness and aardwolves which were not fully habituated could be approached to within 20 m, within two hours, the night after immobilization. Aardwolves not injected with diazepam would have to be followed for at least six hours (and occasionally for a few nights) to be approached this close.

The immobilization procedure, success of various darting methods, response of aardwolves to immobilization and adverse effects encountered in this and a previous study (Richardson 1985), are described in detail in Anderson & Richardson (1992), Richardson & Anderson (1993a,b).

Marking and recognition of aardwolves

Aardwolves were recognized on the basis of (1) their body stripe patterns, (2) their radio-transmitter frequencies, (3) reflective tape colour on the radio-collars, (4) natural ear cuts and nicks and (4) man-made ear markings.

To facilitate later recognition, all aardwolves darted for the first time were earmarked. This was achieved by cutting a small V (or two small Vs) from the aardwolf's ear(s) using a sterile scalpel blade. The wounds were treated (Kemi Spray, C.E. Industries (Pty) Ltd., Kempton Park, RSA) and the animals were injected intramuscularly with a wide spectrum antibiotic (Combimycin, C.E. Industries (Pty) Ltd., Kempton Park, RSA).

Age classification of aardwolves

Richardson (1985) distinguished five broad aardwolf age classes, on the basis of growth and subsequent damage to the canines. Aardwolves have reduced molars and pre-molars and it is therefore not possible to determine their age on the basis of tooth eruption and wear, as is done for other carnivores (e.g., Kruuk 1972; Mills 1981; Lindeque & Skinner 1984). For the purpose of this study only three very broad age-classes were differentiated; namely cubs (<1 year old), sub-adults (1-2 years old) and adults (>2 years old).

Each time an aardwolf was darted and immobilized the body mass was recorded using a 10 kg spring balance (Pesola, Switzerland) or a 25 kg scale (Salter model 235, RSA). The length of all four canines was determined using a pair of calipers. Canine length was measured as the maximum distance from the tip of the tooth to the gum on the lateral side of the tooth.

Mapping of study area

Richardson (1985) used 420 metal stakes to mark middens, dens and prominent landmarks at Benfontein. These 1 m long metal stakes were marked with self-adhesive reflective tape (red, yellow, white and green) which was visible from distances in excess of 200 m at night when shined at with a spotlamp. The stakes were driven into termite mounds which prevented them from being knocked over by black

wildebeest and other animals. In addition all gates and some poles along the length of the fence-lines were marked. Details of the metal stakes, colour coding system and the eventual plotting of the markers is described in detail by Richardson (1985). During this study the reflective tape on the majority of the markers was replaced, and an additional 120 markers were placed in the study area.

Meteorological information

Meteorological information (maximum and minimum temperatures, rainfall, windspeed and relative humidity) was provided by the Kimberley Weather Office at the B.J. Vorster airport, which is approximately 5 km west of Benfontein. Additional temperature measurements were recorded in the field. A maximum-minimum thermometer was mounted behind the window on the back of the vehicle and ambient temperatures (T_as) were recorded. During the latter part of the study a KM 1202 multi-channel temperature recorder (Kane May, Welwyn Garden City) was used to record T_as in the field. One thermistor was attached to a metal stake at a height of 1 m above the ground and shielded from direct sunlight by means of a piece of aluminium foil. Another thermistor was placed on the soil surface and covered with a thin layer of soil. Measurements were taken at hourly intervals.

CHAPTER 3. A FUNCTIONAL ANALYSIS OF THE FEEDING APPARATUS AND DIGESTIVE TRACT ANATOMY OF THE AARDWOLF

Abstract

The aardwolf is unique amongst the myrmecophagous mammals in that it feeds almost exclusively on one genus of termite, *Trinervitermes*, yet it possesses none of the obvious external physical features (elongated snout, powerful limbs and claws) characteristic of this feeding style. Externally it looks simply like a diminutive hyaena. Behaviourally the aardwolf differs from the other typical "anteaters", in that it does not dig for its prey, but licks them off the soil surface. Nevertheless, the aardwolf does have a number of anatomical features which are clearly adaptations to this diet. The most obvious of these are a broad spatulate tongue covered with large, hardened papillae, a broad palate, large mandibular salivary glands, and a muscular pyloric region in the stomach. Some of these features associated with feeding and digestion are compared with those of the domestic dog *Canis familiaris*, the bat-eared fox *Otocyon megalotis* and the black-backed jackal *Canis mesomelas*.

INTRODUCTION

Griffiths (1968) summarized the morphological traits that he considered characteristic of specialized myrmecophagous mammals as the following: (1) extensile vermiform tongues with large salivary glands to lubricate them; (2) long snouts and jaws with highly modified or reduced teeth; (3) anomalous stomachs; and (4) forelimbs adapted for digging. Although the aardwolf does possess some of these features, it is nevertheless very different in body structure from the typical long-snouted and powerfully-limbed myrmecophages, looking more like a slender, diminutive hyaena (Koehler & Richardson 1990). The basic anatomy of the aardwolf has been described by Flower (1869), Pocock (1916) and Wells (1968). This chapter describes the macro-anatomical features of the aardwolf's food-

acquisition and digestive system, paying particular attention to those features which differ from the basic carnivore pattern, and which may be related to its specialization on a diet of termites.

MATERIALS AND METHODS

Anatomical data were obtained from seven fresh, road-killed, adult aardwolves. These specimens were found in the northern Cape Province and in the western Transvaal, South Africa. They were deep-frozen within a few hours of being found. The aardwolves were later sexed, weighed and the complete gastrointestinal tracts removed. Measurements were made of the lengths of the small and large intestines. One of the aardwolves was perfused with 10% formalin prior to dissection. The jaw musculature and salivary glands of three of the aardwolves were removed and weighed separately. Anatomical terminology follows Evans & Christensen (1979).

Measurements of the small intestine and colon of nine adult domestic dogs *Canis familiaris*, weighing between 6-11 kg (i.e. of similar size to the aardwolf), were collected during a student anatomy practical for comparison with the aardwolf. Museum specimens were used in order to determine various cranial measurements, and hence to compare the palate of the aardwolf with an insectivorous (bat-eared fox, *Otocyon megalotis*) and an omnivorous (black-backed jackal, *Canis mesomelas*) African carnivore. The following cranial measurements were taken: (1) skull base - the minimum distance along the midventral line between the basion and the prosthion; (2) skull width (zygomatic breath) - greatest distance between the outer margins of the zygomatic arches; (3) palatal length - from the anterior edge of the maxillae to the anteriormost point on the posterior edge of the palate; (4) inter-canine width - minimum distance between the base of the canines; (5) inter-molar I width - minimum distance between the base of these molars.

Data where more than one sample were utilized are presented as means with standard deviations. For the comparison of two samples the Students t-test (Snedecor & Cochran 1967) was employed. Analysis of covariance (Snedecor & Cohran 1967) was used to compare the cranial measurements of the three carnivores studied. The minimum accepted level of significance was $p < 0,05$.

RESULTS

Tongue

The aardwolf tongue has a long and spatulate shape (length 117-121 mm, maximum breadth 30-32 mm, n=2; Figure 3.1) with typically large and varied papillae present. There are two types of conical papillae. Typical conical papillae are found on the anterior tip, while posterior to them are larger "incisiform" papillae. This appears to be the first record of such papillae on a mammalian tongue. Both types are noticeably large and hardened. In contrast, posterior to these conical papillae, there are numerous filiform papillae which are thin and posteriorly directed. The remaining papillae include fungiform, two lateral foliate (each with five slits) and two circumvallate.

Salivary glands

The mass of the mandibular salivary gland is approximately 15 times greater than the parotid, sublingual and zygomatic glands which are all approximately equal in size (Table 3.1). These masses should not be viewed as absolute values as the aardwolves were in varying stages of dehydration when dissected. Histological sections were prepared from these glands but poor fixation prevented reliable identification of their structure. The mandibular glands appeared to be mucous secreting and the others serous or mixed.

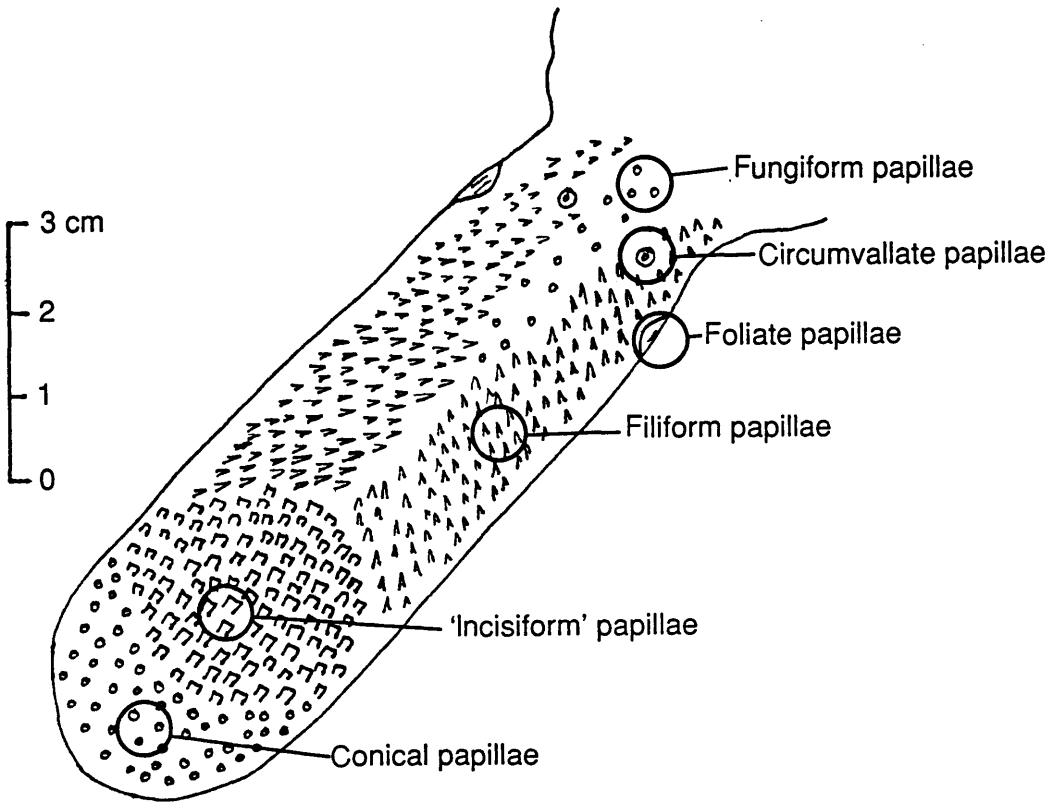


Figure 3.1 The aardwolf has a long and spatulate tongue with a variety of papillae.

Table 3.1 Salivary glands and jaw musculature masses (g) of the aardwolf (±SD; n=3), and the domestic dog (dog salivary glands after Evans & Christensen (1979); dog jaw musculature after Turnbull (1970))

	Aardwolf	Domestic dog
Salivary glands		
Parotid	0,89±0,27	7
Mandibular	14,81±1,63	8
Sublingual	0,58±0,09	1
Zygomatic	0,57±0,08	3
Jaw musculature		
Masseter	5,68±0,78	23-27
Temporal	15,25±1,19	64-67
Pterygoid	2,51±0,72	9-10
Digastric	4,28±0,56	9,5-10,8

Masticatory muscles

The temporal muscle is the largest of the masticatory muscles (Table 3.1) followed by the masseter and the pterygoids. The general location and origins and insertions of the masticatory muscles are similar to those in the domestic dog (Evans & Christensen 1979).

Skull

The most notable features of the aardwolf skull (Figure 3.2) are: (1) the widely spaced and very small peg-like cheek teeth; (2) the contrastingly large canines; and (3) the broad and parallel-sided palate. The anterior regions of the maxillae are bowed out, apparently to accommodate the licking movements of the broad tongue. When the aardwolf's jaw is closed with incisors occluding, the cheek teeth of the upper and lower jaws do not touch. Other features of the skull are the well developed postorbital processes and the extra-ordinarily large tympanic bulla. The permanent dentition generally falls within the formula: i 3/3, c 1/1, p and m 3-4/2-4 (Koehler & Richardson 1990).

Various cranial dimensions of the aardwolf, bat-eared fox and black-backed jackal are compared in Figure 3.3. The aardwolf has significantly larger inter-canine and inter-molar I widths, and thus a broader palate, than the bat-eared fox (ANCOVAR; $F=192,22$; $p<0,001$) and the black-backed jackal (ANCOVAR; $F=201,10$; $p<0,001$). The lengths of the cranial bases of these three species are very different, largely due to their differences in body size. Although the jackal is only slightly smaller than the aardwolf (Smithers 1983; Koehler & Richardson 1990) it has a longer skull. The width of the aardwolf's cranium is nevertheless significantly wider than that of the black-backed jackal (ANCOVAR; $F=4,78$; $p<0,05$), and the bat-eared fox (ANCOVAR; $F=6,91$; $p<0,05$). No significant differences in palate lengths of these three species (ANCOVAR; $F=0,13$, 0,18, 0,75; $p>0,05$) were evident. The aardwolf's palate has deep posteriorly directed transverse ridges, similar to those of the domestic dog.

Digestive tract

The gastrointestinal tract of the aardwolf follows the typical carnivore pattern, and consists of a stomach, small intestine, caecum and colon (Figure 3.4). The stomach

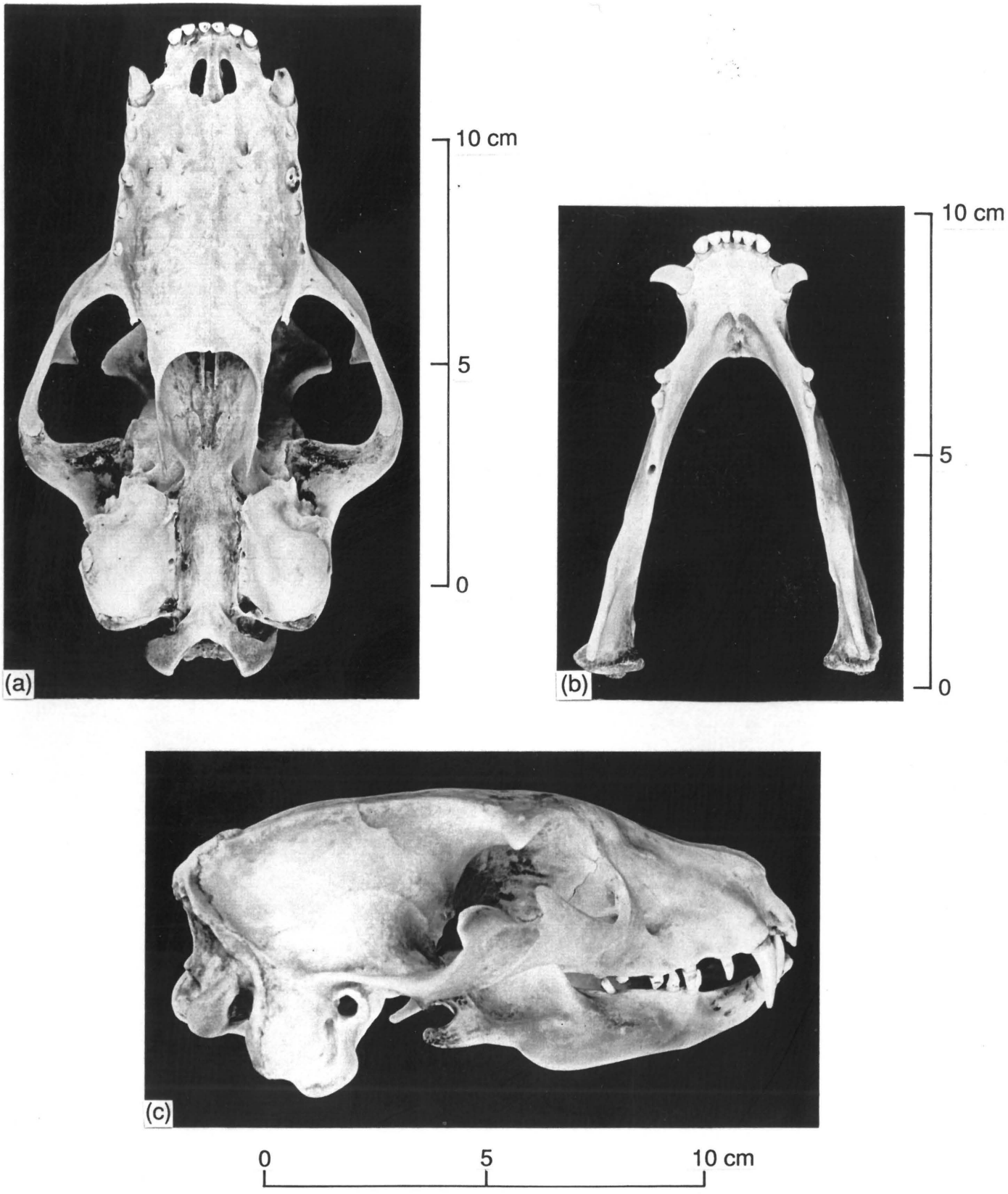


Figure 3.2 Aardwolf skull: (a) ventral view of cranium, (b) dorsal view of maxillae, and (c) lateral view of the skull.

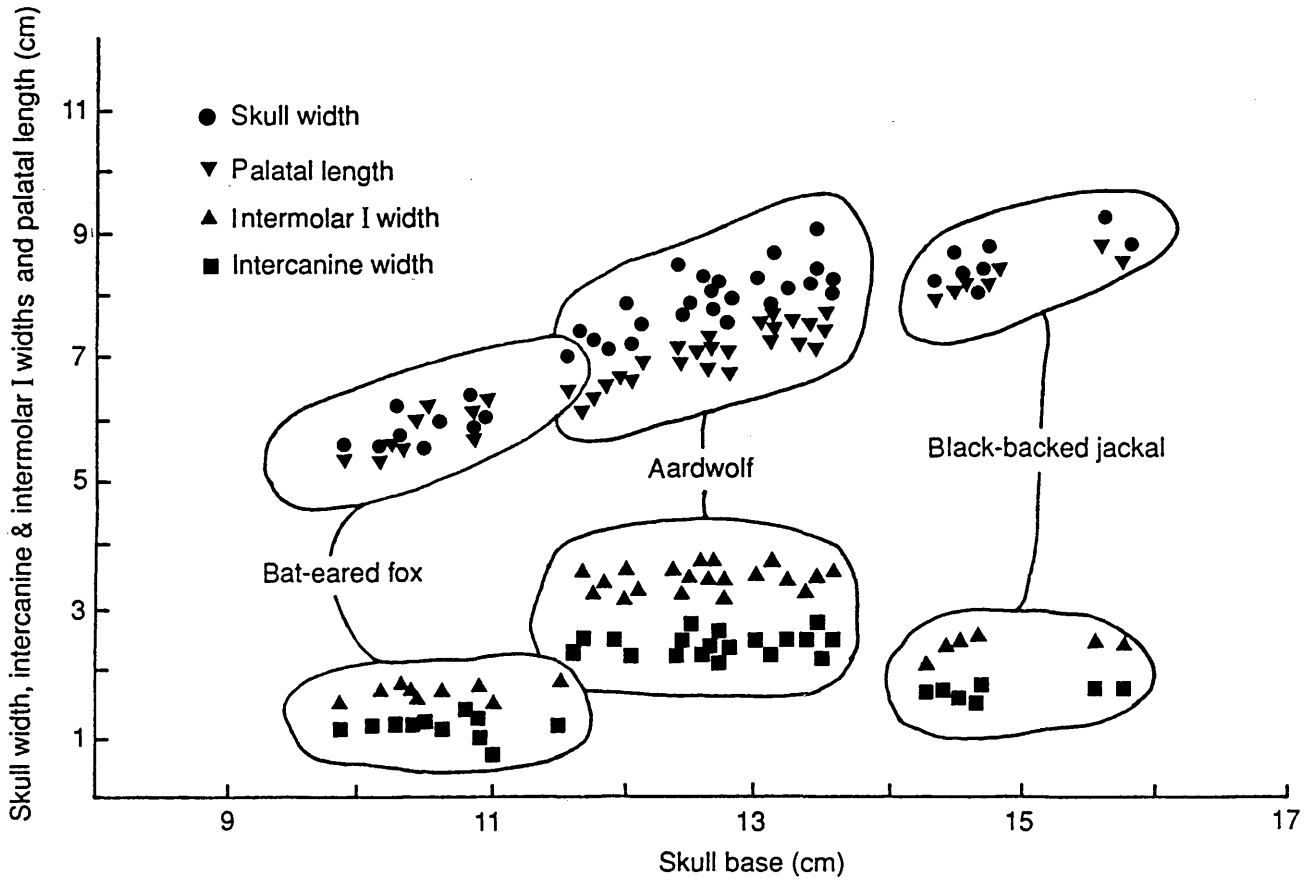


Figure 3.3 Comparison of aardwolf (*Proteles cristatus*), bat-eared fox (*Otocyon megalotis*) and black-backed jackal (*Canis mesomelas*) skull-dimensions.

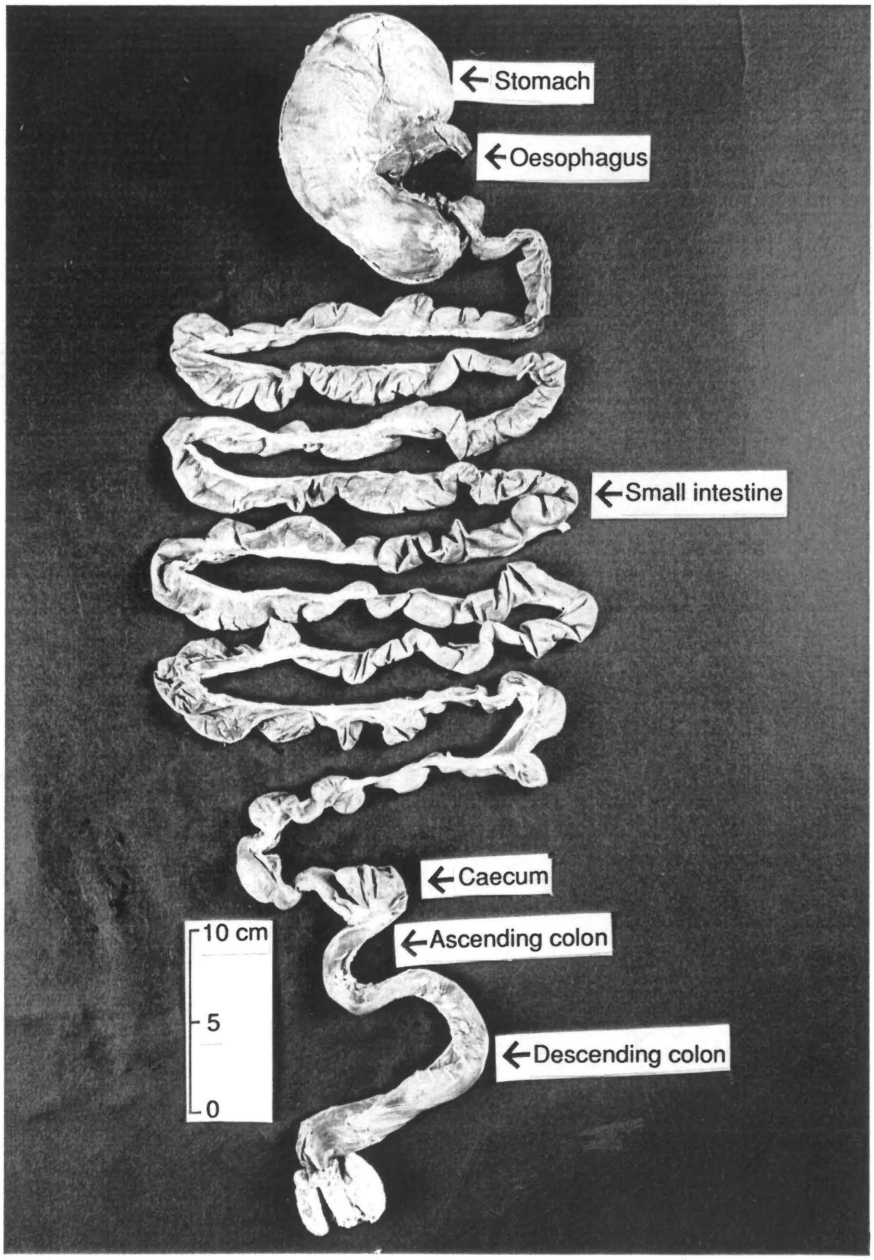


Figure 3.4 The aardwolf gastrointestinal tract.

(Figure 3.5) is simple, elongated, and divided by a constriction into two regions, namely the large fundic region into which the oesophagus opens and the relatively smaller pyloric region. Based on the mucosal surface, the fundic region can be sub-divided in two areas: (1) a smooth-walled cardiac region; and (2) a fundic portion with numerous folds (rugae) of the gastric mucosa. The smooth-walled pyloric region has a few irregular folds, while the walls are thick and muscular.

The small intestine is long (mean length 262±34,4 cm, n=7), while the large intestine (colon) is simple and smooth walled, and has a mean length of 45,3±11,7 cm (n=7) (Table 3.2). The descending (distal) colon is characterized by thick walls with distinct longitudinal bands. The length of the aardwolf large intestine does not differ significantly from that of the domestic dog (t=0,37; d.f.=14; p>0,5). However, the aardwolf small intestine is significantly shorter than that of the domestic dog (t=3,64; d.f.=14; p<0,005). There were no significant differences (t=0,87; d.f.=14; p>0,3) between the body masses of the aardwolves (7,84±1,40 kg) and dogs (8,56±1,67 kg) used in this study. The aardwolf caecum is relatively small in comparison with the Hyaenidae (Flower 1869).

Table 3.2 Intestinal lengths and areas, and body masses, of the seven road-killed adult aardwolves used in this study

Aardwolf no.	1	2	3	4	5	6	7	mean ± S.D.
Sex	F	F	F	F	M	F	F	
Body mass (kg)	8·6	6·8	7·4	6·8	5·8	9·5	10·0	7·8 ± 1·4
Small intestine length (cm)	266	214	209	281	276	309	282	262 ± 34·4
Colon length (cm)	39	31	35	48	41	67	56	45·3 ± 11·7
Small intestine area (cm^2)	931	824	536	—	—	—	—	764 ± 166·8
Large intestine area (cm^2)	153	120	152	—	—	—	—	142 ± 15·3

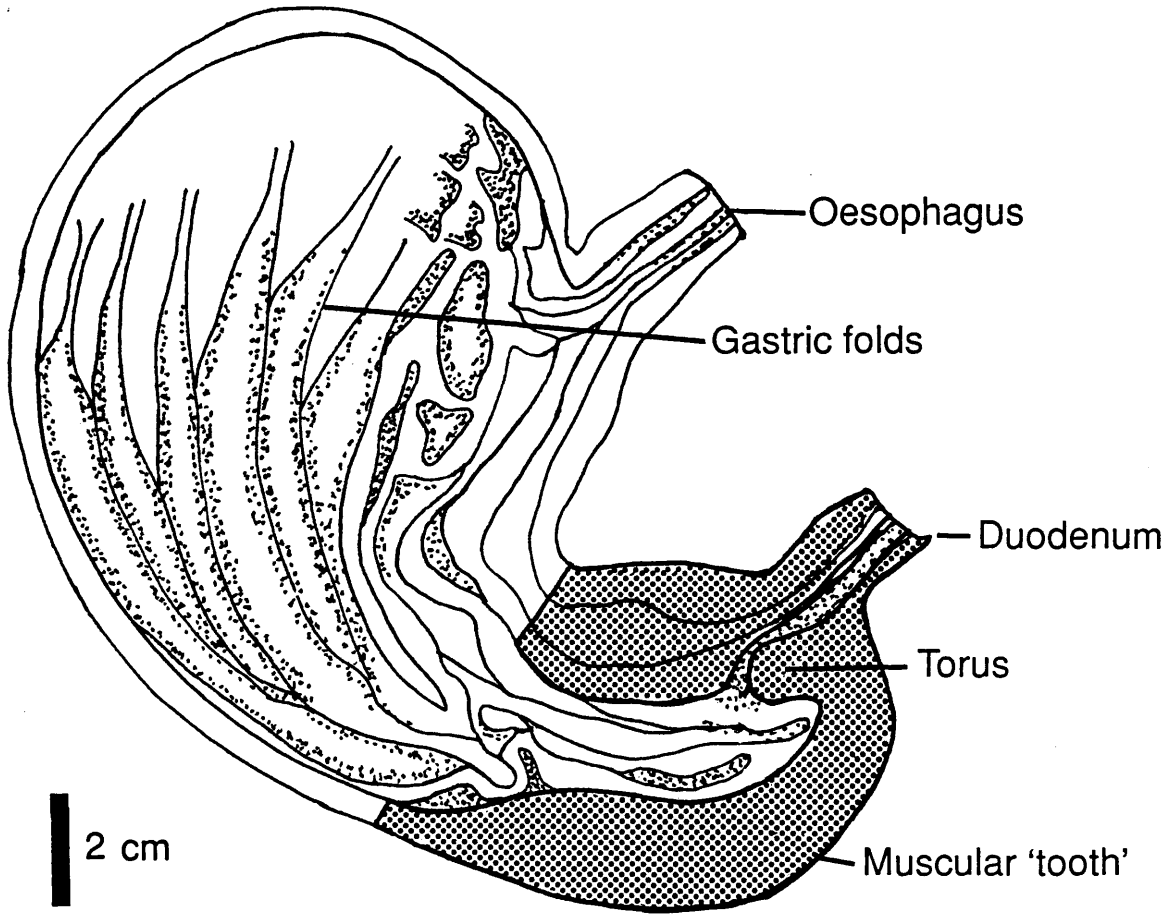


Figure 3.5 The aardwolf stomach indicating the thick pyloric region termed the muscular tooth.

DISCUSSION

Richardson (1987b) has suggested that the aardwolf is possibly the most specialized of all the myrmecophagous mammals, because not only does it feed almost exclusively on termites, but primarily on one genus, *Trinervitermes*. He argued that this specialization was possible, not because the aardwolf outcompeted other myrmecophages like the aardvark *Orycteropus afer* and the pangolins *Manis* spp, but because it feeds in a completely different manner. It licks up surface-foraging termites, as opposed to exposing them by digging and then licking them out of their subterranean nests and tunnels. Thus the aardwolf, having civet-like viverrid ancestors (Ewer 1973; Savage 1978), did not require any major morphological adaptations in order to start feeding on these termites. Concomitantly, a significant pre-adaptation was the ability to tolerate the terpene secretions of *Trinervitermes* soldiers (Richardson 1987b). Thus the ancestral aardwolf, as an omnivorous carnivore, was largely pre-adapted to feeding on surface foraging termites. The modern aardwolf is still a typical looking carnivore, but now possesses certain adaptations which enable it to be very much more efficient at feeding on these termites.

Possibly the most modified anatomical structure in the aardwolf is its tongue. The conical papillae at the front of the tongue are large and hardened. Their distribution is quite different from that in the dog, where the large conical papillae are restricted to the base of the tongue, but is more like the situation in felids where conical papillae are also found rostrally and provide a rasping surface. The "incisiform" papillae, an enlarged form of conical papillae, seem to be unique to the aardwolf. These papillae probably serve the function of protecting the tongue against abrasion by sand.

A remarkable feature of the published records of aardwolf stomach and faecal contents is the variability in the amount of sand they contain (Cooper & Skinner

1979; Bothma & Nel 1980). Richardson (1985) observed that when termites are readily available very little sand is ingested. Aardwolves feed by skimming their tongues just above the soil surface, thereby leaving many termites behind but ingesting little sand and other debris (Kruuk & Sands 1972). In contrast, volumes of faecal content of up to 50% sand have been recorded (Cooper & Skinner 1979). These appear to be from sandy areas and primarily during winter when termite foraging columns are seldom available and less concentrated (Richardson 1987a), so the aardwolf probably licks many more times per 1 000 termites ingested.

The aardwolf's wide, parallel-sided palate clearly accommodates the rapid licking movements of its broad tongue, facilitating the rapid ingestion of thousands of termites. Analysis of film has shown that the aardwolf licks at a rate of approximately five times per second (Richardson pers. comm.). The very broad palate with deep posteriorly directed transverse ridges presumably acts as a catchment area for termites as the tongue is again extruded. The numerous filiform papillae covering the posterior region of the tongue may then feed the termites back down the gullet as the next tongue-load of termites is ingested. The aardwolf has a much broader palate than the bat-eared fox and black-backed jackal, two opportunistic termite-eaters. These two species, however, do not feed on *Trinervitermes* spp. They are both known to feed on the common-harvester termite *Hodotermes mossambicus* when this species is available (Nel 1978; Smithers 1983), but also feed extensively on other insects and small vertebrates and, in the case of the jackal, on vegetable matter and carrion (Smithers 1983; Bothma, Nel & Macdonald 1984). Meller's mongoose, *Rhynchogale melleri*, another small carnivore which subsists primarily on a diet of termites (mainly *Hodotermes* spp. and *Macrotermes* spp.) also has a broad palate and bowed out jaw, although these characters are not as well developed as in the aardwolf (Smithers 1983).

Evans & Christensen (1979) do not give the body masses of the dogs they studied (Table 3.1), so a comparison with the aardwolf of the absolute masses of the salivary

glands is not feasible. However, if one assumes that an "average" dog weighs 20 kg then, relatively speaking, the mandibular is much larger in the aardwolf than in the dog. The mandibular and parotid glands in the dog are roughly equivalent in size. In carnivores (dogs and cats) the parotid produces largely a serous secretion and the mandibular mainly a mucous secretion. This also appears to be true in the aardwolf. Therefore, the aardwolf should produce much greater volumes of mucous than serous secretions. These mucous secretions should, therefore, provide a relatively thick and sticky substrate and facilitate the licking up of termites. In addition, the mucous could provide protection for the oral cavity and oesophagus from the termites' terpene secretions. The saliva may also play a role in the detoxification of *Trinervitermes* terpene secretions. Tannin-binding proteins have been found in the saliva of rats and browsing ruminants, and it has been suggested that these may reduce the absorption of tannins included in their diets and also reduce their toxicity (Menansho, Hagerman, Clements, Butler, Rogler & Carlson 1983; Austin, Suchar, Robbins & Hagerman 1989). Like the aardwolf, browsing ruminants typically have large salivary glands (Kay 1987).

Although tannins are very different from terpenes, a similar function has been proposed for certain glandular secretions in myrmecophagous elephant shrews. Kratzing & Woodall (1988) found dorsal and ventral subdermal tubular glands in *Elephantulus* spp. which extended the length of the snout but released their secretions, together with products of the nasolacrimal and lateral nasal gland ducts, at the tip of the snout. They speculated that these secretions may protect the bare rostral epithelium from the chemical defences of ants and termites. Similarly, it is possible that aardwolf saliva contains proteins which may either neutralize or detoxify terpenes.

A more obvious adaptation against these termites' defence secretions is the aardwolf's large and hairless muzzle. Kruuk & Sands (1972) have suggested that the

smooth and leathery muzzle prevents the soldier termites' defensive secretions, and hence dirt, from adhering to the same extent as they would if the muzzle was haired.

The aardwolf's diet almost certainly explains the degeneration of its cheek teeth. Kruuk & Sands (1972) have argued that the large quantities of grit and sand ingested together with termites make molariform teeth unnecessary and even disadvantageous, and consequently these teeth are greatly reduced. As *Trinervitermes* termites are small and soft bodied, chewing is unnecessary and mastication of termites is performed by a muscular region in the stomach. If an aardwolf were to attempt to chew termites, it would obviously reduce the speed with which they could be licked up and hence reduce the total number ingested. However, possibly the most important factor leading to the degeneration of the aardwolf's cheek teeth, is the reduction of terpene release. By chewing, either purposefully or incidentally while swallowing, an aardwolf would squash the soldier termites' head capsules and release all the terpenes contained therein. By not opening these capsules, an aardwolf needs to contend only with terpenes that are actively squirted.

The aardwolf does, however, still possess well developed canines and relatively well developed jaw masticatory musculature and attachment for these muscles (Ewer 1973). The canines are certainly used in territorial disputes against other aardwolves, and in defence against jackals (Richardson 1985, 1991a,b). An interesting aspect of the aardwolf's musculature is the relatively large digastric muscle, compared to that of the domestic dog (Turnbull 1970). As this muscle is used for opening the jaw, its enlarged size may be explained by the aardwolf's need to open its mouth rapidly and frequently while feeding. The relatively well developed incisors are almost certainly used for grooming.

The muscular region of the pyloric area (or "muscular tooth") of the stomach probably compensates for the lack of cheek teeth for the mastication of termites.

This process may be aided by sand and grit ingested with the termites. A similar structure is found in the stomach of anteaters *Tamandua* spp. and pangolins (Chivers & Hladik 1980), which live exclusively on ants and termites (Kingdon 1971; Best & Harada 1985; Redford 1985, 1987).

Aardwolves may consume up to 300 000 termites (approximately 1,2 kg) per night (Richardson 1985, 1987a). The handling of this volume of food as well as the faeces produced may pose certain problems. Aardwolves usually retire to their dens before daylight and then spend most of the day underground, and only emerge from their burrows that evening. Soon after emergence aardwolves walk to a nearby midden and defecate. The first defecation of the evening is typically very large, weighing up to 1 kg (approximately 10% of the mass of the animal) (Kruuk & Sands 1972; Richardson 1987a). The distensibility of the distal colon may thus be of great importance by allowing the accumulation of this large volume of faeces over a period of up to 18 hours since the last defecation. As aardwolves obtain most of their water from termites and thus very rarely drink (Richardson 1985), the distal colon may also play an important role in the absorption of water.

The aardwolf has a shorter small intestine than the domestic dog. The reason for this is uncertain as animals with easily digested food usually have short intestines, particularly the small intestines. Although the chitinous head capsules of soldiers and workers are not easily digested and remain clearly visible in aardwolf faeces, the workers' bodies are relatively soft and may be easily digested. Aardwolf digestion may therefore be geared more towards processing large volumes and the rapid digestion of the workers' abdomens, as opposed to the more efficient digestion of whole termites. The badger *Meles meles* which feeds on soft-bodied earthworms has a longer small intestine than the aardwolf (Stark, Roper, MacLarnon & Chivers 1987). The function of the aardwolf's caecum is uncertain. It is similar in size to that of the domestic dog. In most carnivores the caecum plays a

small role in the absorption of water and electrolytes (Madge 1975). It may play a similar role in the aardwolf.

Although the aardwolf superficially resembles a typical small carnivore, it has evolved a number of highly specialized features which enable it to feed almost exclusively on surface foraging termites. As these termites require a totally different means of acquisition from those which are located and eaten in tunnels below the soil surface, the aardwolf's external anatomy is very different from that of typical "anteaters", although it does possess some common features associated with the digestion of ants and termites.

CHAPTER 4. THE NUTRITIONAL QUALITY OF THE SNOUTED-HARVESTER TERMITE, WITH EMPHASIS ON ITS UTILIZATION BY THE AARDWOLF

Abstract

The water content, percentage protein, fat, fibre, and ash, and calorific value were determined throughout the year for two castes of *Trinervitermes trinervoides*. Soldier and worker termites were also analyzed for various minerals (P, Ca, Mg, K, Na and Fe) for samples collected during mid-summer and mid-winter. The nutritional quality of *T. trinervoides* was low and in accordance with the values determined for other termite species. Fat content was significantly greater during the winter months. There were significant differences between the two castes for all the parameters tested except for calorific value, Ca, Mg and Fe. The aardwolf feeds on a food source which is nutritionally poor and this may partially account for its low basal metabolic rate.

INTRODUCTION

Termites are eaten by a wide variety of African mammals, ranging in size from tiny elephant shrews (e.g. *Macroscelides proboscideus*, mass 30-50 g) (Smithers 1983) to 60 kg aardvarks, *Orycteropus afer* (Melton 1976). Despite the importance of termites as a food source for myrmecophagous mammals, little information is available on their nutritional quality (Redford & Dorea 1984).

Studies conducted thus far (e.g., Phelps, Struthers & Moho 1975; Redford & Dorea 1984) have indicated that adult termite castes have a low nutritional quality, while larvae and alates are generally high in fat content. Alates are fed on opportunistically by many mammals, while the nutritionally poor adult castes are fed on by more specialized insectivores. This indicates that insectivorous mammals rely on factors other than nutritional quality in determining what prey to consume. A good example is the aardwolf, where Richardson (1987b) has argued that it was largely as a result of the aardwolf's pre-adaptation to tolerate the

termites' defensive secretions that it was able to invade this trophic niche, which was almost entirely devoid of competitors.

McNab (1984, 1986) has shown that there is a correlation between the low metabolic rates of myrmecophagous mammals and their diet of ants and termites. Moreover, he has attributed the seasonal availability of this food source to this trend. The question thus arises whether it is food quality or just the seasonal absence of this food source that affects the aardwolf's metabolism. The aims of this chapter of the study are, therefore:

(1) to determine whether *T. trinervoides* has a low nutritional quality which may thus have a bearing on the aardwolf's low metabolic rate (McNab 1984); and

(2) to determine whether the nutritional quality of *T. trinervoides* varies seasonally which may implicate further nutritional stresses on the aardwolf.

MATERIALS AND METHODS

T. trinervoides were collected monthly for one year (May 1989 - April 1990) on Benfontein. Each month at least three termitaria were collected from the study area by undercutting them with a spade. The termitaria were then broken into smaller pieces by hand. Individual termites were collected with an aspirator, shaken onto a sheet of paper (Richardson 1985), or hand- or tweezer-picked from the mound, nest and grass material. Because there are distinct morphological differences between castes in a termite colony, the soldier and worker castes were separated. No distinction was however made between major and minor soldiers. Approximately 5-10 g of each caste was collected. The termites were cleaned of any sand or grass particles and placed in tightly sealed glass containers, which were frozen at approximately -10^{o}C, within 4 h of collection.

To determine the moisture content of *T. trinervoides*, two 5 g samples of live soldiers and workers were collected monthly and weighed. These samples were oven-dried to constant weight (for approximately 48 h) at 70-80^{o}C, re-weighed, and their moisture content determined.

For the nutritional quality valuations the fat content, calorific value, crude protein, crude fibre and ash content of *T. trinervoides* were determined at the University of Pretoria. Because of the large samples required for these tests and the difficulty in collecting sufficient material, samples collected for two consecutive months (e.g. January and February) were combined for the above analyses. Fat extraction was by petroleum ether distillation using the Soxhelt technique (Allen, Grimshaw, Parkinson & Quarmby 1974; Sawicka-Kapusta 1975). Calorific composition was determined in a bomb-calorimeter (CP400 Mini-Calorimeter: Digital Data Systems, Johannesburg). Nitrogen content of samples was determined by the Kjeldahl method (A.O.A.C. 1975). Crude protein was estimated by multiplying the nitrogen value by 6,25. Crude fibre content of all samples was determined by the methods described by Goering & van Soest (1970). Ash content was measured after incineration in a furnace at 500^{o}C, for approximately 5 h.

A 10 g sample of each caste collected during mid-summer (December/January) and mid-winter (June/July) was also analyzed at the University of the O.F.S. for various minerals; the macro-elements - phosphorous, calcium, magnesium, potassium and sodium, and one micro-element - iron. These minerals were obtained in solution after dry ashing at 550^{o}C (Benton Jones & Steyn 1973). Phosphorous determinations were by colorimetry, while the other five mineral determinations were by atomic absorption (Benton Jones & Steyn 1973).

The Students T-test was used for statistical comparisons (Snedecor & Cochran 1967).

RESULTS

The nutritional quality of soldier and worker termites over the year in terms of crude protein, crude fibre, crude fat, ash, energy and water content are represented in Figure 4.1. Statistical differences between the two castes are presented in Table 4.1. Worker termites had significantly higher values for protein, fibre and water content, and significantly lower values for ash and lipids

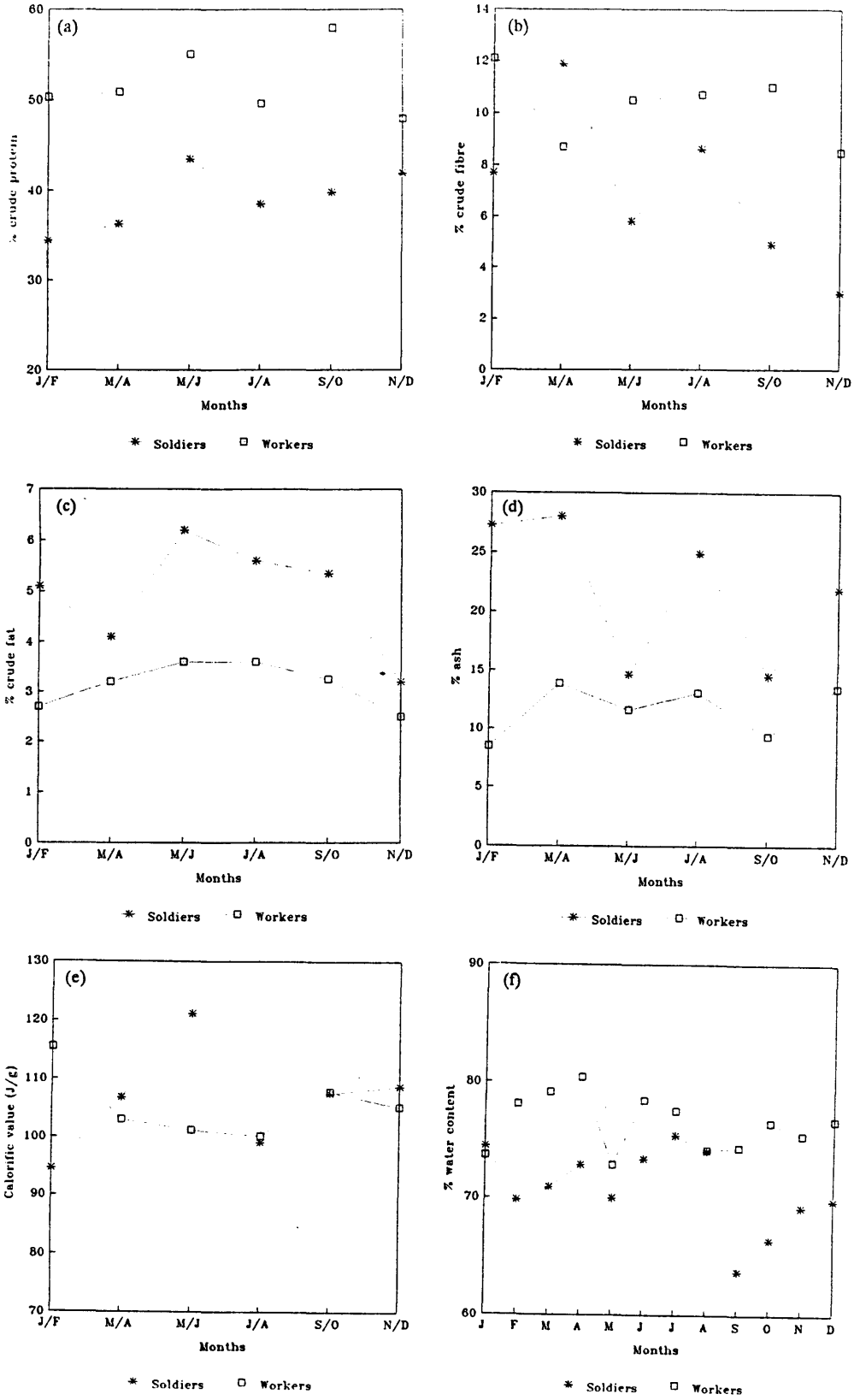


Figure 4.1 The nutritional quality of *Trinervitermes trinervoides* soldier and worker castes over the year: (a) Percentage crude protein, (b) Percentage crude fibre, (c) Percentage crude fat, (d) Percentage ash, (e) Calorific values (J/g), and (f) Percentage water content.

($p<0,05$). There was no significant difference in the calorific value of soldier and worker termites ($p>0,05$).

Due to small sample sizes a statistical comparison for seasonal variation of the nutritional quality of *T. trinervoides* was not possible (Figure 4.1). The crude fat values were however significantly greater during winter (May-August) than summer (September-April) for soldiers ($t=2,76$; $p<0,02$) and workers ($t=2,23$; $p<0,05$) (Figure 4.1).

The mineral determinations of *T. trinervoides* soldier and worker termites for the two seasons is presented in Table 4.2. Summer-winter differences were not apparent and because of small sample sizes this was not tested statistically. There were, however, significant differences between the two castes for N, P, K and Na (Table 4.2). In Table 4.3 the mineral content of *T. trinervoides* is compared with those of the whole body of several wildlife species (Robbins 1983). The mineral content of *T. trinervoides* is lower than the values for these wildlife species for all the minerals tested, except magnesium.

DISCUSSION

Redford and Dorea (1984) noted that most invertebrates, and in particular ants and termites, have a low nutritional value. The nutritional quality of *T. trinervoides* determined during this study is generally in agreement with that of other termite species tested by them, as well as for other insects (ants, locusts, etc.) and other invertebrates (for example, earthworms) determined in previous studies (e.g., Phelps, Struthers & Moho 1975). Moreover, the minerals present in *T. trinervoides* are generally less than those present in the whole body of a variety of wildlife species (Robbins 1983). The mineral content of *T. trinervoides*, however, is well within the nutritional requirements of mammals (Table 4.4).

The nutritional quality of *T. trinervoides* was significantly greater for the worker caste for protein, fibre, N, P, K and Na. Soldier termites were only significantly greater with respect to ash and lipids. Workers are, therefore, more nutritious

Table 4.1 Nutritional quality of the soldier and worker castes of *T. trinervoides*. Data are averages for determinations made throughout the year and include standard deviations and sample sizes in parentheses

	Soldiers	Workers	T test	*p<0,05
Water (%)	70,9±3,2 (24)	76,3±2,5 (24)	t=6,53	*
Protein (%)	39,1±3,6 (12)	51,9±4,3 (12)	t=4,29	*
Fibre (%)	7,0±3,1 (6)	10,3±1,4 (6)	t=3,37	*
Ash (%)	21,9±6,1 (6)	11,6±2,3 (6)	t=3,89	*
Lipids (%)	4,9±1,0 (12)	3,1±0,6 (12)	t=4,90	*
Calorific value (J/g)	106,3±8,9 (12)	105,5±4,7 (12)	t=0,27	

Table 4.2 Summer (December/January) - winter (June/July) comparison of the values for various minerals of soldier and worker castes of *T. trinervoides*; and the results of a statistical comparison of these castes for the data combined for both seasons

	Winter		Summer		T test
	Soldier	Worker	Soldier	Worker	*p<0,05
N (%)	7,05	9,99	6,65	9,60	t=10,50 *
P (%)	0,31	0,52	0,28	0,49	t=9,90 *
Ca (%)	0,29	0,54	0,46	0,50	t=1,70
Mg (%)	0,11	0,17	0,17	0,20	t=1,34
K (%)	0,31	0,47	0,29	0,45	t=11,30 *
Na (ppm)	925	1400	765	1540	t=5,90 *
Fe (ppm)	3400	3550	3500	3100	t=0,54

Table 4.3 Mineral content of *T. trinervoides* and the whole body of several wildlife species (adapted from Robbins (1983))

Mineral	*T. trinervoides*	White-tailed deer	Old-field mouse	Meadow Pipit
P(%)	0,28-0,52	2,26	1,71-1,99	1,40-1,90
Ca(%)	0,29-0,54	3.09	0,57-2,62	1,3-2,77
Mg(%)	0,11-0,20	0,09	0,04-0,08	0,1-0,15
K(%)	0,29-0,47	0,95	0,83-1,57	0,85-1,71
Na(%)	0,08-0,16	0,39	0,27-0,58	0,35-1,30
Fe(%)	0,31-0,36	1,65	2,21-3,96	3,00-5,00

Table 4.4 Mineral content of *T. trinervoides* in relation to the mineral requirements of some mammalian species

Mineral	*T. trinervoides*	Requirement (% of dry diet)
P(%)	0,28-0,52	0,4-0,6 (fox; NRC (1968), cited by Robbins 1983)
Ca(%)	0,29-0,54	0,5-0,6 (fox; NRC (1968), cited by Robbins 1983)
Mg(%)	0,11-0,20	0,03-0,04 (domestic rabbit; NRC (1977), cited by Robbins 1983)
K(%)	0,29-0,47	0,6 (domestic rabbit; NRC (1977), cited by Robbins 1983)
Na(%)	0,08-0,16	0,05-0,15 (mammals; Morris (1980))
Fe(%)	0,31-0,36	$2,5x10^{-5}$-$1,4x10^{-4}$ (various mammals; Robbins (1983))

than the soldiers and are also consumed in greater proportions by foraging aardwolves (Kruuk & Sands 1972; Richardson 1985, 1987a).

The nitrogen content of *T. trinervoides* is congruent with the values for nine Brazilian termite species, which ranged from 2,99-11,89% (Redford & Dorea 1984). The usefulness of these values however are questionable. The nitrogen and protein assays incorporate the nitrogen present in the indigestible chitin exoskeletons and, therefore, determination of the protein content of invertebrates is difficult (Redford & Dorea 1984). The level of crude protein in food is normally calculated from total nitrogen content by multiplying by a conversion factor, usually 6,25 (A.O.A.C. 1975). This conversion assumes that nitrogen in a sample is present solely as protein. However, in arthropods the presence of chitin renders this assumption invalid. Chitin, which makes up a large proportion of the exoskeleton in many arthropods, is a structural carbohydrate (Redford & Dorea 1984), with nitrogen as a component. Tihon (1946, cited by Redford & Dorea 1984) and Hubert, Gillon & Adam (1981, cited by Redford & Dorea 1984) calculated the chitin content of termites to be 5,1% for termite queens and 16,5% for unspecified termite workers, respectively, and according to Hubert, Gillon & Adam (1981) chitin in the exoskeleton of ants and termites represents up to 18% of their dry mass. Therefore, because of the comparatively large quantity of the body mass of ants and termites being taken up by ash and exoskeleton, Green, Griffiths & Newgrain (1992) calculated that approximately 49% of the dry matter ingested by ant- and termite-eaters is in the form of indigestible materials.

Cornelius, Dandrifosse & Jeuniaux (1976) have indicated that certain animals, including insectivores, may be capable of producing an enzyme, chitinase, which digests chitin. Thus, determination of chitin content and subtraction of the nitrogen in this chitin from total nitrogen does not give a reliable indication of available nitrogen for all animals. As a result, all values in this study are presented as a percentage of total nitrogen; the percentage of available nitrogen is, however, not known. Experiments should, therefore, be conducted to determine the extent of the aardwolf's capability to digest chitin. However, in view of the persistence of the termite's chitinous exoskeleton and heads in their faeces (Kruuk & Sands 1972;

Cooper & Skinner 1979; Richardson 1985, 1987a) it appears as if the aardwolf does not have the ability to digest the whole termite.

As with nitrogen determinations, the calorific determinations are of limited use only as the values incorporate the largely indigestible chitinous exoskeleton of the termites. This is supported by the findings in a previous study where Anderson (1987) examined the heads and bodies of *T. trinervoides* separately and found that the frontal glands of the soldiers contributed significantly to the overall calorific value of the termite body. The head capsule is not digested by the aardwolf and persists in its faeces (Cooper & Skinner 1979). Furthermore, the terpenoid contents of the head capsules appear largely to pass through the aardwolf's digestive system as the characteristic terpenoid smell is evident in its faeces (Kruuk & Sands 1972; Richardson 1987b).

No data are available for the fibre content of other termite species and, therefore, comparisons are not possible. It is unlikely that aardwolves are able to process the fibre present in the termites and, although aardwolves possess a small caecum, it is unlikely that any fermentation occurs in their digestive tract (Anderson, Richardson & Woodall 1992).

The fat content of *T. trinervoides*, determined during this study, is similar to the values obtained in a previous study for the same species (soldiers - 8,1%, workers - 5,6%; Anderson (1987)). The fat content of Brazilian termite species varied between 1,5-14,0%, with a similarly higher content in the soldier caste of three of the five species studied (Redford & Dorea 1984). The higher fat content in the soldier caste may be augmented by the terpene secretions (Prestwich 1983) in the large frontal gland. Soldier and worker castes are generally low in fat content, while alates have much higher fat values (Redford & Dorea 1984). Although aardwolves feed predominantly on foraging soldier and worker termites, alates are fed on when available during the summer months (pers. obs.).

The higher ash content of the soldier caste determined during this study is incongruent with previous studies. Redford & Dorea (1984) and Matsumoto

(1976) found that worker termites had a higher ash content for all the species they examined. Redford & Dorea (1984) attributed this to the presence of higher concentrations of indigestible materials in the worker's digestive tracts. The higher ash content of *T. trinervoides* soldiers may be attributed to their large, indigestible, sclerotinised frontal glands and its contents, and their chitinous exoskeleton.

The percentage moisture determinations (63,1%-80,5%) are in accordance with that determined in previous studies: unspecified *T. trinervoides* caste - 78% (Cooper 1977); *T. geminatus* - 73-80% (Redford & Dorea 1984); nine Brazilian species - 66,4-79,7% (Redford & Dorea 1984). The high water content of *T. trinervoides* is important for aardwolves and during summer, when termites are available, they rarely drink water, thus fulfilling all their water requirements from their diet (Anderson, Richardson & Woodall 1992). However, during winter when termites are generally unavailable aardwolves have occasionally been observed to drink water (pers. obs.).

The lack of seasonal variation in the nutritional quality of *T. trinervoides* may be attributed to the foraging habits of these termites. *T. trinervoides* are harvester termites and during winter, when they are generally not active above-ground, they rely on grass that was harvested and stored in the termitarium during the summer months (Richardson 1985). It can then be assumed that winter is not a nutritionally stressful period for these termites as long as there is an adequate supply of harvested grass in the mound. Furthermore, as is apparent from the higher fat values during winter, *T. trinervoides* may in fact be in a slightly better condition during this season. This may be related to reduced energy expenditure due to inactivity in the termitarium during these colder months. Aardwolves feed on *T. trinervitermes* primarily during the summer months (Richardson 1987a) and, as they do not possess the morphological features typical of other myrmecophagous mammals (Anderson, Richardson & Woodall 1992), they are unable to excavate these termites from their termitaria during the winter months.

Redford & Dorea (1984) have suggested that differences in nutritional quality may affect a predator's choice between two specific prey items, but availability and

abundance of prey probably determine the type of prey taken by most invertebrate-eating mammals. The reason for the aardwolf's preference for *Trinervitermes* may best be explained by these termites foraging behaviour (Kruuk & Sands 1972). Some *Trinervitermes spp.*, in contrast to most African termites which forage under the protection of mud galleries, forage openly on the soil surface and are thus freely available for aardwolves. The reason *Trinervitermes* can afford to forage so openly is due to their chemical defence system (Prestwich 1983). Originally *Trinervitermes* represented a food source available, without competition, to any mammal that could overcome this defense system (Richardson 1987b). Aardwolves were probably pre-adapted to tolerate noxious foodstuffs and this specialization proceeded simultaneously with the development of various anatomical and morphological adaptations (Richardson 1987b; Anderson, Richardson & Woodall 1992). Dietary selection, therefore, was not for nutritional quality but for an abundant food source which was not being exploited by other mammals.

Due to the small size of termites and their low nutritional quality, aardwolves have to consume vast quantities of termites, and Richardson (1987a) has estimated that during a single warm summer night an aardwolf can consume as many as 300 000 termites. The consumption of these termites off the soil surface means that large quantities of indigestible materials such as sand and grass litter may enter their digestive system (Cooper & Skinner 1979; Bothma & Nel 1980). It is McNab's (1984) contention that ant- and termite-eating mammals have low metabolic rates because they feed on a diet which is nutritionally poor, often filled with chemical poisons, ingested with indigestible materials and often seasonally unavailable.

To conclude, as has been determined for other termites species, and other invertebrates, *T. trinervoides* have a low nutritional quality when compared to a few selected mammal and bird species. Ancestral aardwolves probably selected this food source not on the basis of its nutritional quality but for its accessibility, its locally abundant availability and the absence of competitors feeding on it. The seasonal unavailability of the aardwolf's food source, as well as the termites' low nutritional value, may be partly responsible for its low metabolic rate.

CHAPTER 5. BODY CONDITION OF THE AARDWOLF IN RELATION TO SEASONAL AVAILABILITY OF FOOD

Abstract

Body condition data were collected from free-ranging aardwolves in order to relate various condition parameters to the seasonal availability of their principle food source, *Trinervitermes* termites. Body masses (n=137), and subcutaneous fat indices for six body localities, were analysed. The body masses of aardwolves decreased significantly from late-summer to late-winter, and during this period (April-August) aardwolves lost an average of 613 g body weight per month. Aardwolves also showed a decrease in subcutaneous fat during winter. Blood samples from 49 captures of 17 aardwolves were analyzed during summer and winter for 16 blood chemistry and eight blood haematology parameters. Six blood chemistry parameters were found to differ between the sexes; while eight blood chemistry values and one blood haematology value differed between the two age classes. Significant differences between summer and winter for eight blood chemistry values and one blood haematology value were also apparent.

INTRODUCTION

The seasonal availability of *Trinervitermes trinervoides* places stress on aardwolves during winter (Richardson 1987a). Due to their specialization on this diet, and various anatomical and morphological adaptations (Richardson 1987b; Anderson, Richardson & Woodall 1992), aardwolves are to a large extent precluded from feeding on alternative food items (Richardson 1987a). During winter aardwolves feed to a limited extent on *Hodotermes mossambicus* but during this season there is still a significant decrease in their body mass and also increased mortality of aardwolf cubs during particularly severe years (Richardson 1985, 1987a). Nevertheless, most aardwolves survive through winter by behavioural (Chapter 6) and physiological

adjustments (Chapter 7 & 8) which reduce the associated stresses. Through an evaluation of the body condition of aardwolves, I undertook this study in order to understand the energy status of these animals during winter and their ability to withstand prolonged periods of food deprivation.

Traditionally the body condition and nutritional status of free-ranging animals has been assessed by determining their body masses or by measuring, either directly or indirectly, their fat reserves. In more recent years, the body condition of animals has also been indexed using a variety of other parameters, including adrenal cortical hypertrophy, blood chemistry and haematology, urinary excretion of hydroxyproline, and aspects of body growth (Hanks 1981). Haematology and blood chemistry, particularly during the past 20 years, have been found to be useful indicators of an animal's physiological response to stress, seasonality, and/or nutritional status (e.g. Halloran & Pearson 1972; Seal & Hoskinson 1978). I investigated the body condition of free-ranging aardwolves throughout the year by examining their body masses, subcutaneous fat, blood chemistry and haematology.

MATERIALS AND METHODS

Body mass

Free-ranging aardwolves were immobilized using the methods described by Anderson & Richardson (1992) and Richardson & Anderson (1993b). Each immobilized aardwolf was weighed to the nearest 0,1 kg by suspending it on a canvas sling from a 10 kg spring balance (Pesola, Switzerland) or a 25 kg scale (Salter model 235, RSA). Additional body masses of aardwolves were obtained from southern African museums, Cape Nature Conservation, and Richardson (unpubl. data). Only the body masses of subadult (1-2 years old) and adult (>2 years old) aardwolves were incorporated into the data analysis. As the juveniles generally approach adult body mass by May, when they are seven months old (Van Jaarsveld, Richardson &

Anderson unpubl. data), to prevent complications with the analysis of the data, and the interpretation thereof, these individuals (<7 months old) were excluded from the calculations.

Subcutaneous fat index

Each time an aardwolf was darted an index of the amount of subcutaneous fat (SFI) present was determined at six body localities (upperback, lowerback, chest-side, chest-front, waist and belly) by measuring the thickness of a pinch of skin using a pair of calipers. In order to compare variation in the amount of subcutaneous fat by season the indices for summer (data for the months of February, March and April - when aardwolves are in their best condition according to body mass) were pooled and compared to the indices obtained for winter (June, July and August - when aardwolves are in their poorest condition according to body mass). In order to determine the extent of seasonal variation in the SFIs of individual aardwolves, data were also compared for animals for which a few sets of measurements for different months of the year were available.

Blood chemistry and haematology

During 1989 and 1990 blood was collected from 17 aardwolves (49 captures). Blood was drawn from the cephalic vein of recumbent animals into 2 ml sterile (no anti-coagulant) vacutainers for serum, and heparinized vacutainers for plasma. Blood for the determination of glucose concentration was collected in vacutainers containing potassium oxalate and sodium fluoride as anti-coagulants. Blood samples were placed in a cold-box in the field, and within a few hours placed in a fridge (0-5^{o}C) and stored overnight. The analyses were conducted the following day at the South African Institute for Medical Research in Kimberley.

Heparinized blood samples were analyzed for haemoglobin (Hb), number of red blood cells (RBC), number of white blood cells (WBC), haematocrit (Hct), mean corpuscular volume (MCV), mean corpuscular haemoglobin (MCH), mean haemoglobin concentration (MCHC) and platelet counts (PLT) using a Coulter T660 analyzer (Coulter Electronics, USA). The remaining blood samples were centrifuged at 3 600 rpm for 10 min. Serum and plasma was collected and measured on an Astra-8 analyzer (Beckman Instruments, USA) using prescribed methods for glucose, acetone, urea, creatinine, chlorides, sodium and potassium. Albumin, total plasma proteins, cholesterol, triglycerides, iron, calcium, phosphorous, total and direct bilirubin, and magnesium were measured on a Cobas Mira analyzer (Roche, Switzerland).

Statistical analysis of data utilized t-tests for paired and unpaired variates (Snedecor & Cochran 1967). Data for summer (February, March and April) and winter (June, July and August) were tested for differences between the age classes and between the sexes, and pooled if there were no differences between these groups. Analysis of covariance was used to compare the body masses and subcutaneous fat indices by season (Snedecor & Cochran 1967).

RESULTS

Body mass

The body masses of male and female aardwolves only differed significantly during June ($t=2,80$; $p<0,05$) (Table 5.1). There was a significant monthly variation in the body mass of aardwolves ($F=4,86$; $p<0,05$), with the body masses of individuals during late-summer ($9,6\pm1,2$ kg; $n=33$; February, March and April) differing significantly from the body masses of individuals during mid-winter ($8,4\pm1,1$ kg; $n=55$; June, July and August) ($t=4,85$; $p<0,05$) (Figure 5.1). From April to August there was a constant weight loss, with the body mass of aardwolves decreasing by an

average of 613 g per month. The body mass of aardwolves then increased significantly from August to September ($t=2,86$; $p<0,05$) and then again from January to February ($t=2,60$; $p<0,05$).

Table 5.1 The body masses (kg±SD; with sample sizes) of male and female aardwolves

Month	Males	Females	t-test $^{*}p<0,05$
January	7,0 (n=1)	8,5±0,4	(n=5)
February	9,2±0,9 (n=5)	10,0±0,9 (n=5)	t=1,45
March	9,9±0,7 (n=5)	8,9±1,1 (n=7)	t=1,49
April	9,6±1,1 (n=4)	10,1±1,4 (n=7)	t=0,52
May	9,7±1,1 (n=7)	9,0±1,1 (n=6)	t=0,99
June	8,2±1.1 (n=11)	9,5±0,8 (n=10)	t=2,80*
July	8,2±1,3 (n=17)	8,4±0,9 (n=9)	t=0,42
August	7,6±0,8 (n=10)	7,4±0,9 (n=3)	t=0,18
September	8,7±0,5 (n=4)	8,9 (n=1)	
October	8,0 (n=1)	8,2±0,5 (n=3)	
November	8,7±0,6 (n=6)	7,9±1,0 (n=4)	t=1,53
December	9,1 (n=1)	8,7±0,9 (n=4)	
Average	8,6±1,2 (n=72)	9,0±1,2 (n=64)	t=1,82

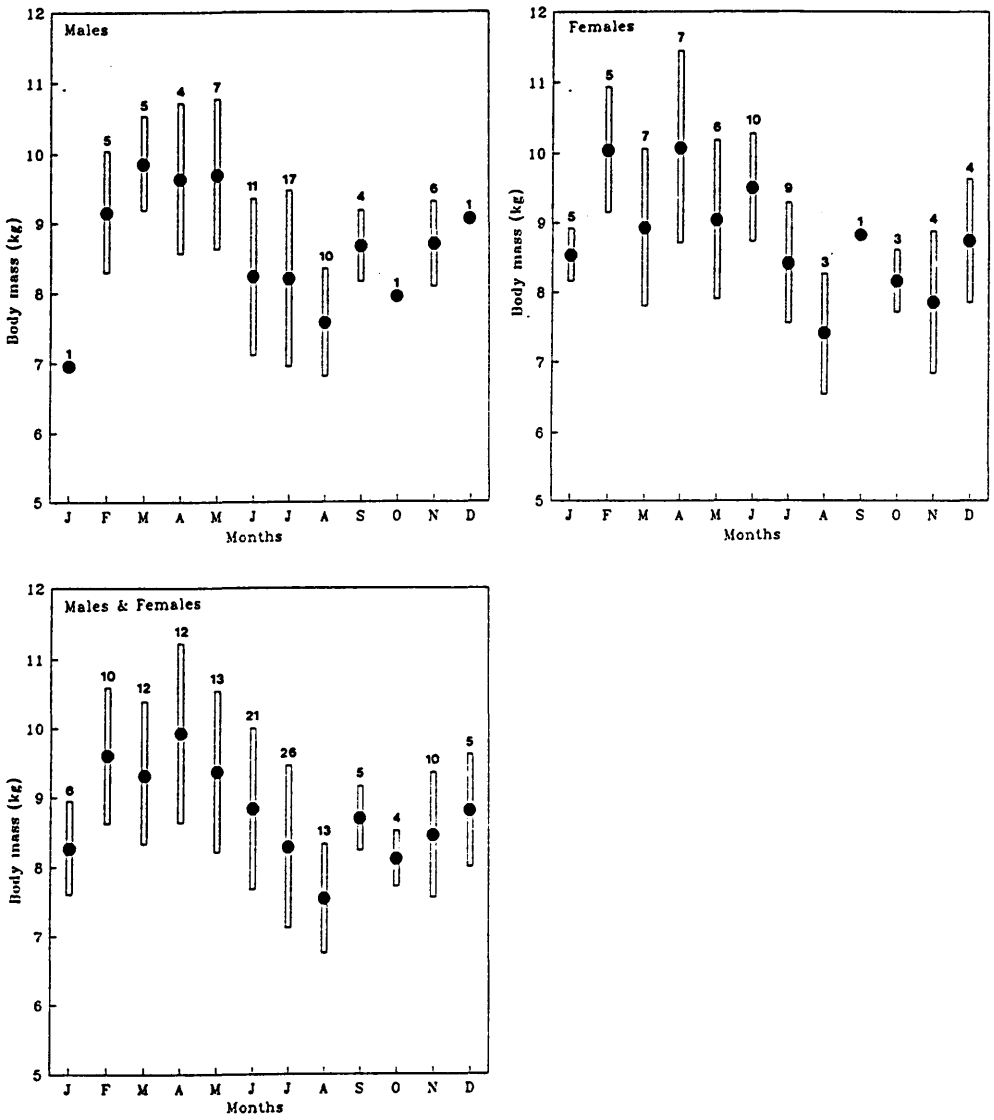


Figure 5.1 Seasonal variation in mean body masses (kg±SD; with sample sizes indicated) of adult male aardwolves (n=72), adult female aardwolves (n=64) and all adult aardwolves (n=136).

Subcutaneous fat index

The subcutaneous fat indices (SFI) of juvenile and adult aardwolves were compared statistically by season (Table 5.2), and data where no differences occurred were pooled to facilitate analysis. There was no significant seasonal change (i.e. late-summer *vs* mid-winter) in subcutaneous fat at these six body localities for these groups ($p>0,05$) (Table 5.3). However, the SFI of the upperback, lowerback and waist showed monthly differences at these three localities ($F=6,22$; $F=2,53$; $F=4,31$; $p<0,05$). What is most noticeable is the increase in SFI from July to August followed by a decrease during the subsequent months (Figure 5.2). This trend was not observed for the measurements taken from the belly and the chest (side and front) (Figure 5.2), localities for which there was little seasonal variation or small sample sizes. Essentially skin thickness follows the same seasonal pattern as body mass with a general decline over winter, staying low during the first half of summer.

Patterns in the seasonal change of subcutaneous fat were clearer when measurements taken from individual aardwolves over the year were compared (Figure 5.3), with the SFI of aardwolves A-D (adults) showing a clear decline from late-summer to winter/early summer. The SFI of aardwolf E (a cub) increased markedly from February to July (Figure 5.3).

Blood chemistry and haematology

Blood samples were obtained from 17 aardwolves immobilized on 49 occasions. Seven aardwolves were captured in autumn (April), 21 in winter (May-August), 21 in summer (October-March) and none during spring (September). For the purpose of this study the blood values of aardwolves captured in mid/late-summer (February-

Table 5.2 Subcutaneous fat indices (mm; mean±SD with sample sizes) from different body localities for aardwolves (juveniles and adults) during late-summer (February, March and April) and winter (June, July and August)

	Juveniles	Adults	t-test ($^{*}p<0,05$)
SUMMER			
Upperback	4,9±1,2 (n=13)	5,8±1,5 (n=16)	t=1,74
Lowerback	4,7±1,6 (n=13)	5,3±1,7 (n=15)	t=1.02
Waist	3,2±1,9 (n=13)	5,0±2,3 (n=15)	t=2,24*
Belly	2,3±0,9 (n=12)	3,8±1,4 (n=13)	t=3.17*
Chest#	3,1±2,1 (n=13)	4,6±2,5 (n=17)	t=1,74
Chest - side	3,7 (n=1)	6,9±2,9 (n=4)	
Chest - front	2,7±1,6 (n=12)	3,9±1,9 (n=13)	t=1,63
WINTER			
Upperback	5,2±1,8 (n=2)	4,8±1,0 (n=25)	t=0,42
Lowerback	4,9±0,0 (n=2)	4,6±1,3 (n=26)	t=0,33
Waist	4,2±0,8 (n=2)	3,9±1,8 (n=26)	t=0,29
Belly	2,8±0,0 (n=2)	3,0±0,9 (n=21)	t=0,38
Chest#	3,6±0,0 (n=2)	3,9±1,8 (n=29)	t=0,24
Chest - side	- (n=0)	4,8±2,0 (n=15)	
Chest - front	3,6±0,0 (n=2)	2,9±0,7 (n=14)	t=1,40

Measurements from chest (front) and chest (side) combined for an average subcutaneous fat index for the chest

Table 5.3 Subcutaneous fat indices (mm; mean±SD with sample sizes) from different body localities for aardwolves during late-summer (February, March and April) and winter (June, July and August)

	Summer	Winter	t-test
Upperback#	5,5±1,4 (n=29)	4,8±1,0 (n=28)	t=1,93
Lowerback#	5,0±1,6 (n=28)	4,6±1,3 (n=28)	t=1,13
Waist (adults)	5,0±2,3 (n=15)	3,9±1,8 (n=26)	t=1,83
Waist (cubs)	3,2±1,9 (n=13)	4,2±0,8 (n=2)	t=0,71
Belly (adults)	3,8±1,4 (n=13)	3,0±0,9 (n=21)	t=2,01
Belly (cubs)	2,3±0,9 (n=12)	2,8±0,0 (n=2)	t=0,75
Chest (side & front)#	4,0±2,4 (n=29)	3,9±1,7(n=31)	t=0,24
Chest - side#	6,9±2,5 (n=5)	4,8±2,0 (n=15)	t=1,87
Chest - front#	3,3±1,9 (n=24)	3,0±0,6 (n=16)	t=0,66

combined data for adults and cubs

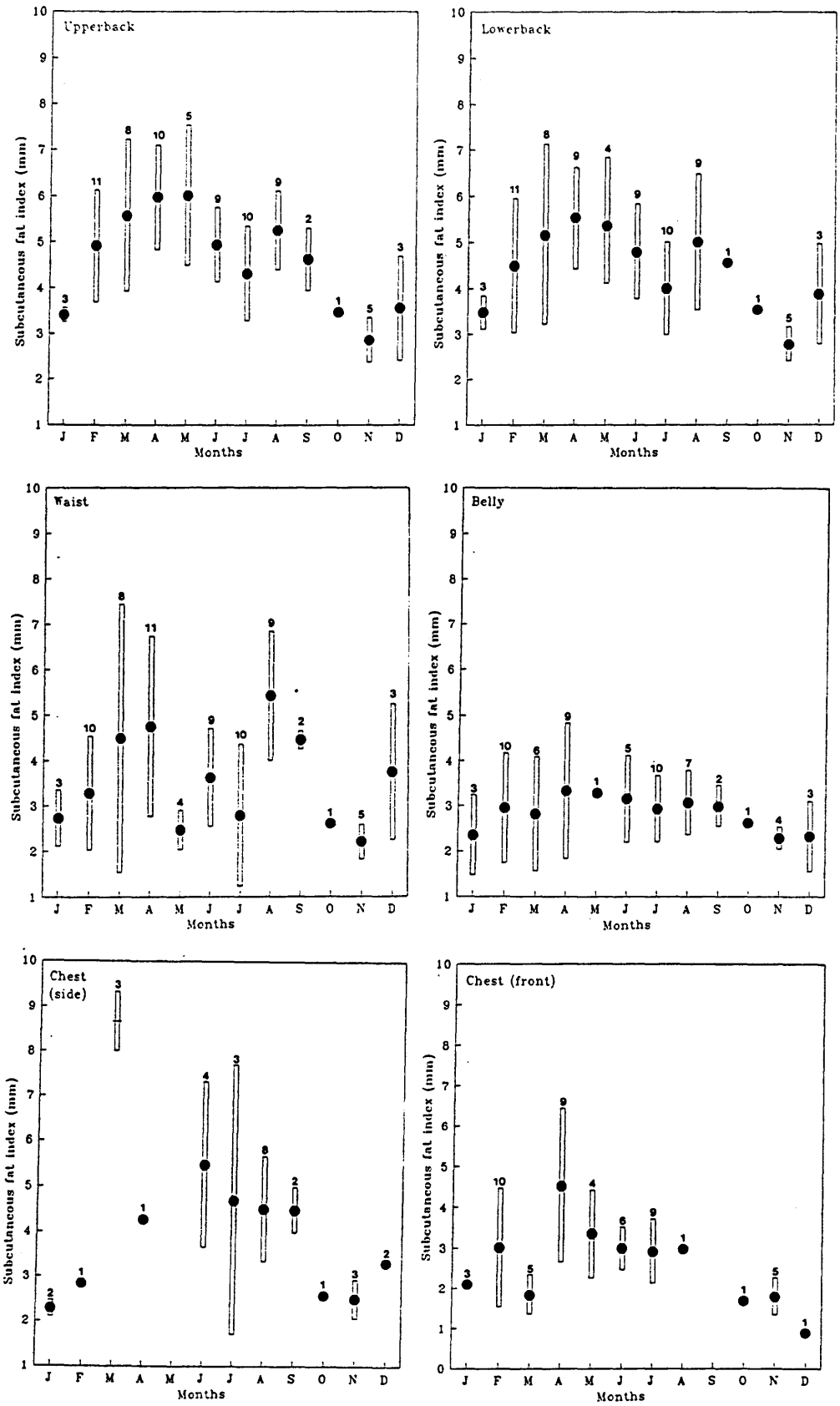


Figure 5.2 Seasonal change in subcutaneous fat indices (mm±SD, with sample sizes indicated) for measurements determined at the upperback (n=76), lowerback (n=73), waist (n=75), belly (n=61), chest-side (n=30) and chest-front (n=54).

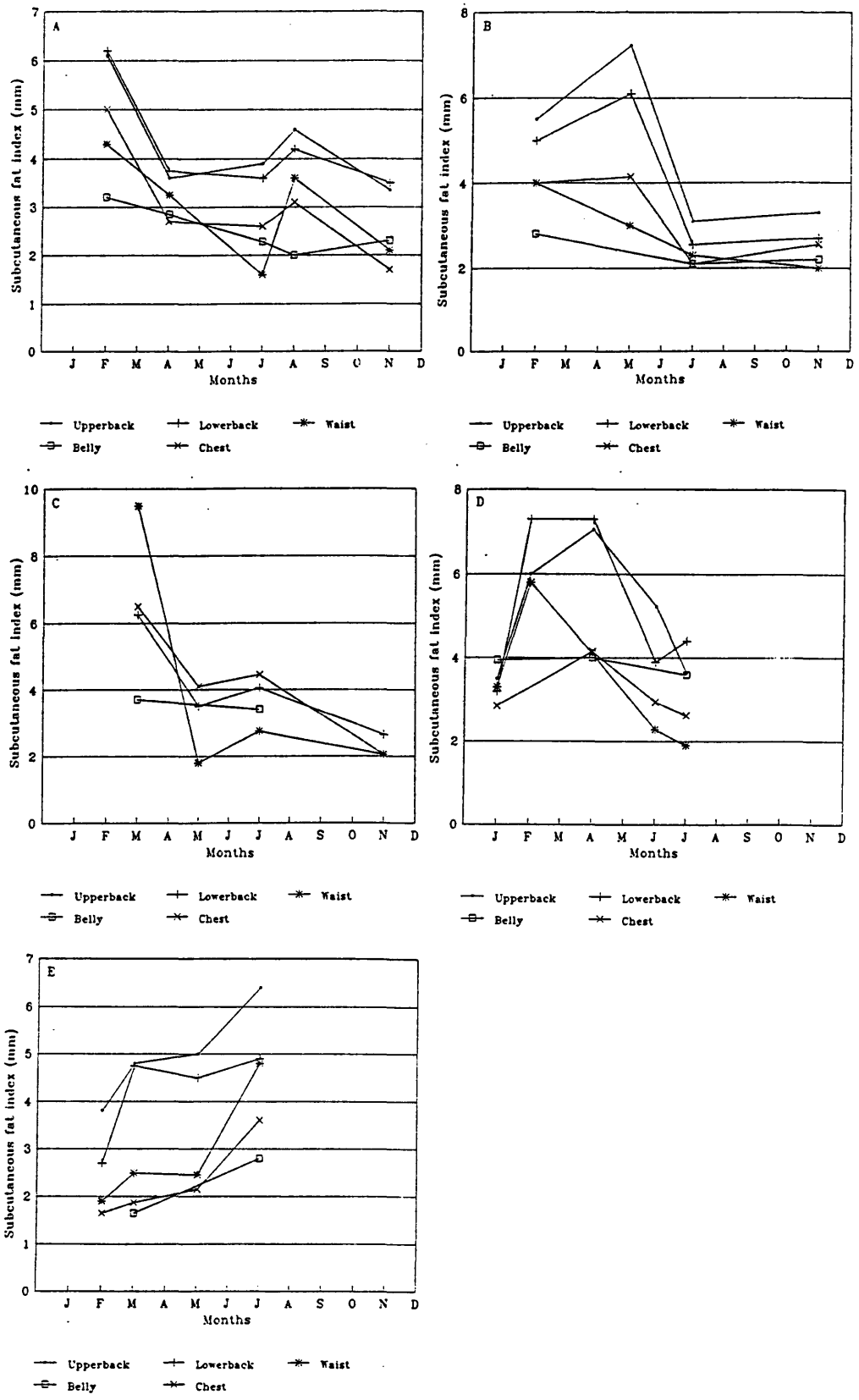


Figure 5.3 Seasonal change in subcutaneous fat indices (mm) for five aardwolves for measurements determined at the upperback, lowerback, waist, belly and chest (side and front). Aardwolves A-D are adults and aardwolf E is a cub.

April; n=14) were compared with the blood values of aardwolves captured during winter (June-August; n=16).

During summer, male and female aardwolves differed significantly with respect to the following blood chemistry values: globulin, total plasma proteins, cholesterol, triglycerides and potassium (Table 5.4). Significant differences between the sexes during winter were only apparent for cholesterol and chlorides (Table 5.5). With respect to blood haematology, there were no significant differences between the sexes during summer and winter (Table 5.6). Age class differences were apparent during summer between a number of blood chemistry values (globulins, total plasma proteins, cholesterol, triglycerides and phosphorous) (Table 5.7) and a single blood haematology value, namely platelets (Table 5.8). During winter a statistical comparison between the two age classes was not possible as too few data for juveniles were obtained (Tables 5.8 & 5.9).

For a seasonal comparison data were analyzed separately if there were differences between the two age classes or between the sexes, and to facilitate data analysis the blood chemistry and blood haematology values were pooled if there were no significant differences between these groups. There was a number of significant summer-winter differences in the blood chemistry values of aardwolves: albumin (Figure 5.4), total plasma protein and creatinine (Figure 5.4) values were significantly higher during winter, and similar differences were also observed for males for total plasma proteins and chlorides (Table 5.10). Urea, cholesterol, triglycerides and phosphorous values were significantly greater during summer (Figure 5.5) (Table 5.10). Inter-age class and/or sex differences were observed with higher globulin, cholesterol and triglyceride values during summer. The only significant differences between the two seasons for blood haematology values were the significantly higher WBC counts during summer (Table 5.11).

Table 5.4 Blood chemistry (means ±SD; with sample sizes) of male and female aardwolves during late-summer (February, March and April)

Blood parameter	Males	Females	t-test *p<0,05
Glucose (mmol/l)	5,0±2,1 (6)	4,2±0,8 (8)	t=0,93
Albumin (g/l)	9,8±2,8 (6)	22,1±1,1 (8)	t=2,13
Globulin (g/l)	19,5±2,9 (6)	29,1±9,8 (8)	t=2,32*
TPP (g/l)	41,0±7,1 (6)	53,6±9,4 (8)	t=2,76*
Urea (mmol/l)	16,7±3,0 (6)	13,7±2,3 (8)	t=1,98
Creatinine (umol/l)	77,5±7,5 (6)	67,0±10,6 (8)	t=2,06
Cholesterol (mmol/l)	3,43±0,26 (6)	4,61±0,94 (8)	t=2,97*
Triglycerides (mmol/l)	1,48±0,66 (14)	0,80±0,28 (8)	t=2,66*
Chlorides (mmol/l)	105,5±3,9 (6)	105,9±5,2 (8)	t=0,15
Sodium (mmol/l)	140,7±1,0 (6)	141,0±3,2 (8)	t=0,25
Potassium (mmol/l)	5,2±0,6 (6)	4,5±0,3 (8)	t=2,80*
Iron (umol/l)	47,2±37,8 (6)	46,0±43,9 (7)	t=0,05
Calcium (mmol/l)	2,24±0,11 (6)	2,06±0,96 (6)	t=0,46
Phosphorous (mmol/l)	1,74±0,50 (6)	1,52±0,47 (7)	t=0,79
Bilirubin (d) (umol/l)	1,8±2,0 (6)	2,4±2,2 (7)	t=0,50
Bilirubin (t) (umol/l)	7,0±2,7 (6)	6,6±2,2 (7)	t=0,32
Magnesium (mmol/l)	0,75±0,01 (6)	0,72±0,33 (5)	t=0,17

Table 5.5 Blood chemistry (means ±SD; with sample sizes) of male and female aardwolves during winter (June, July and August)

Blood parameter	Males	Females	t-test *p<0,05
Glucose (mmol/l)	4,3±0,9 (6)	4,8±0,6 (7)	t=1,22
Albumin (g/l)	33,1±6,9 (8)	28,9±5,3 (9)	t=1,48
Globulin (g/l)	27,3±5,8 (8)	28,6±4,8 (9)	t=0,51
TPP (g/l)	60,5±9,9 (8)	57,0±8,2 (9)	t=0,80
Urea (mmol/l)	10,0±1,0 (8)	11,0±3,3 (9)	t=0,89
Creatinine (umol/l)	128,5±44,3 (8)	116,6±25,3 (9)	t=0,69
Cholesterol (mmol/l)	2,82±0,42 (8)	3,86±0,65 (9)	t=3,90*
Triglycerides (mmol/l)	0,34±0,08 (8)	0,49±0,23 (9)	t=1,79
Chlorides (mmol/l)	111,8±2,3 (8)	105,2±7,1 (9)	t=2,47*
Sodium (mmol/l)	143,5±3,6 (8)	139,9±5,1 (9)	t=1,66
Potassium (mmol/l)	4,7±0,3 (8)	4,5±0,5 (9)	t=0,89
Iron (umol/l)	24,2±17,1 (8)	33,9±13,5 (9)	t=1,31
Calcium (mmol/l)	2,41±0,16 (6)	2,40±0,32 (7)	t=0,92
Phosphorous (mmol/l)	0,78±0,42 (8)	0,98±0,58 (9)	t=0,81
Bilirubin (d) (umol/l)	2,9±2,8 (8)	1,6±0,9 (9)	t=1,35
Bilirubin (t) (umol/l)	4,9±3,6 (8)	5,9±4,8 (9)	t=0,49
Magnesium (mmol/l)	0,98±0,29 (8)	0,89±0,29 (9)	t=0,59

Table 5.6 Blood haematology (means ±SD; with sample sizes) of male and female aardwolves during late-summer (February, March and April) and winter (June, July and August)

Blood parameter	Males	Females	t-test
SUMMER			
WBC ($x10^9$/l)	8,2±1,9 (6)	7,8±2,5 (8)	t=0,32
RBC ($x10^{12}$/l)	6,98±1,23 (6)	6,19±0,58 (8)	t=1,62
Hb (g/dl)	13,5±2,2 (6)	11,8±1,1 (8)	t=1,91
Hct (RATIO)	40,7±6,6 (6)	36,4±2,9 (8)	t=1,66
MCV (fl)	58,5±1,4 (6)	58,8±1,6 (8)	t=0,57
MCH (pg)	19,4±0,7 (6)	19,1±1,2 (8)	t=0,45
MCHC (g/dl)	33,2±1,2 (6)	33,6±2,0 (8)	t=0,65
PLT ($x10^9$/l)	322±85 (6)	220±88 (8)	t=2,17
WINTER			
WBC ($x10^9$/l)	5,2±1,6 (6)	5,4±3,3 (4)	t=0,20
RBC ($x10^{12}$/l)	7,1±0,6 (6)	6,73±0,95 (5)	t=0,74
Hb (g/dl)	14,0±1,3 (6)	13,0±1,8 (5)	t=1,12
Hct (RATIO)	41,7±3,6 (6)	39,5±4,9 (5)	t=0,86
MCV (fl)	58,8±0,9 (6)	58,7±1,2 (5)	t=0,22
MCH (pg)	19,8±0,6 (6)	19,3±0,2 (5)	t=0,22
MCHC (g/dl)	33,7±0,6 (6)	32,9±0,7 (5)	t=2,00
PLT ($x10^9$/l)	196±28 (6)	185±154 (5)	t=0,18

Table 5.7 Blood chemistry (means ±SD; with sample sizes) of adult and juvenile aardwolves during late-summer (February, March and April)

Blood parameter	Juveniles	Adults	t-test *p<0,05
Glucose (mmol/l)	5,0±2,1 (6)	4,2±0,8 (8)	t=0,93
Albumin (g/l)	19,8±2,8 (6)	22,1±1,1 (8)	t=2,13
Globulin (g/l)	20,1±3,0 (6)	30,9±10,1 (8)	t=2,88*
TPP (g/l)	40,2±4,1 (6)	54,3±9,6 (8)	t=3,35*
Urea (mmol/l)	16,1±3,7 (6)	14,2±2,4 (8)	t=1,22
Creatinine (umol/l)	71,7±6,4 (6)	71,4±13,3 (8)	t=0,05
Cholesterol (mmol/l)	3,47±0,45 (6)	4,57±0,93 (8)	t=2,65*
Triglycerides (mmol/l)	1,46±0,69 (6)	0,81±0,08 (8)	t=2,42*
Chlorides (mmol/l)	104,3±4,5 (6)	107,1±4,6 (8)	t=1,14
Sodium (mmol/l)	140,8±2,2 (6)	140,9±2,7 (8)	t=0,03
Potassium (mmol/l)	4,8±0,3 (6)	4,7±0,7 (8)	t=0,33
Iron (umol/l)	46,3±38,7 (6)	46,7±43,3 (7)	t=0,02
Calcium (mmol/l)	2,32±0,18 (6)	1,98±0,92 (6)	t=0,88
Phosphorous (mmol/l)	2,05±0,23 (6)	1,25±0,26 (7)	t=5,84*
Bilirubin (d; umol/l)	1,3±0,8 (6)	2,9±2,6 (7)	t=1,37
Bilirubin (t; umol/l)	6,3±3,1 (6)	7,1±1,5 (7)	t=0,55
Magnesium (mmol/l)	0,77±0,06 (6)	0,70±0,29 (6)	t=0,51

Table 5.8 Blood haematology (means ±SD; with sample sizes) of adult and juvenile aardwolves during late-summer (February, March and April) and winter (June, July and August)

Blood parameter	Juvenile	Adult	t-test $p<0,05^*$
SUMMER			
WBC ($x10^9/l$)	9,0±1,9 (6)	7,2±2,1 (8)	t=1,65
RBC ($x10^{12}/l$)	6,27±1,61 (6)	6,35±0,80 (8)	t=0,91
Hb (g/dl)	12,8±2,1 (6)	12,4±1,6 (8)	t=0,38
Hct (RATIO)	39,7±6,3 (6)	37,2±4,1 (8)	t=0,38
MCV (fl)	58,8±1,7 (6)	58,6±1,3 (8)	t=0,32
MCH (pg)	18,9±1,0 (6)	19,5±0,9 (8)	t=0,27
MCHC (g/dl)	32,3±1,2 (6)	33,3±1,8 (8)	t=0,27
PLT ($x10^9/l$)	339±83 (6)	204±71 (8)	$t=3,30^*$
WINTER			
WBC ($x10^9/l$)	-	5,2±1,6 (11)	
RBC ($x10^{12}/l$)	8,27 (1)	6,92±0,78 (11)	
Hb (g/dl)	15,9 (1)	13,5±1,6 (11)	
Hct (RATIO)	47,5 (1)	40,7±4,2 (11)	
MCV (fl)	57,4 (1)	58,7±1,0 (11)	
MCH (pg)	19,3 (1)	19,6±0,5 (11)	
MCHC (g/dl)	33,6 (1)	33,3±0,8 (11)	
PLT ($x10^9/l$)	447 (1)	192±99 (11)	

Table 5.9 Blood chemistry (means ±SD; with sample sizes) of adult and juvenile aardwolves during winter (June, July and August)

Blood parameter	Juveniles	Adults
Glucose (mmmol/l)	5,0 (1)	4,5±0,8 (13)
Albumin (g/l)	27,0 (1)	30,9±6,3 (17)
Globulin (g/l)	33,0 (1)	27,8±5,3 (17)
TPP (g/l)	60,0 (1)	58,6±8,9 (17)
Urea (mmol/l)	17,1 (1)	10,5±2,4 (17)
Creatinine (umol/l)	72,0 (1)	122,2±34,9 (17)
Cholesterol (mmol/l)	4,50 (1)	3,37±0,76 (17)
Triglycerides (mmol/l)	1,10 (1)	0,42±0,19 (17)
Chlorides (mmol/l)	97,0 (1)	108,3±6,3 (17)
Sodium (mmol/l)	138,0 (1)	141,6±4,7 (17)
Potassium (mmol/l)	4,5 (1)	4,6±0,43 (17)
Iron (umol/l)	37,0 (1)	29,3±15,6 (17)
Calcium (mmol/l)	2,7 (1)	2,4±0,6 (13)
Phosphorous (mmol/l)	2,28 (1)	0,89±0,5 (17)
Bilirubin (d; umol/l)	1,0 (1)	2,2±2,1 (17)
Bilirubin (t; umol/l)	18,0 (1)	4,6±2,7 (16)
Magnesium (mmol/l)	1,21 (1)	0,93±0,28 (17)

Table 5.10 Blood chemistry of aardwolves during late-summer (February, March and April) [n=9 aardwolves; 15 dartings; mean±SD (n)] and winter (June, July and August) [n=9 aardwolves; 17 dartings; mean±SD (n)]

Blood parameter	Summer	Winter	t-test p<0,05
Glucose (mmol/l)#	4,5±1,5 (14)	4,5±0,8 (13)	t=0,01
Albumin (g/l)#	21,1±5,1 (14)	30,9±6,3 (17)	t=5,52*
Globulin (g/l)#	5,5±9,1 (14)	27,9±5,1 (17)	t=0,96
Globulin M	19,5±2,9 (6)	27,3±5,8 (8)	t=3,01*
Globulin F	29,1±9,8 (10)	28,6±4,8 (9)	t=0,15
Globulin A	30,9±10,1 (8)	27,8±5,3 (15)	t=0,97
Globulin J	20,1±3,0 (8)	33,0 (1)	
TPP (g/l)#	8,2±10,4 (14)	58,7±8,9 (17)	t=3,00*
TPP M	41,0±7,1 (6)	60,5±9,9 (8)	t=4,08*
TPP F	53,6±9,3 (8)	57,0±8,2 (8)	t=0,79
TPP A	54,3±9,6 (8)	58,6±8,9 (17)	t=1,12
TPP J	40,2±4,1 (6)	60,0 (1)	
Urea (mmol/l)#	15,0±3,0 (14)	10,5±2,5 (17)	t=4,55*
Creatinine (umol/l)#	71,5±10,5 (14)	122,2±34,9 (17)	t=5,23*
Cholesterol (mmol/l)#	4,10±0,93 (14)	3,37±0,76 (17)	t=2,41*
Cholesterol M	3,43±0,26 (6)	2,82±0,42 (8)	t=3,12*
Cholesterol F	4,61±0,94 (8)	3,86±0,65 (9)	t=1,93
Cholesterol A	4,58±0,93 (8)	3,37±0,76 (17)	t=3,44*
Cholesterol J	3,47±0,45 (6)	4,45 (1)	

#combined data for both sexes and age groups

M = males, F = females, A = adults, J = juveniles

Table 5.10 continued

Blood parameter	Summer	Winter	t-test *p<0,05
Triglycerides (mmol/l)#	1,09±0,58 (14)	0,38±0,08 (16)	t=4,91*
Triglycerides M	1,48±0,66 (6)	0,34±0,08 (8)	t=4,92*
Triglycerides F	0,80±0,28 (8)	0,49±0,23 (9)	t=2,46*
Triglycerides A	0,81±0,28 (8)	0,42±0,19 (17)	t=4,18*
Triglycerides J	1,46±0,69 (6)	1,1 (1)	
Chlorides (mmol/l)#	05,9±4,6 (14)	108,3±6,3 (17)	t=1,17
Chlorides M	105,5±3,9 (6)	111,8±2,3 (8)	t=3,77*
Chlorides F	105,9±5,2 (8)	105,2±7,1 (9)	t=0,83
Sodium (mmol/l)#	140,9±2,4 (14)	141,6±4,7 (17)	t=0,53
Potassium (mmol/l)#	4,8±0,6 (14)	4,6±0,4 (17)	t=1,02
Potassium M	5,2±0,6 (6)	4,7±0,3 (8)	t=1,89
Potassium F	4,7±0,3 (8)	4,9±0,5 (9)	t=0,13
Iron (umol/l)#	46,6±39,5 (13)	29,3±15,6 (17)	t=1,64
Calcium (mmol/l)#	2,34±0,15 (11)	2,41±0,25 (13)	t=0,79
Phosphorous (mmol/l)#	1,62±0,48 (13)	0,89±0,51 (17)	t=4,03*
Phosphorous A	1,25±0,26 (7)	0,89±0,51 (17)	t=1.79
Phosphorous J	2,05±0,23 (6)	2,28 (1)	
Bilirubin (d, umol/l)#	2,2±2,1 (13)	2,2±2,1 (17)	t=0,03
Bilirubin (t, umol/l)#	6,8±2,3 (13)	5,4±4,2 (17)	t=0,30
Magnesium (mmol/l)#	0,73±0,21 (11)	0,93±0,28 (17)	t=0,06

combined data for both sexes and age groups

M = males, F = females, A = adults, J = juveniles

Table 5.11 Blood haematology of aardwolves during late-summer (February, March and April) [n=9 aardwolves; 15 dartings; mean±SD (n)] and winter (June, July and August) [n=9 aardwolves; 17 dartings; mean±SD (n)]

Blood parameter	Summer	Winter	t-test *p<0,05
WBC ($x10^9/l$)#	7,9±2,2 (14)	5,3±1,6 (10)	t=3,30*
RBC ($x10^{12}/l$)	6,53±0,96 (14)	6,92±0,77 (11)	t=1,11
Hb (g/dl)	12,5±1,8 (14)	13,5±1,6 (11)	t=1,45
Hct (RATIO)	38,3±5,1 (14)	40,7±4,2 (11)	t=1,25
MCV (fl)	58,7±1,4 (14)	58,7±0,9 (11)	t=0,13
MCH (pg)	19,2±1,0 (14)	19,6±0,5 (11)	t=0,98
MCHC (g/dl)	32,8±1,7 (14)	33,3±0,8 (11)	t=0,91
PLT ($x10^9/l$)#	264±98 (14)	191±99 (11)	t=1,83
PLT A	204±71 (8)	192±99 (10)	t=0,31
PLT J	339±83 (6)	447 (1)	

combined data for both sexes and age groups

A = adults; J = juveniles

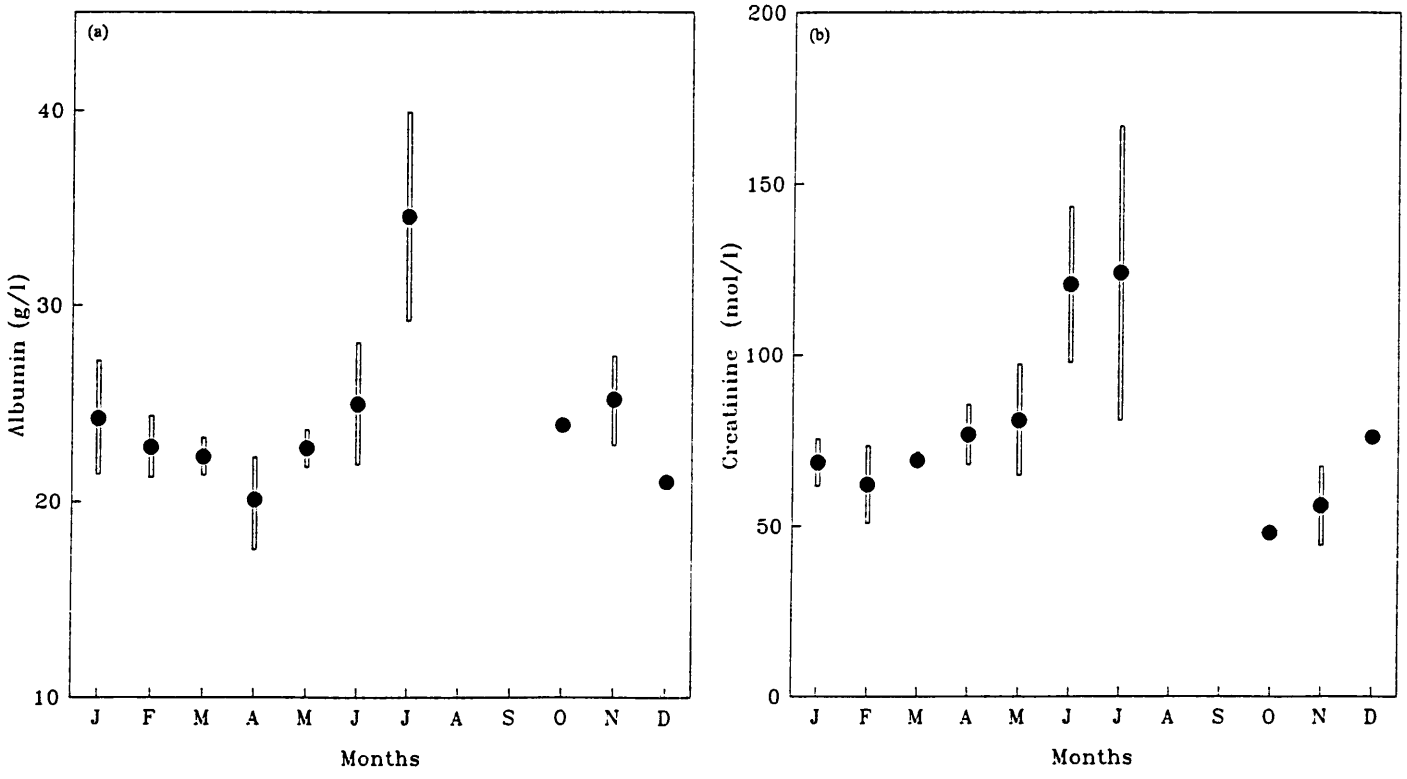


Figure 5.4 Seasonal change (means; with standard deviations) of (a) albumin values (g/l; n=31) and (b) creatinine values (umol/l; n=31) for free-ranging aardwolves.

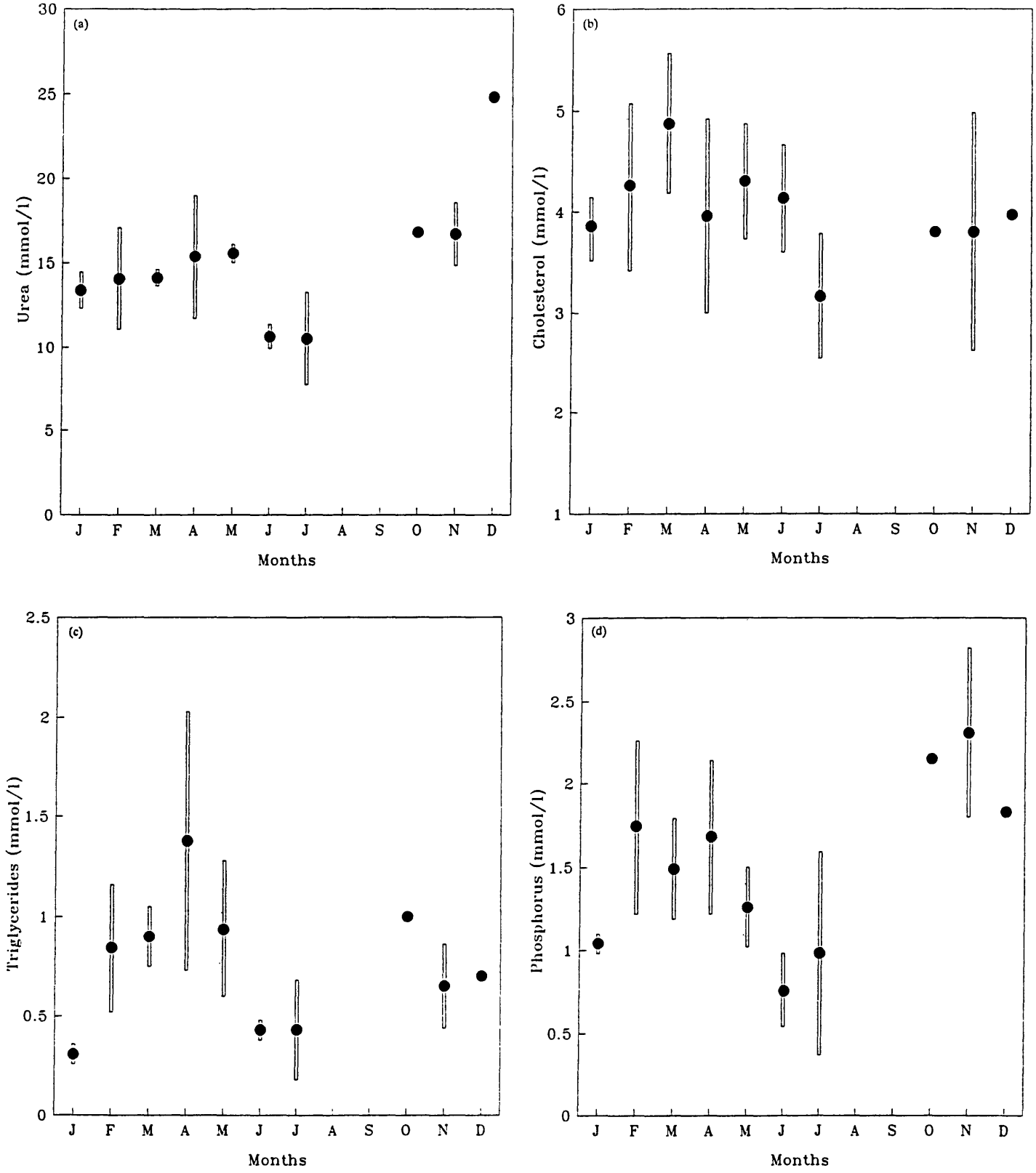


Figure 5.5 Seasonal change (means; with standard deviations) of (a) urea values (mmol/l; n=31), (b) cholesterol values (mmol/l; n=31), (c) triglyceride values (mmol/l; n=30) and (d) phosphorous values (mmol/l; n=30) for free-ranging aardwolves.

DISCUSSION

The decline in body mass of aardwolves during winter is congruent with Richardson's (1987a) observations. He noted a decline of up to 20% in the body mass of aardwolves during winter, with a subsequent increase during early summer. The only other records of aardwolf body masses are found in Smithers (1983). Smithers gives the average body mass of males as 8,91 kg (range 7,83-9,99; n=10) and females as 8,73 kg (range 7,72-9,99 kg; n=5); however, no information is given as to the time of year these animals were weighed.

The body mass of aardwolves declines significantly from April to August. During this period, when food is scarce, aardwolves must rely heavily on their fat reserves. From August to September there is an increase in body mass followed by a decrease during October. These changes are probably related to an increase in termite activity and hence food availability during August and September, and an increase in the mass of females due to pregnancy. The subsequent drop in mass during October may be associated with parturition and an increased period of parental care at the den after the cubs are born during early-mid October (and therefore less time spent feeding) (Richardson 1987c). During the subsequent 3-4 months, lactation also places demands on the females energy reserves. Only during late-summer, when the cubs are largely independent of their parents and when the adults can allocate more time to foraging, was there an increase in the body mass of these adults. The only difference in the body mass of males and females was during June with the males weighing significantly less than the females during this month. During June, even though there is very little food available, the males are very active - scent marking and attempting to procure matings (Richardson 1987c). Males, during this period, will therefore be tapping at their energy reserves with a consequent decrease in body mass. Seasonal weight changes have been observed in other carnivores, for example gray wolves *Canis lupus* (Seal & Mesh 1983), European badgers *Meles meles* (Kruuk &

Parish 1983) and Blanford's fox *Vulpes cana* (Geffen, Hefner, Macdonald & Ucko 1992).

During this study there were no significant summer-winter differences in the SFIs of aardwolves. This could be related either to variation between individuals (as is obvious from the large standard deviations) or an error or bias in the technique. During winter there is a significant increase in insulation (Chapter 8) and this may result in a larger measurement during this season. Furthermore, variation in the use of the calipers (e.g. amount of pressure applied to the pinched skin) may result in biases. Nevertheless, trends were observed with a decrease in the SFI determined at three localities, *viz.* upperback, lowerback and waist (Figure 5.2). Changes were also apparent when the SFI of individual aardwolves was compared (Figure 5.3), with aardwolves A-D (adults) showing a definite decline in subcutaneous fat from late-summer to mid-winter.

Subcutaneous fat is viewed as a latent metabolic energy which can be mobilized in response to caloric demands imposed by climatic stresses, nutritionally harsh periods (Rock & Williams 1979), or changed physiological state (Schmidt-Nielsen 1985). The aardwolf's subcutaneous fat reserves must be one of its keys to survival during the winter months. Examination of aardwolf carcasses has revealed that adult animals have a thick, yellow subcutaneous fat layer during mid/late-summer. This fat is mobilized during winter and consequently is almost totally absent from carcasses examined during late-winter/spring. The ability to accumulate, store and use body fat is important to mammals which may have to face periods of uncertain food availability or environmental stress (Young 1976), and it appears as if these fat reserves, which are deposited when food is plentiful, are essential for the survival of adult aardwolves. Adults are more likely than juveniles to survive through the winter months because by this time they would have reached a suitable mass with a supply of fat (Hanks 1981; Kruuk & Parish 1983). The first winter is a critical period for juveniles aardwolves. The cubs do not have the resilience of the adults with their

accumulated fat reserves which were laid down during the preceding summer. This may explain the high mortality of immature animals during this season during bad years (Richardson 1985, 1987a). The fast growth rate recorded in juvenile aardwolves (Van Jaarsveld, Richardson & Anderson unpubl. data), and their apparent rapid deposition of subcutaneous fat (Figure 5.3; aardwolf E), may reflect their need to obtain a suitable body weight (and energy status) which would enable them to survive through their first winter.

In aardwolves a number of blood parameters varied between summer and winter and these changes may reflect nutritional differences between the seasons. The albumin and globulin values were significantly higher during winter and this, and particularly the elevated albumin levels, may be related to dehydration (Coles 1974). In two other studies, albumin and haematological characteristics were found to be the most sensitive indicators of bear *Ursus americanus* nutritional condition (Franzmann & Schwartz 1988). Increased values for total plasma proteins during winter may also be related to dehydration in aardwolves, as elevated total plasma protein concentrations have been observed in mammals on a restricted water regime (e.g. rabbits *Oryctolagus cuniculus*; Wood & Lee 1985). During winter aardwolves obtain less water due to a reduced food intake, and the fact that aardwolves are probably water stressed during this period is confirmed by observations in the field: winter is the only time when they have been observed to drink water (Richardson 1985; Anderson, Richardson & Woodall 1992). In the study on rabbits (Wood & Lee 1985), the sodium and potassium concentrations also decreased when the rabbits were maintained on a restricted water regime. In the present study, however, there were no differences between the sodium and potassium concentrations of summer and winter.

Urea in the aardwolves was higher in summer than winter and this implies a higher average food intake during the former season. Blood urea nitrogen (BUN) levels will rise within a normal range as the quality and quantity of protein ingested increases, however abnormal elevation can occur if protein is catabolized during food shortage

or owing to renal dysfunction (Searcy 1969). Blood urea in domestic dogs is dependent upon protein intake and can increase significantly for a number of hours after a meal (Bressani & Braham 1977, cited by Seal & Mech 1983). The lower values of urea nitrogen during winter also suggest that gluconeogenesis from amino acids decreases during this period of low food availability. However, when approaching starvation, mammals catabolize muscle protein to maintain adequate levels of energy metabolites. Under such circumstances BUN levels may be elevated, and consequently give a false impression of physiological condition. This has been found in fasted gray wolves where serum urea nitrogen levels were elevated during the fast (Delgiudice, Seal & Mech 1987).

Creatinine levels were greater for aardwolves during winter. Elevated creatinine has also been found in hibernating black bears which was attributed to reduced renal function during hibernation (Hellgren, Vaughan & KirkPatrick 1979). High creatinine during winter in aardwolves may be due to reduced excretion and defecation during this season as a result of hypophagia. Higher creatinine levels during fasting in wolves (Delgiudice, Seal & Mech 1987) conforms with the findings in the present study. Creatinine levels were higher in adult aardwolves than juveniles during winter. Blood creatinine concentration is proportional to total muscle loss (McGlivery 1983, cited by Hellgren *et al.* 1989) and thus would therefore tend to be higher in larger individuals (*viz.* adults aardwolves).

Serum lipids also varied on a seasonal basis, with cholesterol and triglycerides values for aardwolves being higher during summer, and this also conforms with the study on wolves (Delgiudice, Seal & Mech 1987). Hellgren *et al.* (1989) also reported a seasonal variation in triglycerides in black bears. Seal, Mech & van Ballenberghe (1975) equated lower cholesterol values with a lower intake of animal flesh in wild gray wolves. Cholesterol is synthesized in the liver and other tissues from various amino acids, carbohydrates and fatty acids when they are supplied in excess of metabolic needs (Gordon 1982). Thus a reduction in cholesterol levels should either

indicate a reduction in the quality of the diet (Coblentz 1975) or a reduced food intake, and chronic malnutrition would be expected to promote hypocholesteremia (Searcy 1969). Cholesterol is a good indicator of the nutritional status of mammals as it is directly proportional to the quantity and quality of the diet and less affected by severe, short term physiological stresses (Coblentz 1975).

Juvenile aardwolves had significantly higher inorganic phosphorous levels than adults. Phosphorous absorption correlates positively with calcium metabolism and is important in bone metabolism (Searcy 1969). Higher phosphorous levels have also been found in juvenile coyotes *Canis latrans* (Smith & Rongstad 1980) and black bears (Hellgren *et al.* 1989). High levels of phosphorous in juvenile aardwolves can be attributed to greater osteoblastic activity in these animals, while higher phosphorous levels during summer may be attributed to a higher dietary intake. The summer elevations in WBC counts may reflect a greater vulnerability to infections during this period of increased activity.

No significant sex, age or seasonal differences were found in serum glucose levels of aardwolves. Glucose varies with diet, time of day, age, environmental condition, activity and stress (Seal & Mech 1987) and, unless all these conditions are taken into account, plasma glucose can only be of limited value for estimation of physiological condition.

To conclude, winter food stress in aardwolves is manifested in a seasonal change in body mass which can be partly attributed to a depletion of subcutaneous fat reserves. Changes in blood chemistry and blood haematology characteristics can be ascribed to a reduced intake of food and water during the winter months. Body mass, together with a seasonal variation of certain of these blood parameters, such as albumin, total plasma proteins, creatinine, urea, cholesterol and triglycerides, provide a reliable indication of the body condition of free-ranging aardwolves.

CHAPTER 6. THE DEN ENVIRONMENT AND ITS USE BY THE AARDWOLF

Abstract

Den use by aardwolves and the physical characteristics of these dens was examined. Aardwolf dens usually only had one entrance with a single, long tunnel. One of three dens excavated had a slightly enlarged chamber at the end. Aardwolves did not dig their own burrows but enlarged the burrows of springhares *Pedetes capensis*, although in the absence of springhares they can dig their own. The amount of time spent in the den each day varied from approximately 15 h during summer to 20 h during winter. The aardwolf den provides a favourable thermally stable environment, is used for the rearing of young, and as a refuge to evade predation from black-backed jackals.

INTRODUCTION

In arid or semi-arid environments there are considerable daily and seasonal temperature fluctuations. Small- and medium-sized mammals which inhabit these areas use behavioural and physiological means to escape the associated environmental stresses (Louw & Seely 1982). These animals often escape from the heat or cold by retreating to the thermally stable microclimate of the den. The aardwolf is one such mammal.

During winter, when *Trinervitermes* termites are unavailable (Richardson 1987a,b), aardwolves spend a greater proportion of time in the den. An increased period of inactivity (Richardson 1987b), a thermally stable den environment, and huddling and hypothermy (Chapter 8) while inactive, contribute to the aardwolf's ability to survive through this stressful period. Dens are also important for the rearing of young and as a refuge to evade predation from black-backed jackals *Canis mesomelas* (Richardson 1985).

Despite the important ecological significance of dens, very little information is available on their characteristics and the usage of these refugia by aardwolves (Richardson 1985; Smithers 1983). The purpose of this chapter, therefore, is to describe the physical characteristics of aardwolf dens and to elaborate on their significance to the ecology of the aardwolf. Comparisons are also made with the denning behaviour of the closely related, and often sympatric, hyaenids.

MATERIALS AND METHODS

Dens were located by following aardwolves (Richardson 1985; Anderson & Richardson 1992) until they retired to these refugia late at night, or during the early hours of the morning. Alternatively, dens were located by determining the position of inactive, radio-collared aardwolves in their dens. The position of all dens were marked by placing a metal stake in a termitarium within a few metres of the den entrance.

The length of time (i.e. per day) that aardwolves spent underground in the shelter of their dens was determined by noting the time of emergence from, and time of retirement to, their dens. The period of time (i.e. number of days) that specific dens were utilized by individual aardwolves was also noted.

Several characteristics were determined for active aardwolf dens: (1) slope of the burrow entrance, determined using a clinometer (Suunto CO., Helinsky, Finland); (2) burrow entrance orientation, determined with a compass; (3) number of burrow entrances; and (4) the width, height and depth (measured from ground surface above the centre of the entrance to the roof of the entrance) of each burrow entrance was measured.

Two dens were excavated to determine the internal structure of the burrow architecture. The width, height and depth of the burrows were determined at the

entrance and then at intervals along their length. In addition, the compass orientation of the entrances were determined and the orientation of the burrows were noted if there was a change in burrow direction. The burrow architecture of a den excavated by Richardson (1985) is also presented in this chapter.

The temperature of an unoccupied aardwolf den was determined during mid-summer (December) and mid-winter (June) using a KM 1202 multi-channel temperature recorder (Kane May, Welwyn Garden City). Den temperatures (T_ds) were recorded by inserting a thermistor 2,5 m down the length of the burrow from the entrance. An additional thermistor was placed in a black ball on the ground, outside the den. T_d and black ball temperatures were determined every hour, and hourly ambient temperatures (T_as) were obtained from the Kimberley Weather Station at the B.J. Vorster airport, approximately 5 km west of the study area.

Air samples were taken from two occupied aardwolf dens to determine the CO_2 content of the den air. One was occupied by an adult aardwolf and her three cubs, and the other by an adult male. The occupants had been present in their dens for at least 6 h prior to the air samples being taken. Samples were taken 3 m from the entrance after extraction of all the "dead-air" from the tubing. Samples were collected and stored in Douglas air bags. The CO_2 concentration of the samples was determined using a model Li-6262 CO_2/H_2O analyzer (Li Cor, Nebraska, USA).

RESULTS

Den usage

Dens were regularly slept in for about 6-8 weeks before a different den was used. Adult females, however, regularly (as often as every 3-5 days) moved their cubs to alternative dens once the cubs were two months old. One female was observed to move her cubs to alternative dens six times during a period of eight weeks. The time

lapse between when a den ceased to be slept in, and then became active again, was highly variable but was generally between 6-18 months. The time of departure from dens and time of retirement to dens was highly variable throughout the year but more consistent within a specific season (Table 6.1), with aardwolves spending a significantly longer period in their dens per day during winter ($t=5,2$; $p<0,001$) (Figure 6.1a-c).

Den characteristics

The entrance to a typical aardwolf den is illustrated in Figure 6.2. All 42 dens examined had only one entrance. Den entrances were randomly orientated ($x^2=2,0$; $df=3$; $p>0,5$), with nine entrances facing south (135-225^o), 14 facing east (45-135^o), 11 facing north (315-360^o, 0-45^o), and eight facing west (225-315^o). The characteristics of the aardwolf den entrances are presented in Table 6.2. The aardwolf burrow entrances were half-circle shaped, approximately 150% wider than high, and easily distinguished from aardvark *Orycteropus afer* and springhare *Pedetes capensis* burrows (Figure 6.3), the two prominent burrowing species in the study area. The slope of the den entrances were steep (Table 6.2), while the slope of the ground into which the burrows were excavated was usually flat or with a gentle slope.

The tunnels of the three excavated dens were narrow and well defined (Table 6.3) (Figures 6.4-6.6). Two of these burrows (A & B, Figures 6.4 & 6.5) narrowed into smaller springhare burrows, with a tunnel height and width of approximately 10 cm and 15,5 cm, respectively. The most noticeable features of these three aardwolf dens, and the 42 dens from which measurements were taken, were the single entrances and the single, narrow passages. The tunnels of dens A and B had no obvious enlargement at the end. The tunnel of den C, however, had a slight chamber enlargement (approximately twice as wide as the tunnel). The ends of the three excavated burrows were not lined with any insulative material such as grass, litter or fur, although the chamber floor of den C was covered with very fine sand.

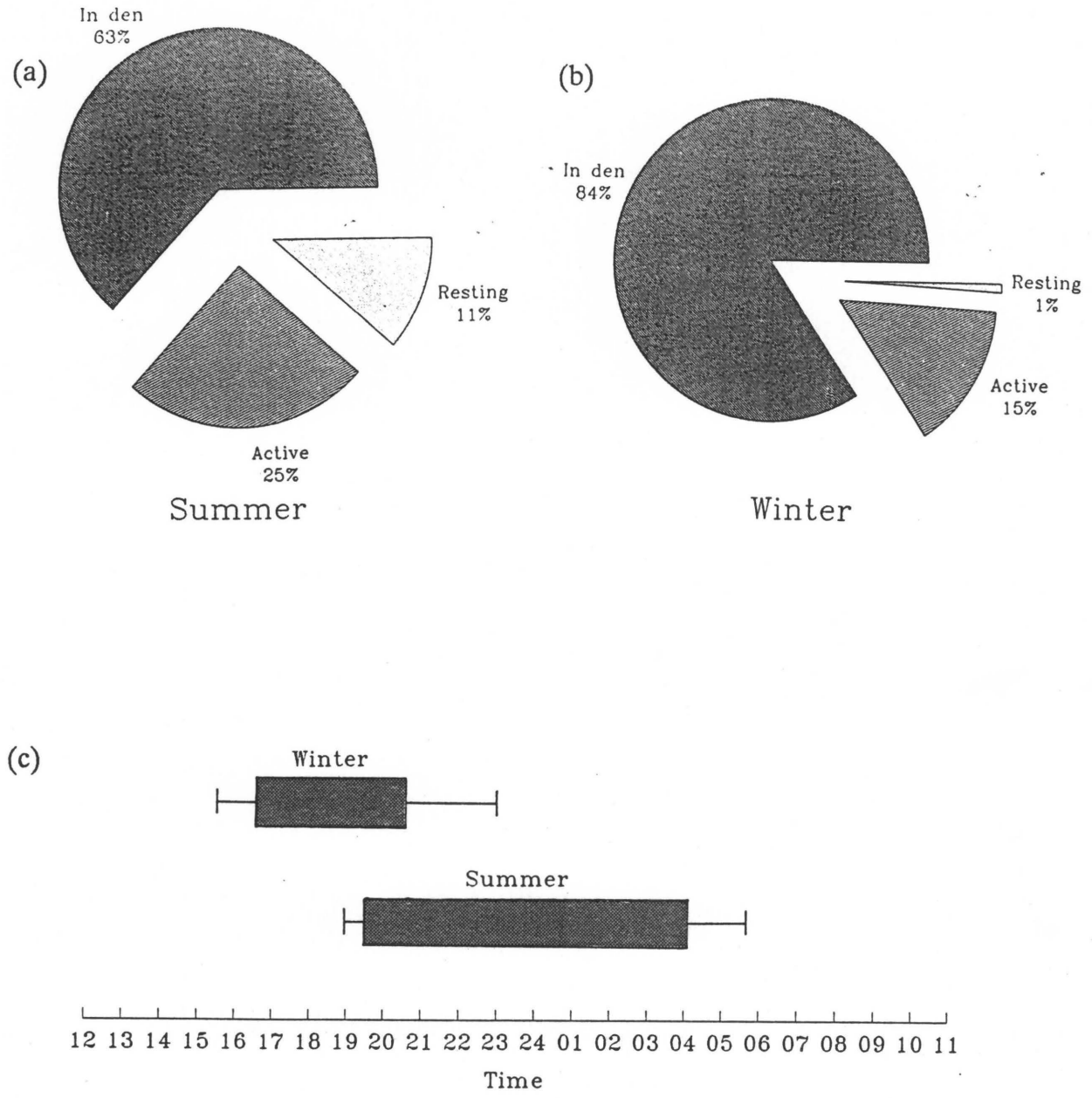


Figure 6.1 The time six aardwolves, followed for two nights each during summer and winter, were active above ground, inactive in the den, and inactive outside the den (i.e. resting) during (a) summer and (b) winter. The time spent out of the den (with standard deviations) is illustrated in (c) for summer and winter.

Figure 6.2 An aardwolf den.

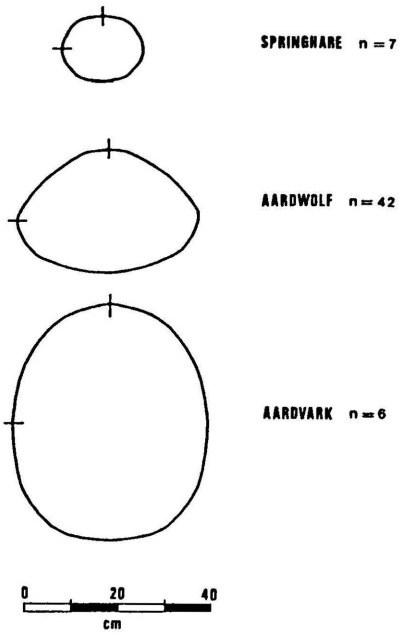
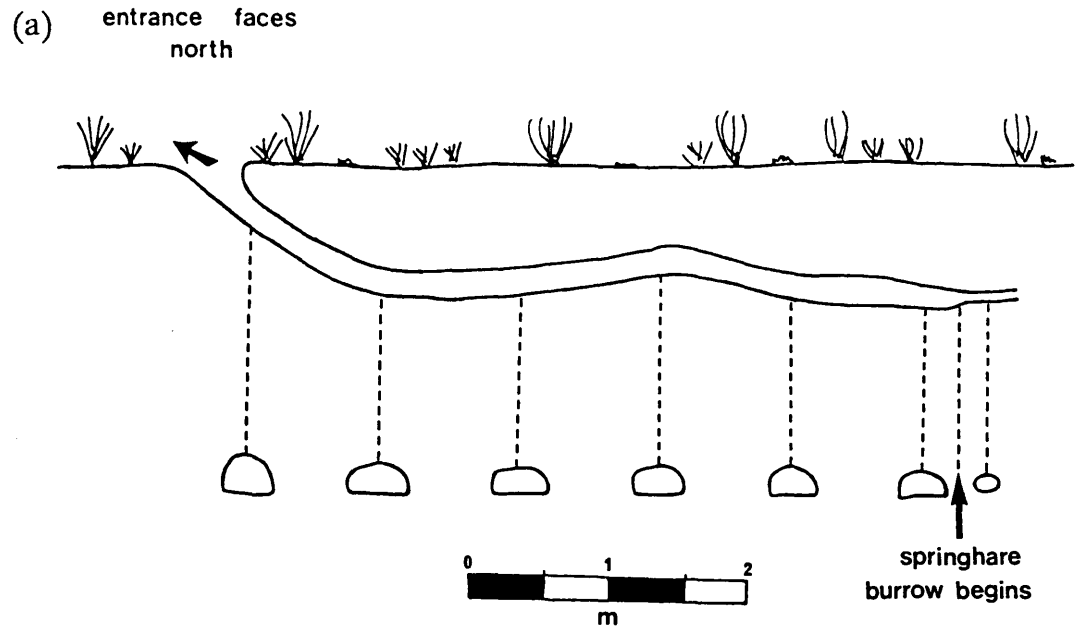


Figure 6.3 The size (with standard deviations) and shape of springhare *Pedetes capensis*, aardwolf and aardvark *Orycteropus afer* dens (springhare and aardvark den entrance measurements are from Richardson (1985)).



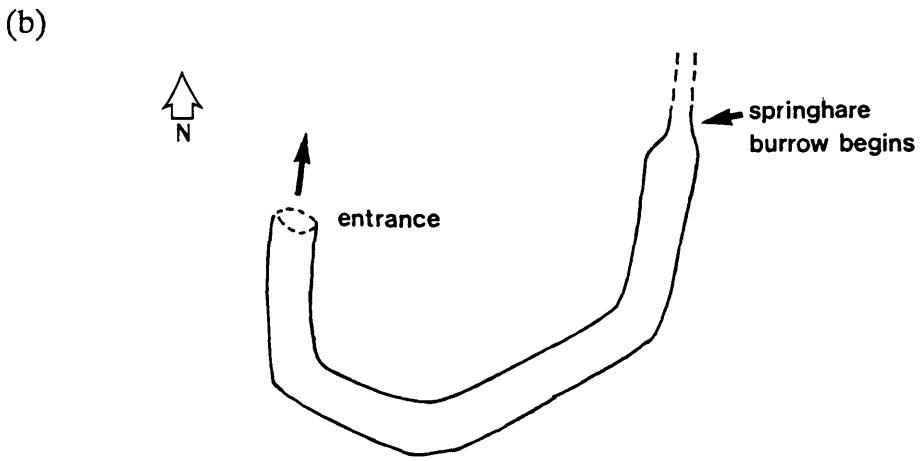


Figure 6.4 Diagrammatic representation of an excavated aardwolf den (Den A): (a) lateral view, (b) view from above.

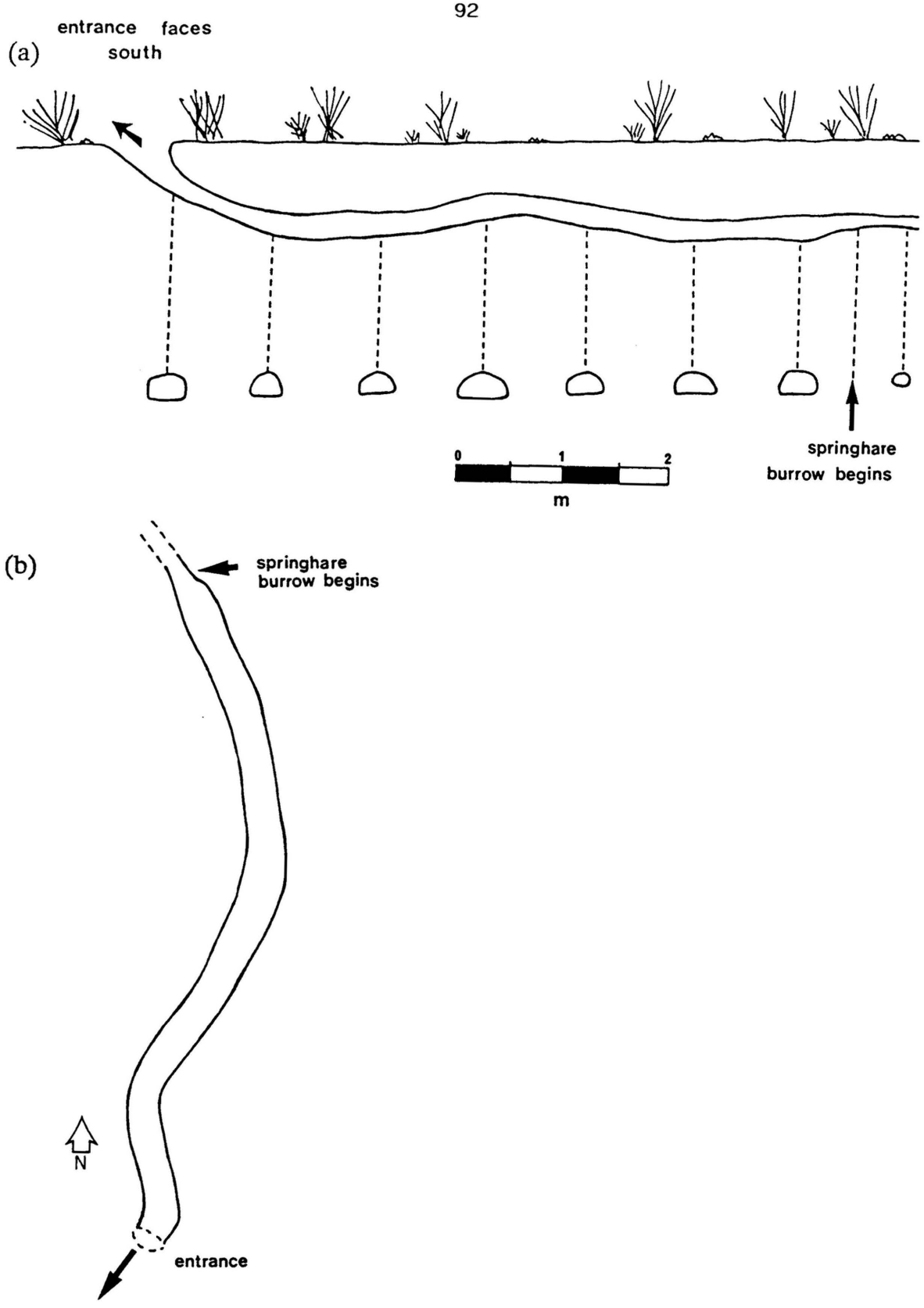


Figure 6.5 Diagrammatic representation of an excavated aardwolf den (Den B): (a) lateral view, (b) view from above.

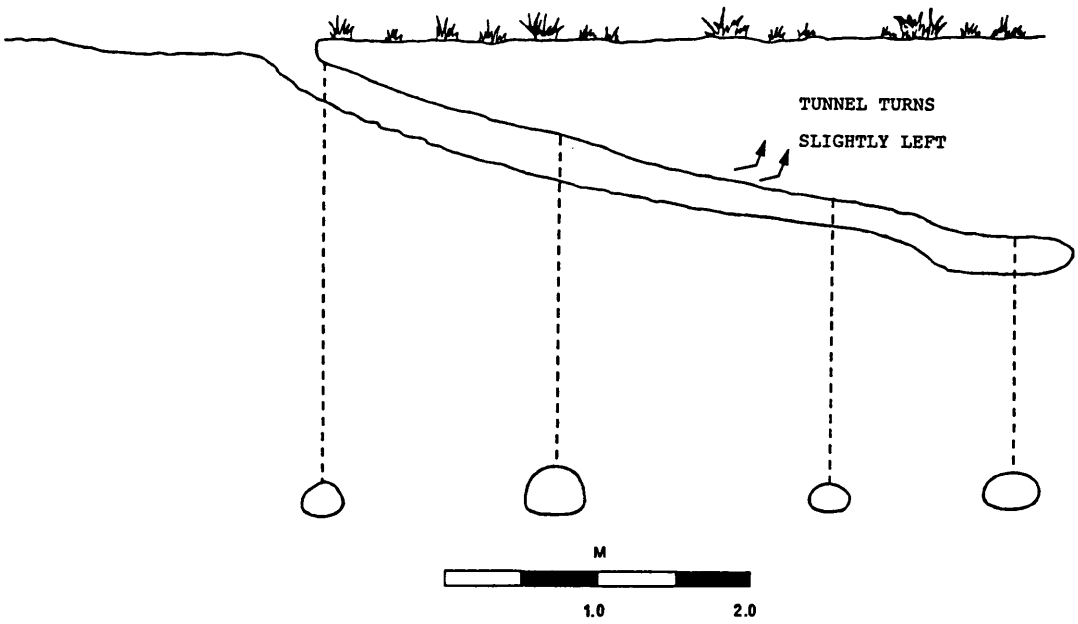


Figure 6.6 Diagrammatic representation of the lateral view of an excavated aardwolf den (Den C) (after Richardson (1985)).

Table 6.1 Den utilisation by adult male (n=3) and female (n=3) aardwolves during mid-summer (December/January) and mid-winter (June/July) (standard deviations and the number of observations are indicated in parentheses)

	Summer	Winter
time of emergence	19h20 min (±30 min, n=18)	16h28 min (±57 min, n=23)
time of retirement	04h04 min (±91 min, n=12)	20h28 min (±239 min, n=18)
time spent in the den	15h12 min (±86 min, n=12)	19h57 min (±239 min, n=18)

Table 6.2 The mean depth, width and height (mm), and slope (^{o}) (with standard deviations) of 42 aardwolf den entrances

	Depth	Width	Height	Slope
mean	49,6	38,0	25,5	19,1
SD	14,0	6,9	6,0	5,7

Table 6.3 Tunnel dimensions of the three excavated aardwolf dens (with standard deviations and number of measurements in parentheses). Data for den C are from Richardson (1985)

	Den A	Den B	Den C	mean
Tunnel length (m)	6,5	5,1	5,4	5,7
Tunnel height (cm)	20,7±1,8 (n=7)	21,7±2,7 (n=6)	22,4±5,5 (n=4)	21,6
Tunnel width (cm)	34,8±4,4 (n=7)	36,8±3,6 (n=6)	32,0±5,7 (n=4)	34,5

The average daily T_ds were 27,2±0,2°C and 12,2±1,2°C during summer and winter, respectively (Figure 6.7). The CO_2 content of the den air samples were 0,180% (den occupied by the female with her three cubs) and 0,338% (den occupied by the adult male).

DISCUSSION

An advantage of occupying a subterranean den is that it provides protection from predators. This is of particular importance to aardwolves when they have young cubs which are prone to predation by black-backed jackals (Richardson 1985); and also to adults when they are inactive and in a state of lethargy (hypothermy) during winter (Chapter 7). Aardwolves have well developed canines which can be used in defence against jackals, but denning appears to be an equally important anti-predatory strategy. Similarly, Carter & Encarnacao (1983) suggest that digging abilities and burrows afford armadillos greater protection from predators than does their carapace.

Relative to their body size, aardwolf burrows are very narrow. This suggests that they do not require very much space inside their dens and keep them as narrow as possible to limit air flow and to offer protection against large carnivores. A single entrance into an aardwolf den is also advantageous because it limits access by predators; however, this may preclude the use of an alternative exit as an escape route should a predator enter the den. In an attempt to evade predation an aardwolf was observed to block the burrow entrance with sand while she was being excavated (pers. obs.). On the same occasion, 4-5 week old cubs attempted to evade being caught by moving up the very narrow springhare burrow extension (see Figure 6.4 & 6.5), filling this passage with soil behind them. This is an advantage of utilizing/enlarging springhare burrows, and this digging behaviour recorded in the aardwolf cubs may explain why they have well developed claws at a young age (pers. obs.). The prime function of brown hyaena *Hyaenna brunnea* and spotted hyaena *Crocuta crocuta* dens is also to

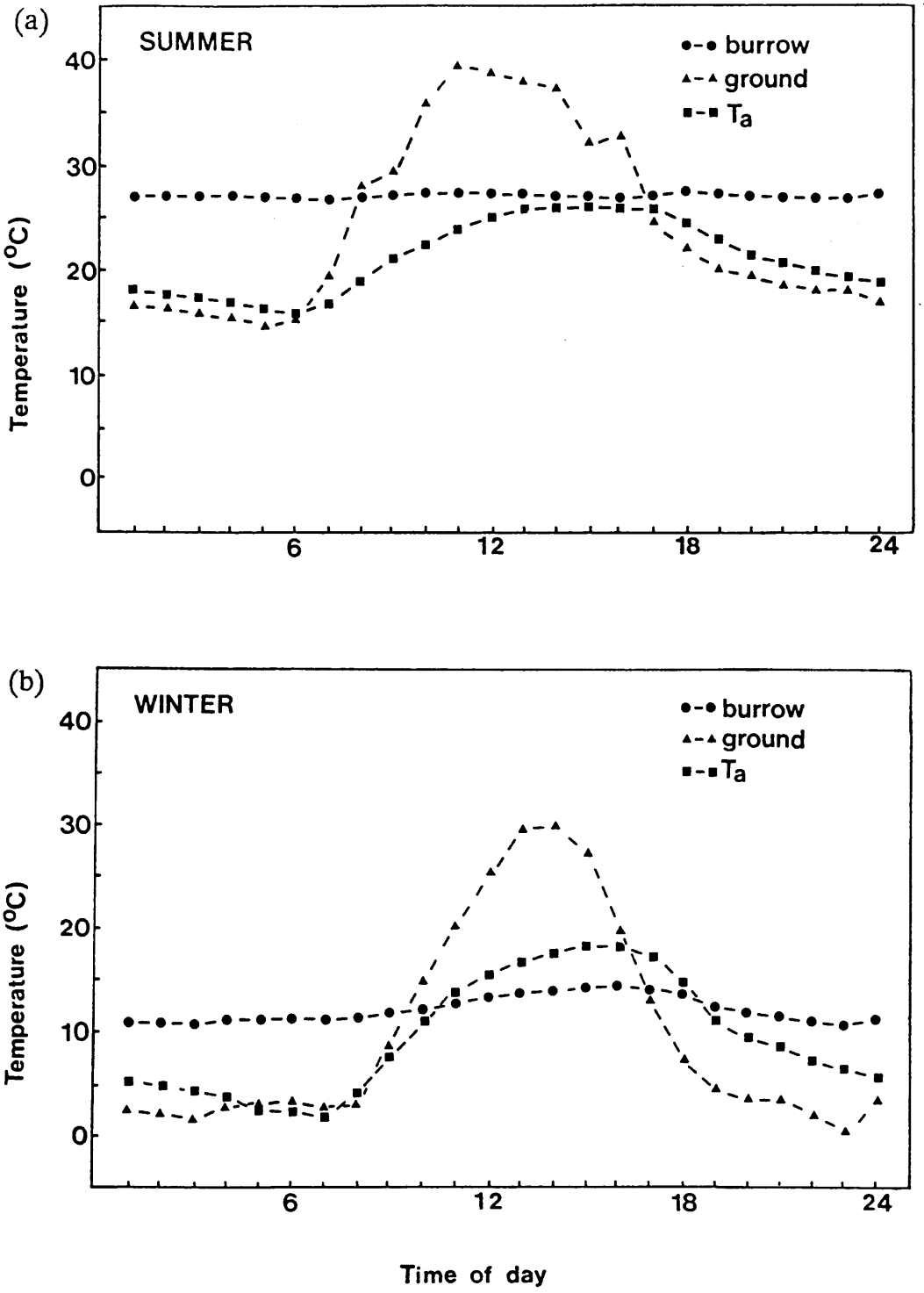


Figure 6.7 The temperatures of an aardwolf den, the soil surface temperature in the vicinity of the den and ambient temperatures from the Kimberley Weather Office (B.J. Vorster airport) during (a) summer and (b) winter.

provide protection for the cubs (Mills 1990). The entrances of the dens are large but they narrow down to small, oval-shaped tunnels, which are large enough for the cubs but not large enough for adult hyaenas or other large carnivores, such as lions *Panthera leo*, to enter (Mills 1990). The narrow "springhare tunnel" extension in the aardwolf dens and the narrow tunnel in hyaena dens appear to serve a similar function.

Aardwolves have been observed to move their cubs to new dens on a regular basis once the cubs are 7-8 weeks old (pers. obs.). Frequent den movement when the cubs are young is almost certainly an anti-predatory strategy. With a number of aardwolves occupying a den (adult female and her 1-4 cubs), the scent of the occupants must be easily detectable. Aardwolves are hygienic and den entrances are always devoid of scats but, nevertheless, regular den movement may limit jackals and other carnivores detecting their presence at the den. It has been suggested that brown and spotted hyaenas may move dens as a result of a build up of fleas in the dens (Mills 1990), and it is possible that this may also be the case with aardwolves, although there is no evidence to support this.

Until aardwolf cubs are three months old there is almost a constant vigil by adult aardwolves at the den (Richardson 1987c). In contrast, brown and spotted hyaenas rarely guard their cubs and Mills (1990) has suggested that the need to leave guards is obviated by the structure of the dens. Aardwolf cubs of all ages immediately run into the den if alarmed. Adult aardwolves seem to know the location of their dens well because when chased at night in the lights of a vehicle (Smithers 1983), or by another aardwolf, or a threatening black-backed jackal, they head straight for the den (pers. obs.), even running distances in excess of 1 000 m (Smithers 1983).

Aardwolves are not well adapted diggers (Anderson, Richardson & Woodall 1992) like other ant- and termite-eating mammals (e.g. Redford 1987). They do not dig for their prey but lick foraging termites off the soil surface, and hence they do not possess

well developed claws and powerful limbs necessary to excavate a subterranean food source. Consequently, aardwolves are not proficient at excavating burrows and they preferably enlarge the burrows of springhares to suit their own requirements. The closely related and often sympatric hyaenas also do not dig their own dens. Spotted hyaenas may often take over porcupine *Hystrix africaeaustralis* dens, while brown hyaenas regularly occupy abandoned aardvark dens (Mills 1990). In captivity, however, aardwolves occasionally excavate burrows (pers. obs.). Moreover, Smithers (1983) observed that aardwolves may be able to dig their own burrows in the absence of existing holes. Aardwolf burrows examined by Smithers (1983) originated in springbok *Antidorcas marsupialis* middens where the hard calcareous surface layer had been broken.

Most aardwolf dens only have one entrance, although Richardson (1985) found that a few dens have two entrances. This is in contrast to some species which may have more complex den systems with many entrances and chambers. For example, the dens of the aardvark may have many entrances and underground chambers, interconnected by an extensive burrow system (Melton 1976). The direction of aardwolf burrow entrances are randomly orientated, and dens are therefore not selected with the entrance facing away from the prevailing wind, as has been found in armadillos (Carter & Encarnacao 1983). This may be because aardwolves generally enlarge springhare burrows and do not dig their own, which would enable them to select for specific requirements. It has been suggested that armadillos position their burrow entrances away from direct exposure to the wind to limit heat loss, while coyotes *Canis latrans* orientate their dens to the south to maximize solar radiation (Harrison & Gilbert 1985). The entrances of aardwolf dens, however, are sufficiently below ground level with little direct exposure to the prevailing wind and it is unlikely that wind affects the occupants. The effect of wind on the den occupants would also be greater if there was more than one den entrance. The size and shape of the entrance of aardwolf dens are very characteristic, with distinct differences between these and the burrows of other burrowing species, such as the aardvark and springhare.

The aardwolf den provides an important refuge for the successful rearing of cubs. During early to mid-October, 1-4 cubs (Smithers 1983; Richardson 1987c) are born in the protective confinement of the subterranean dens. Here they remain for approximately 5-6 weeks. From the age of four weeks they emerge from the den for short periods when a parent is present. Extended excursions from the den are only undertaken once the cubs are 12 weeks old, and by the time they are five to six months old they readily occupy alternative dens, either sleeping alone or with a partner (a sibling or a parent) (Richardson 1985). During mid-winter (June/July) the cubs often return to share a den with the adult female. The cubs rarely shared a den with the adult male.

Aardwolf dens, particularly dens in the Kalahari sandveld area of Benfontein, do not have a very long "life" and may collapse after it has rained. Dens are, however, re-excavated, and one den which collapsed was re-excavated and re-occupied 18 months later. Aardwolves only occupy dens for short periods, usually varying between 1-12 weeks. However, this depends on the time of the year, whether cubs are present, and whether the occupant was disturbed at the den. One female was observed to use a specific den for 14 months, and the den was only deserted after it partially collapsed during a thunderstorm. Dens for aardwolves are readily available (due to the large number of springhares in the study area) and therefore these refuges are apparently not a limiting factor.

Dens are not distributed uniformly within the aardwolf territories. Richardson (1985; 1991a,b) determined the positions of all the aardwolf dens in a single intensively studied territory, and found that there tended to be more dens in the border areas of the territory. These dens served as focal points of territorial activity and they were scent marked more frequently (together with peripheral middens) than dens and middens in the centre of the territory. The den is the centre of social activity in social carnivores, such as in brown and spotted hyaenas (Mills 1990), while in the aardwolf

the preference for a greater frequency of scent marking at the peripheral dens indicates that they may serve more of a territorial function (Richardson 1991). Within a single aardwolf territory an average of 5,8 dens (range 2-9, n=5) is used by the adult aardwolf pair each year, and approximately 18% (range 8-29%) of these dens used during any specific year are also utilized the following year (Richardson 1985).

There is considerable annual variation in the time aardwolves emerge from and retire to their dens, and consequently variation in the length of time spent in the den (Richardson 1987a). The daily and seasonal activity periods of aardwolves can, however, be directly attributed to the availability of *T. trinervoides* and *Hodotermes mossambicus* (Richardson 1987a) and to a lesser extent to the aardwolf's mating behaviour (Richardson 1987c).

The CO_2 content of the air samples taken from the aardwolf dens was greater than atmospheric CO_2 but still considerably lower than the CO_2 concentration recorded in the burrows of some other species. For example, the CO_2 concentration in the burrows of golden hamsters has been recorded to be as high as 5,7-10,8% (Kuhnen 1986). CO_2 concentration in other mammalian burrows may escalate to 10-15% (Kennerley 1964, Studier & Baca 1968, cited by Kuhnen 1986; Studier & Proctor 1971; Williams & Rausch 1973).

Living or resting in burrows offers a favourable microclimate in terms of stable T_a and humidity. In a semi-arid region, such as the northern Cape, there are extreme temperature fluctuations on a daily and a seasonal basis. Daily T_a during summer regularly exceeds 35°C, while the T_a during winter frequently drops below freezing point. The daily T_d within a season is fairly constant, while there is a considerable variation between the seasons. T_ds during summer are high but within the thermoneutral zone (TNZ) of aardwolves (McNab 1984, Chapter 8). Although the T_d during winter is below the TNZ of aardwolves, it is still considerably warmer than the T_a outside the den. It is likely that the relatively low T_d, together with an increased

CO_2 concentration in the den during winter (exacerbated by the extended period spent underground, and den sharing), may stimulate hypothermy in this species (see Kuhnen 1986). Aardwolves lower their body temperature (T_b) by up to 4-6^oC while inactive in their dens during winter (Chapter 7). The den during winter, therefore, may not only provide the cues (hypercapnic and hypothermic conditions) necessary for a lowering of metabolism and drop in T_b, but also provide a protective environment to enter into this hypothermic state. During winter aardwolves frequently share their dens with siblings or one of their parents and it can be assumed that huddling takes place. Huddling reduces their effective surface area, resulting in a reduction in heat loss. Owing to the small size of the den chamber, heat produced by the occupant(s) will also raise the T_d to some extent. A large den chamber would be advantageous in that it would facilitate movement, but would contribute to greater heat loss during winter. The three dens examined in this study were not lined with insulative material, as is found in the dens of other animals, and in particular hibernating mammals, such as black bears (Tietje & Ruff 1980).

CHAPTER 7. SEASONAL AND CIRCADIAN TEMPERATURE PATTERNS IN THE AARDWOLF

Abstract

Body temperatures (T_b) of six aardwolves were monitored in the field during summer and winter with implanted temperature-sensitive radio transmitters. An annual T_b pattern was apparent with mean daily summer T_b greater than mean daily winter T_b. A daily T_b rhythm was also evident during these two seasons. The greatest difference between mean active and mean inactive T_b occurred during winter, with averages of 37,3°C and 35,5°C, respectively. The T_b of two aardwolves during winter, however, dropped to an average of 33,2°C at 09h00 during their inactive phase. The lowest recorded T_b in any individual animal was 31,2°C. Activity times were shorter during winter, with aardwolves spending a significantly greater proportion of time in the den. As a result of the drop in T_b, savings in energy of up to 17,7% occurred during winter. Two captive aardwolves, acclimated to a summer photoperiod and temperature regime, but on a restricted diet, also showed an exaggerated daily T_b fluctuation. This suggests that hypothermy may be related to winter food limitations, rather than seasonal changes in T_a or photoperiod. I propose that the observed drop in T_b during winter is a physiological adaptation that enables the aardwolf to cope with periodic limitations in energy supplies.

INTRODUCTION

Nocturnal endotherms living in semi-arid areas are confronted with physical and ecological stresses which they have to overcome on a daily and a seasonal basis. Typically these include ambient temperature (T_a) fluctuations, water scarcity and unpredictable food resources (Louw & Seely 1982). Endotherms living in these areas cannot be adapted to the environmental conditions of a specific season, as they may be at a disadvantage with the stresses imposed by a contrasting season. Therefore,

many small endotherms use torpor (hypothermy) to avoid the extremely high costs of maintaining normothermic T_bs during periods of low food availability (Snyder & Nestler 1990). The most obvious effect of hypothermia on the biology of endotherms is a reduction of their energy requirements for the maintenance of T_b. How much energy is conserved depends on body size and the degree of hypothermia the animal attains. It has been determined that changes in core or skin temperature of an endotherm result in significant energy and water savings (McClure & Porter 1983; Bakko, Porter & Wunder 1988). Hypothermy could, therefore, be advantageous to the aardwolf, particularly during winter when *T. trinervoides* are largely unavailable (Richardson 1987a).

The purpose of this study was (1) to monitor the T_b patterns of free-ranging aardwolves during summer and winter to determine whether significant changes in T_b occur on a daily and/or seasonal basis; and (2) to determine the implications of a variable T_b (if it does occur) on energy and water conservation.

MATERIALS AND METHODS

Six free-ranging aardwolves (two adult males, three adult females and one subadult female) were immobilized (Anderson & Richardson 1992) and transported to a veterinary theatre in Kimberley for the implantation of temperature-sensitive radio transmitters.

The transmitters (IMP/400/L; Telonics Inc., Arizona, USA) were cylindrically shaped, 100 mm long and 35 mm in diameter, and encapsulated in a physiologically inert material (Figure 7.1). The transmitters weighed approximately 120 g, which is 1,2-1,6% of the body weight of the aardwolves and less than the 3-5% transmitter weight/body weight ratio recommended by MacDonald & Amlaner (1980).

The transmitters were calibrated before implantation in a stirred waterbath at 3°C intervals between 20-40°C, and re-calibrated after removal 8-12 months later to determine whether there was a drift in pulse rate. The transmitters were sterilized by immersing them in a Hibitane (ICI Pharmaceuticals, Johannesburg, RSA) and alcohol solution for 3-6 h before implantation, and then rinsed thoroughly in sterile water immediately prior to implantation.

Anaesthesia during surgery was maintained by administering an initial 1 ml dose of Intraval (50 mg/ml; Maybaker Animal Health, (Pty) Ltd, Halfway House, RSA), followed by subsequent 0,5 ml doses of this drug when necessary. The animals were placed in dorsal recumbency and a 12 cm^2 area of the abdominal wall was shaved, disinfected and prepared for surgery. A 5 cm ventral, longitudinal incision was made through the skin along the midline. The peritoneal cavity was entered by cutting through the *linea alba* and the temperature telemeters were implanted into the peritoneal cavity.

In four aardwolves a portion of the omentum was externalized and wrapped around the transmitter as recommended by Guynn, Davis & Von Recum (1987) (Figure 7.1). This method has been used successfully in the implantation of transmitters in leopards *Panthera pardus* and spotted hyaenas *Crocuta crocuta* (McKenzie, Meltzer, le Roux & Goss 1990). Guynn *et al.* (1987) have suggested that enclosing the transmitters in a fold of the omentum may prevent adhesion between the implanted capsule and peritoneal structures. In the other two aardwolves the transmitters were placed inside the peritoneal cavity and allowed to float freely (see Philo, Follman & Reynolds 1981). The transmitters were not attached to the body wall (which would facilitate retrieval) as this has had negative results in other studies, for example hernia development in a polar bear *Thalarctos maritimus* (Philo, Wolfe & Fassig 1979). The minor differences in core T_b, which would occur as a result of the transmitters being located at various positions within the abdomen, was not judged important enough to

warrant the risks involved with a transmitter secured to the peritoneal surface of the ventral abdominal wall.

The incision area was flushed with Pendistrep (Phenix SA (Pty) Ltd, Honeydew, RSA). The peritoneum, *linea alba* and subcutaneous fat were subsequently sutured using simple interrupted sutures of No. 1 chromic gut absorbable suture material. Skin wounds were closed with interrupted nylon sutures (Figure 7.2). Sutured wounds were topically treated with Kemi Spray (Panvet, C.E. Industries (Pty) Ltd, Kempton Park, RSA) and all the animals were given an antibiotic (Combimycin (Panvet, C.E. Industries (Pty) Ltd, Kempton Park, RSA) or Peni La (Phenix SA (Pty) Ltd, Honeydew, RSA)) by intramuscular injection immediately after surgery.

After surgery the animals were weighed. They were then returned to the study area and placed on the ground in lateral recumbency near the place of capture. Recovery was monitored from a vehicle from a distance of 20-30 m (Anderson & Richardson 1992). The immobilization and anaesthesia of the study animals was satisfactory in all cases. The duration of the surgical procedure was 30-45 min and the entire implantation procedure from darting to release lasted 2-3 h. All implants were successful and no post-operative complications, behaviour aberrations, pathology in the peritoneal cavity or mortalities occurred. The two males subsequently mated, as did the three adult females which also gave birth to cubs.

Four transmitters were recovered 8-12 months later. Two of the four transmitters originally wrapped in the omentum were encapsulated in a thin layer of slightly vascular, necrotic fibrous tissue originating from the omentum, and this may have resulted from bacterial contamination of the transmitters during surgery (Eagle, Choromanski-Norris & Kuechle 1984). One transmitter became loosely attached to the peritoneal wall but was removed with little difficulty. The other transmitter was not attached to any peritoneal structures or encapsulated in tissue and was recovered without difficulty. Compensation was made for the limited drift in pulse rate which

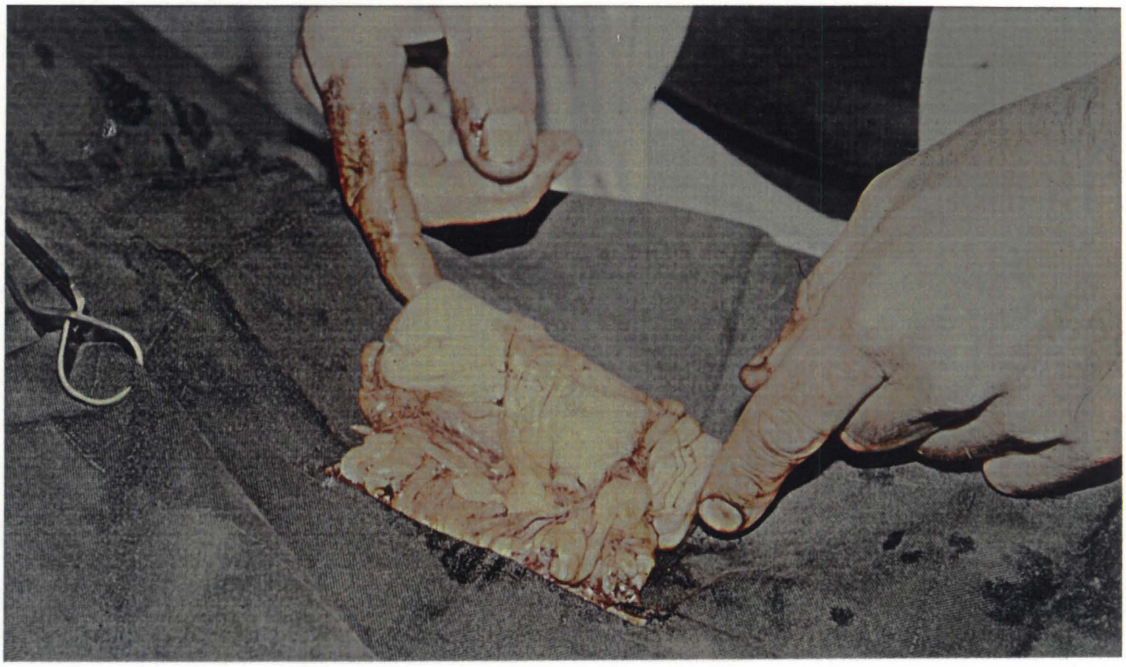


Figure 7.1 A temperature telemeter wrapped in a portion of the externalized omentum.

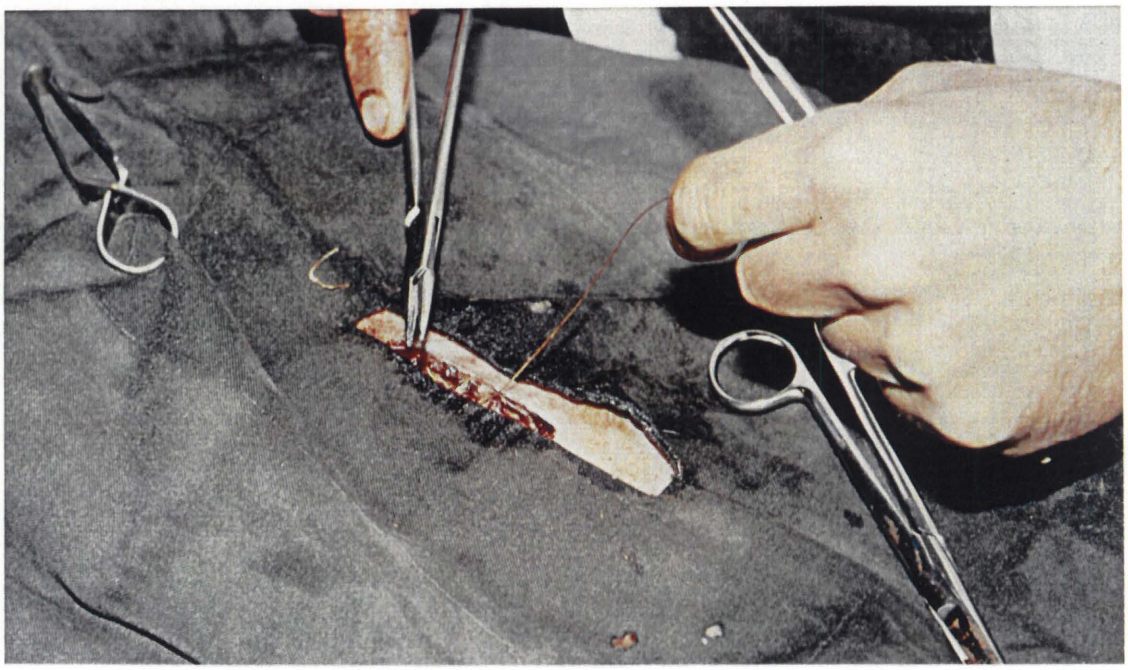


Figure 7.2 The 5 cm long skin wound being closed using No. 0 monofilament nylon sutures.

occurred between the initial calibration of the transmitters and the re-calibration after removal.

A Yaesu FT29OR receiver (Yaesu Musen Co., Tokyo, Japan) and a Yagi-type antenna were used to locate and record the T_bs of the aardwolves. T_b was monitored after a recovery period of at least three weeks. The ground-to-ground signal range was between 0-300 m for aardwolves inside burrows and approximately 0-800 m for active aardwolves. Optimal receiving range was approximately 50 m from underground animals and 100 m from above-ground animals. This enabled observations and T_b measurements to be made without disturbing the animals or interfering with their natural behaviour.

The T_b of each aardwolf was recorded at hourly intervals over two 24 h periods during summer (November-March) and two 24 h periods during winter (June/July). The number of pulses were counted for two minutes, in duplicate, and these two readings were averaged to obtain a mean count at each hourly interval. Activity times and denning times (i.e. time from retirement to, and departure from, the den) were determined, and the behaviour of each animal was noted at the time of T_b measurement.

Temperature telemeters were also implanted into the peritoneal cavity of two captive aardwolves (adult females). They were housed in concrete enclosures at the Experimental Farm, University of Pretoria (see Chapter 8 for further details). The T_b of these two aardwolves was recorded during November (i.e. summer photoperiod and temperature regime), at hourly intervals, for two 24 hour periods. In order to determine the influence of a reduced diet on T_b, these animals were maintained on a restricted diet (from three weeks prior to the experiment), simulating dietary conditions in the wild during winter. They were fed a daily diet of 67 g Pronutro (Cerebos food Corporation Ltd., Randburg, RSA) and 23 g dry, ground dogfood (Dogmor, S.A. Oil Mills, Universal Group Ltd., Randfontein, RSA).

The Mann-Whitney U test was used to compare the T_bs of aardwolves between, and within, the seasons (Siegel 1956). The Students t-test was used to compare the body masses of aardwolves and for a comparison between the summer and winter denning times (Snedecor & Cochran 1967). Results are presented as means with one standard deviation.

RESULTS

T_b of free-ranging aardwolves

The mean daily T_b of aardwolves during summer (T_b=36,6^{o}C) was significantly greater than the mean daily T_b recorded during winter (T_b=35,8^{o}C) (Z=8,90; p<0,01) (Table 7.1). However, this result is entirely due to the differences in T_b during the inactive phase of these two seasons (Z=8,41; p<0,01), as there was no difference between their T_b during the active phase of summer and winter (Z=0,55; p>0,2).

Aardwolves demonstrated a daily T_b cycle which was evident during summer and winter (Figures 7.3-7.4), but with the pattern being more exaggerated during winter. This cyclic pattern and the T_bs were similar for males and females during winter (Z=1,69; p>0,05) (Figure 7.3) and during summer (Z=1,28; p>0,05) (Figure 7.4) (Table 7.2). These data for each season were then combined.

The greatest amplitude of the daily T_b cycle occurred during winter (Figure 7.3) and during this season the mean T_b of active aardwolves was significantly greater than the mean T_b of inactive aardwolves (Z=8,30; p<0,01) (Table 7.3). During winter active aardwolves maintained an average T_b of approximately 37,3^{o}C but after returning to their dens their T_b decreased through the rest of the night and early morning until the middle of their inactive period (08h00-10h00). At 09h00 their average T_b was

Table 7.1 The mean body temperatures ($^{o}C \pm SD$) of six aardwolves during summer and winter. The sample size refers to the total number of hourly measurements

	Summer	Winter	Mann-Whitney U-test
24-h mean	36,6±0,6 (n=264)	35,8±1,2 (n=265)	(Z=8,90; p<0,01)
Active period	37,2±0,4 (n=79)	37,3±0,7 (n=38)	(Z=0,55; p>0,05)
Inactive period	36,3±0,5 (n=185)	35,5±1,1 (n=227)	(Z=8,41; p<0,01)
ΔT_b*	0,9	1,8	
09h00	36,1±0,3 (n=12)	34,1±1,6 (n=12)	(Z=2,71; p<0,01)

*ΔT_b = (T_b when active) - (T_b when inactive)

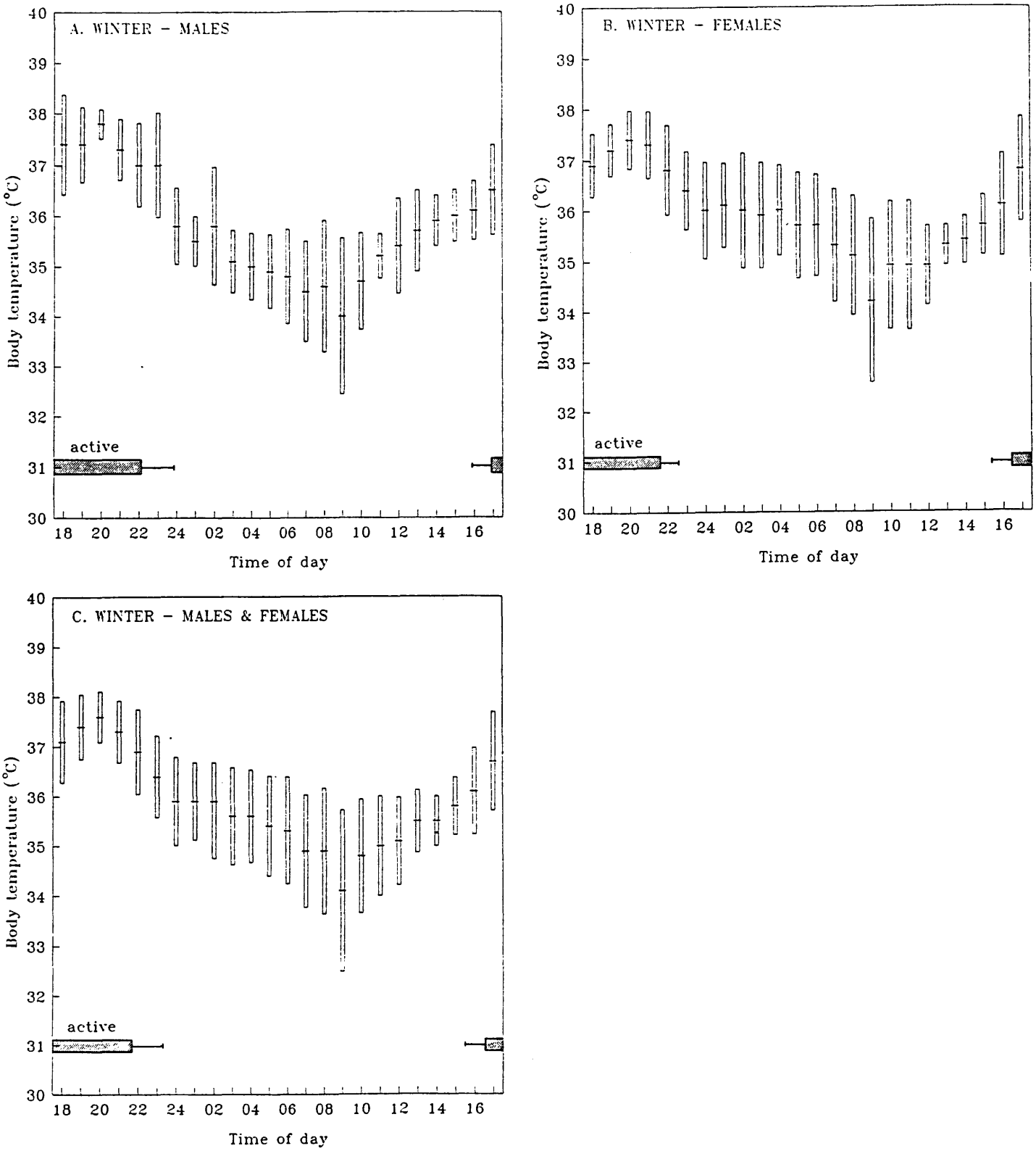


Figure 7.3 The body temperatures ($^{o}C \pm SD$) of six aardwolves measured at hourly intervals during winter. The activity period ($\pm SD$) is also indicated.

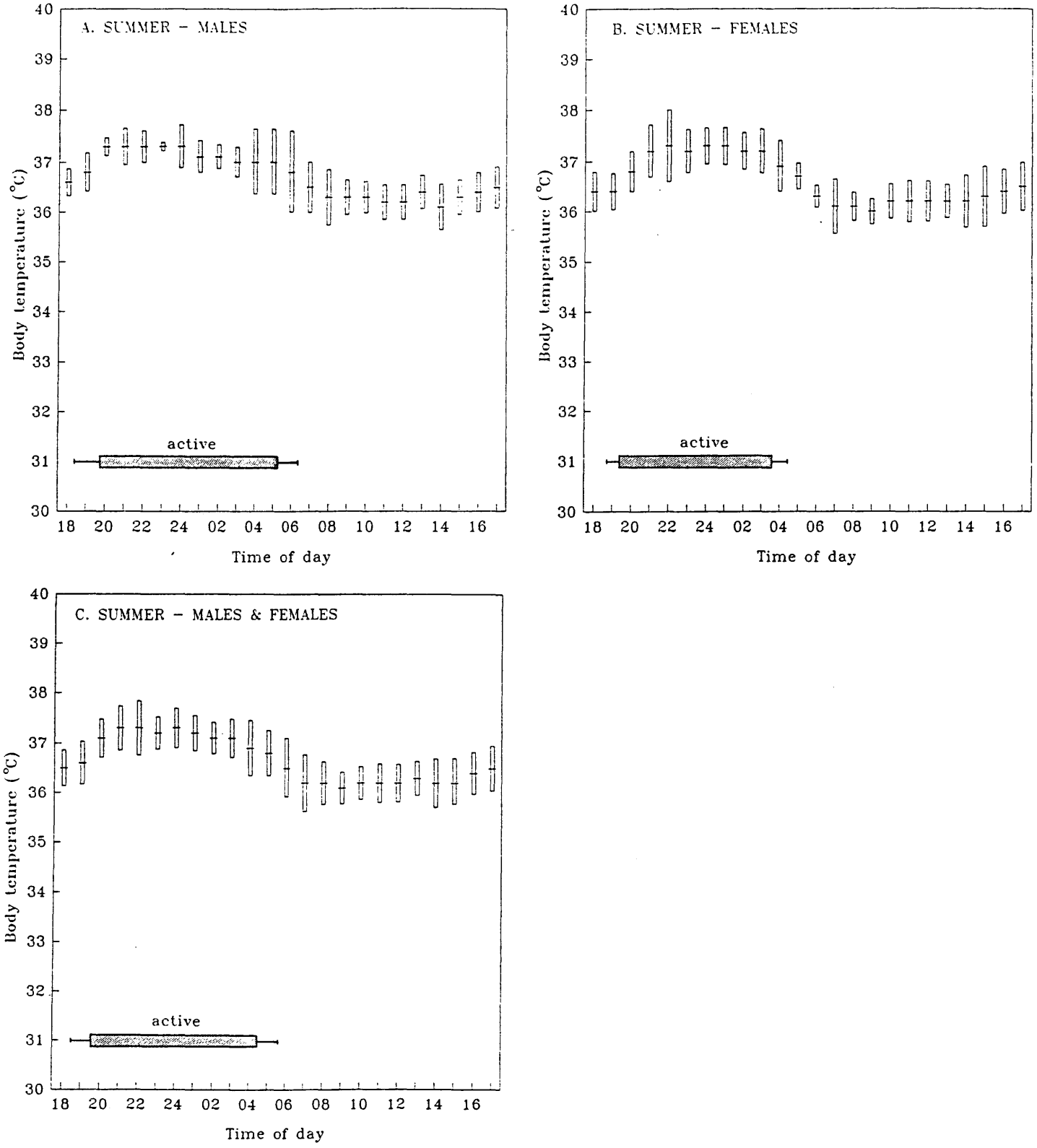


Figure 7.4 The body temperatures ($^{o}C \pm SD$) of six aardwolves measured at hourly intervals during summer. The activity period ($\pm SD$) is also indicated.

Table 7.2 The mean body temperatures ($^{o}C \pm SD$) of male (n=3) and female (n=3) aardwolves during summer and winter

	Males	Females	Mann Whitney U-test
Winter			
All T_bs	35,6±1,2	35,8±1,4	(Z=1,69; p>0,1)
Active	37,3±0,7	37,3±0,7	(Z=0,24; P>0,1)
Inactive	35,2±1,0	35,7±1,1	(Z=0,82; p>0,1)
Summer			
All T_bs	36,7±0,6	36,5±0,6	(Z=0,28; p>0,1)
Active	37,2±0,4	37,2±0,5	(Z=0,40; p>0,1)
Inactive	36,4±0,4	36,3±0,5	(Z=1,08; p>0,1)

34,1±1,6°C. The lowest T_b recorded during winter was 31,2°C in one female (group A) at 09h00.

During summer the mean T_b of active aardwolves was greater than the mean T_b of inactive animals (Z=10,95; p<0,01) (Figure 7.3), but the variation in T_b was not as great as that during winter (Table 7.3). The lowest T_b was recorded between 07h00-15h00, during the inactive period (Figure 7.4). Denning times were longer during winter than summer, with aardwolves spending an average of 19 h 06 min (±1 h 13 min) and 15 h 5 min (±1 h 43 min) in their dens during winter and summer respectively (t=6,04; p<0,01) (Figures 7.3-7.4).

Table 7.3 The mean body temperatures (°C±SD) of six aardwolves while active and inactive during winter and summer. The sample size refers to the total number of hourly measurements

	Active	Inactive	Mann Whitney U-test
Winter	37,3±0,7 (n=38)	35,5±1,1 (n=185)	(Z=8,30; p<0,01)
Summer	37,2±0,4 (n=79)	36,3±0,5 (n=227)	(Z=10,9; p<0,01)

During winter, two of the aardwolves (an adult male and female, group A) dropped their T_b to a greater extent than the other four aardwolves (group B) (Figure 7.5; Table 7.4). At 09h00, the middle of the inactive period during winter, and the time at which T_b was generally at its lowest, the mean T_b of group A was 33,2±0,3°C. The mean active T_b of group A (37,1°C) and group B (37,3°C) was similar (Z=1,01;

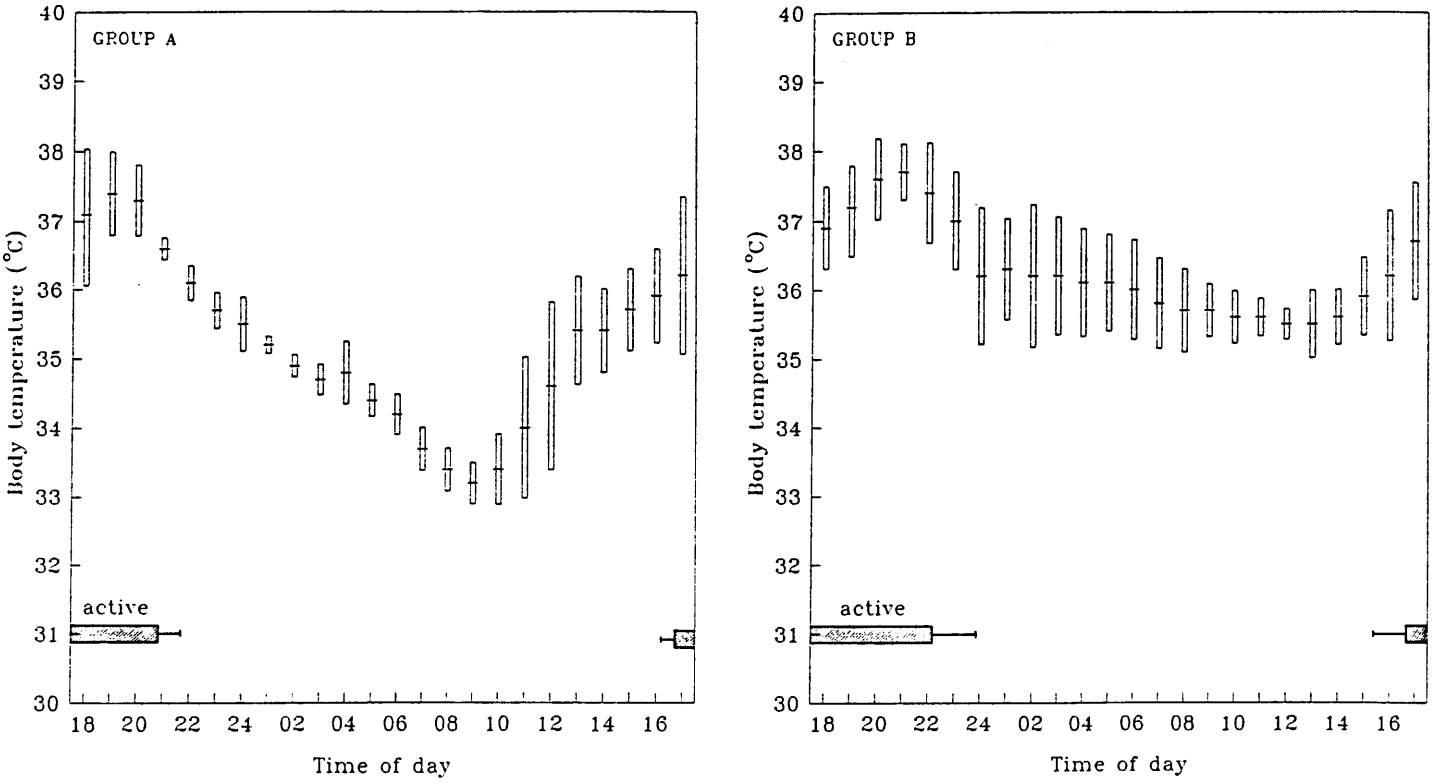


Figure 7.5 The body temperatures ($^{o}C \pm SD$) of two aardwolves (group A) where a marked daily T_b variation was apparent and four aardwolves (group B) which showed limited T_b variation during winter. The activity period ($\pm SD$) is also indicated.

Table 7.4 The mean body temperatures ($^{O}C \pm SD$) of six aardwolves (group A and group B) during winter. The sample size refers to the total number of hourly measurements

	Group A	Group B	Mann Whitney U-test
Active period	37,1±0,8 (n=14)	37,3±0,7 (n=24)	(Z=1,01; p>0,1)
Inactive period	34,8±1,0 (n=79)	35,5±1,0 (n=112)	(Z=4,66; p<0,01)
T_b*	2,3	1,8	
09h00	33,2±0,3 (n=4)	35,7±0,4 (n=8)	(Z=2,49; p<0,01)

* T_b = (T_b when active) - (T_b when inactive)

$p>0,1$). However, the mean inactive T_b of group A (34,8°C) was significantly lower than the mean inactive T_b of group B (35,5°C) ($Z=4,66$; $p<0,01$). When it became apparent during winter that there were intraspecific differences in the magnitude of T_b drop, the study area was visited on seven additional occasions at 09h00-10h00 in order to determine whether the observed variation always occurred. The pattern was always apparent, except for the sub-adult female (of group B) whose T_b was 32,1°C at 10h00 on one occasion.

In order to measure the energy saving by a drop in T_b, Wunder's (1975) model for estimating metabolic rate (MR) was used:

$MR = alpha(3,8^{-0,25})+1,05W^{-0,50}[T_b-4W^{0,25})-T_a]-(8,46W^{-0,40})$; where

MR = metabolic rate;

alpha = body posture coefficient (animal at rest = 1; active animal = 1,7);

W = body mass in grams;

T_b = body temperature; and

T_a = ambient temperature (in this case den temperature).

This formula was used to calculate an estimated MR for group A and group B for each hour while inactive (23h00-15h00) during winter, using the actual T_b measurements at these hourly intervals (Table 7.5). The average body mass of aardwolves during winter (8,5 kg) (Chapter 5) and average winter den temperature (T_{den}) (12,2°C) (Chapter 6) were used in this equation. A hypothetical MR was also calculated for this time period (23h00-15h00) for an aardwolf during winter assuming (1) a T_b of 36,3°C (the average T_b of inactive aardwolves during summer) and, (2) a T_b of 37,2°C (the average T_b of active aardwolves during winter) (Table 7.5). The estimated MR for group A while inactive was 0,307 ml $O_2g^{-1}h^{-1}$ which is 4,9% lower than the estimated inactive MR determined for the other four aardwolves (Group B) (Table 7.5). Furthermore, these results show that group A exhibited significantly greater energy savings than group B, in relation to (i) the MRs calculated using

Table 7.5 The metabolic rates (MR; ml O_2 $g^{-1}h^{-1}$) of aardwolves while inactive (23h00-15h00) during winter, determined using Wunder's (1975) model, for two aardwolves (group A) which exhibited a significant daily T_b fluctuation, and four aardwolves (group B) which exhibited a limited daily T_b fluctuation. These MRs are presented as a percentage (energy saved) of two hypothetically predicted MRs assuming (1) a summer inactive T_b (36,2°C) was maintained during the winter inactive period and, (2) a winter active T_b (37,2°C) was maintained during the winter inactive period. Furthermore, they are presented as a percentage of energy saved in relation to the average BMR determined for five aardwolves at 12,2°C (winter den temperature) in the laboratory (these aardwolves maintained normothermic T_bs) (Chapter 8)

	MR	Hypothetical MRs		BMR
	(observed T_b)	(1) 0,325	(2) 0,336	0,373
Group A	0,307	5,5%	8,6%	17,7%
Group B	0,322	0,9%	4,2%	13,7%

hypothetical mean inactive T_b (i.e. summer inactive and winter active) and (ii) the resting metabolic rates determined in the laboratory (Chapter 8).

T_b of captive aardwolves

The captive aardwolves on a reduced diet during summer exhibited a pronounced daily cycle in T_b. This variation was greater than that observed in the field during summer, but of similar magnitude to the variation during winter (Figure 7.6). The mean T_b of these aardwolves was $38,4 \pm 0,4^{o}C$ between 18h00-03h00 (which corresponds to the active period of wild aardwolves during summer). This is higher than that recorded for free-ranging aardwolves during their active period during summer ($T_b=37,2^{o}C$) ($Z=8,57$; $p<0,01$) and winter ($T_b=37,3^{o}C$) ($Z=5,96$; $p<0,01$).

DISCUSSION

To date pronounced daily hypothermy has been only observed in small endotherms (Prothero & Jurgens 1986; Geiser 1988), and the largest mammal which exhibits daily hypothermy is the dwarf lemur *Cheirogaleus* spp. which weighs *ca* 300 g (Russel 1975, cited by Prothero & Jurgens 1986). Although a number of medium- to large-sized mammals undergo hypothermy (e.g., Tucker 1965; Heldmaier & Steinlechner 1981; Bakko & Nahorniak 1986; Wang & Holowyk 1988), the aardwolf is the largest recorded to do so on a daily basis.

In aardwolves a daily T_b drop results in a potential energy saving of 17,7%. This estimated reduction in metabolism is lower than the typical 18-31% saving observed in most small mammalian species which exhibit daily hypothermy (Vogt & Lynch 1982; Wang & Wolowyk 1988). This suggests that aardwolves do not fully exploit the energetic advantages of hypothermia. Resting at a lower T_b would lower metabolic rate further, but perhaps the T_b at which aardwolves rest during the day facilitates the lowest rate of energy expenditure needed to maintain physical agility for predator

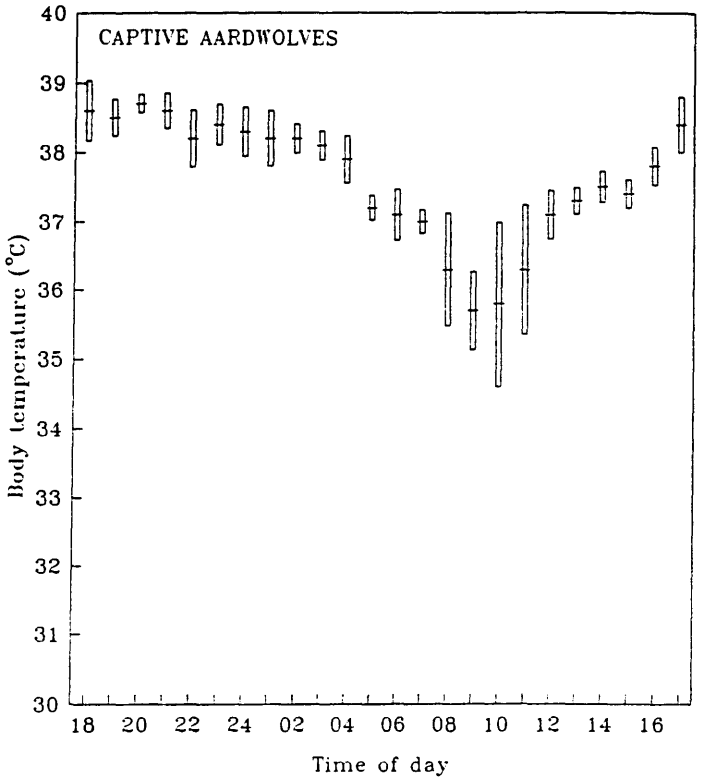


Figure 7.6 The body temperatures ($^{O}C \pm SD$) of two captive aardwolves on a restricted diet during summer.

avoidance. On one occasion during winter an aardwolf was observed lying at her den entrance at 10h00. Her T_b was 31,5^{o}C but, nevertheless, she stood up and retreated into her burrow when approached by the vehicle. If necessary, therefore, aardwolves are able to evade predation while hypothermic. The increased T_b at the onset of activity (observed during the late afternoon/early evening) would provide an increase in speed when susceptibility to predation is increased.

During winter, from mid-morning, the aardwolves T_b gradually increases until late afternoon/early evening when they were, once again, euthermic. In hibernating mammals, which undergo dramatic hypothermia, much energy is consumed in warming the body to a state of euthermia (Bailey & Davis 1965). The size limit to hypothermy is set by the costs of rewarming (Prothero & Jurgens 1986). The rewarming costs are directly proportional to body mass, so the larger the animal the greater the costs (Geiser 1988). The decrease in T_b in aardwolves is, however, limited (when compared to hibernators) and warming may be expedited by radiation energy from the sun. Aardwolves regularly sunbathe during the late afternoon during winter (pers. obs.) and this passive warming may serve to reduce the thermal gap over which the animal has to actively warm itself (Arnold 1988). The gradual rise of T_b observed in this study (Figures 7.3 & 7.4) clearly contrasts to the steep increase during spontaneous arousal, typical of true hibernators (Prothero & Jurgens 1986).

The daily aardwolf T_b rhythm observed during summer is similar to the typical activity-rest cycle (circadian rhythm) of endotherms (Stanier, Mount & Bligh 1984). However, during winter, particularly in two aardwolves, the cyclical pattern was exaggerated. The question arises as to why only two aardwolves (group A) exhibited pronounced hypothermy. Many previous studies have shown that only a fraction of the population undergoes hypothermy at a time (e.g., Hill 1975; Heldmaier & Steinlechner 1981) and the specific environmental cues that regulate the expression of temporal heterothermy may vary inter- (Bartholomew 1972) and intraspecifically (Heath & Lynch 1983, cited by Tannenbaum & Pivorum 1984). Intraspecific variation

in hypothermy can be in response to differences in body condition (body mass), food availability, differences in climatic regimes experienced (Chaplin, Diesel & Kasparie 1984; Geiser & Kenagy 1987) or be related to age (Smith, Peterson, Drummer & Sheputis 1991). Chaplin, Diesel & Kasparie (1984) found that the most important factor which affected the T_b of inactive red-tailed hawks *Buteo jamaicensis* was the change in their body mass induced by fasting, and not as a direct result of fasting. During the present study, however, there were no significant differences in the winter body masses of the six aardwolves (group A *vs* group B; $t=0,08$; $p>0,05$).

Food restriction is perhaps the most effective inductive agent for hypothermy, as it elicits daily torpor in the greatest number of species (Hudson 1974) and individuals within species (Morhardt 1970; Tannenbaum & Pivorun 1984). Geiser & Kenagy (1987) found that intraspecific differences in T_b variation may be related to diet. They found that chipmunks fed a diet rich in polyunsaturated fats had longer bouts of hibernation with a lower T_b than chipmunks on a diet of saturated fatty acids. Variation in food availability or dietary differences are, however, unlikely to be the reason for the intraspecific variation in T_b drop observed in this study as the six aardwolves occur in the same area with a similar food availability.

Age related T_b depression differenes have also been observed, for example in beavers *Castor canadensis* (Smith, Peterson, Drummer & Sheputis 1991). During the present study, the two aardwolves which showed a marked T_b drop were adults while the other four animals (group B) were three adults and one subadult. Hence there appears to be no apparent relation between age and T_b in these aardwolves.

Any conclusions, of course, will be tempered by the fact that only six individuals were studied, but this is always a common limitation of physiological studies. The intraspecific variation in T_b drop in aardwolves clearly warrants further investigation and it is probable that a combination of factors are responsible for the observed differences.

The aardwolves in captivity experienced hypothermy during summer on a low diet. It therefore appears as if the lowering of T_b might be independent of photoperiod and T_a, as these two aardwolves were exposed to a summer photoperiod and T_a regime. Therefore, the annual phasing of hypothermy during winter would appear to be primarily dependent on food restriction (nutritional status/body condition) and unaffected by photoperiod and T_a.

The aardwolves in captivity maintained a higher "active" T_b than the free-ranging aardwolves. The reason for this is uncertain but the observed difference may be attributed to the physical environment of the captive aardwolves enclosures. The enclosures were very small, permitting very little air movement, and consequently the T_a was high (Chapter 8; minimum=18,8$\pm$1,2^{o}C, maximum=32,1$\pm$1,5^{o}C). The insulated dens were not extensively utilized by the captive aardwolves and thus these animals were exposed to the high T_as of the enclosure during the day. It is possible that conductive and convective heating and radiation may have contributed to this high T_b. An alternative explantation may be that specific dynamic action, resulting from the comparatively energy-rich captive diet, may have augmented the T_b of these animals.

Free-ranging aardwolves conserve energy by spending a greater proportion of time in the den, which has a thermally stable microclimate (Richardson 1987a; Chapter 6). During winter aardwolves become active during the late afternoon and retire to their dens in the early evening when termites are no longer available (Richardson 1985, 1987a). In the den energy is presumably also saved through social thermoregulation. During winter aardwolf cubs return to share the maternal den (Richardson 1985). Individual energy consumption could be reduced by huddling (decreasing the effective surface area for heat exchange and decreasing heat lost) and hence increase winter survival by reducing energy requirements. During this study no obvious effect of den sharing (huddling) on the T_b of the occupants was noted but this was not sufficiently

assessed during these experiments. Aardwolf cubs particularly should profit from huddling as they have lower fat reserves than the adults, and their smaller size would involve a greater heat loss. Social thermoregulation is an important survival strategy for many species, for example, alpine marmots, *Marmota marmota* (Arnold 1988). The positive effect of clustered animals on the local microclimate may also be important during winter. The temperature of aardwolf dens is very constant and favourable (Chapter 6) and the physical characteristics of the den provides a protective environment for aardwolves to become hypothermic.

Lowered T_b also has adaptive potential for water conservation by reduction of evaporative water loss. If the effective temperature of the evaporative surface is lowered, the vapor pressure that drives evaporative water loss also decreases (Thornwaite 1940; Weast 1985). Aardwolves very seldom drink water (Richardson 1985; Anderson, Richardson & Woodall 1992), with their requirements being met by water derived from termites.

Therefore, aardwolves conserve energy and water during periods of cold stress and food shortage by both physiological and behavioural means. They respond physiologically by lowering their T_b during inactive periods, and behaviourally by increasing the amount of time spent in the den, thereby saving energy by inactivity and simultaneously prolonging the daily period of the lower (inactive) T_b. Hypothermy was observed in all the study animals during winter but was more pronounced in two individuals. It is calculated that hypothermy will reduce the energy requirements of aardwolves by up to 17,7%. Therefore, it is concluded that hypothermy is primarily aimed to reduce energy requirements and thus to facilitate survival during periods of low food availability.

CHAPTER 8. LABORATORY METABOLISM AND EVAPORATIVE WATER LOSS OF THE AARDWOLF

Abstract

Rates of oxygen consumption, evaporative water loss and body temperatures were measured for five aardwolves during short term exposures (1-3 h) to ambient temperatures of 7,5-32^{o}C, during summer and winter. Body temperatures between 35,2-37,6^{o}C were recorded. Low rates of evaporative cooling are hypothesized as adaptations for saving energy and reducing water loss. Measurement of basal metabolic rates (BMR) established a thermal neutral zone from 20-32^{o}C during winter, and from 24-32^{o}C during summer. BMR averaged 1869,5 ml O_2 h^{-1} during winter and 2194,3 ml O_2 h^{-1} during summer. These metabolic rates are significantly lower (58,9% - winter; 67,1% - summer) than that predicted by Hayssen & Lacy's (1985) allometric equation and are in accordance with the BMR of other myrmecophagous mammals.

INTRODUCTION

There is a paucity of information available on the metabolic responses of wild carnivores in arid and semi-arid environments (Noll-Banholzer 1979; Golightly & Ohmart 1983; McNab 1989). Furthermore, there is almost no information available on the thermal energetics of the single African myrmecophagous (ant- and termite-eating) carnivore, the aardwolf, which occurs in much of the semi-arid grasslands of south and east Africa (Smithers 1983). The aardwolf's occurrence in these environments (Smithers 1983; Koehler & Richardson 1990) demands effective thermoregulatory mechanisms to cope with a broad range of ambient temperatures and other environmental stresses. Furthermore, due to its specialized feeding habits (Kruuk & Sands 1972; Richardson 1987a) the aardwolf has to endure a seasonal unavailability of its principle food source, *Trinervitermes* termites (Richardson 1987a).

An advantage of a low metabolic rate for the aardwolf would be to reduce energy requirements, which would be of particular importance to this animal during winter when termites are largely unavailable (Richardson 1987a,b).

McNab (1984) hypothesized that the metabolic rates of ant- and termite-eating mammals were low because they use a food that: (1) has a seasonally limited availability, (2) a low energy density, (3) is often filled with chemical deterrents and (4) is eaten with indigestible materials. *T. trinervoides* are seasonally unavailable, have a low nutritional quality (water - 74%; per g dry mass: protein - 46%; carbohydrates - 33%; ash - 17%; lipids - 4%; calorific value - 105J/g) (see Chapter 4), are filled with noxious terpene chemicals (Prestwich 1983) and are ingested with sand and grass litter (up to 45,5% indigestible materials: sand - 42,4%, grass - 3,1%; Bothma & Nel 1980). McNab (1984) measured the basal metabolic rate (BMR) of a single captive aardwolf (11 measurements, ambient temperature range: 16-31^{o}C) and found it to be 70% of that predicted using Kleiber's (1961) allometric equation. With data from only one animal, McNab's (1984) results and conclusions were tentative. In this chapter I test the hypothesis that aardwolves have a reduced metabolic rate and evaporative water loss which facilitates survival through the period of low food availability during winter.

MATERIALS AND METHODS

Study Animals and Housing Facilities

Five adult aardwolves, three females and two males, were used for these experiments. Four aardwolves were obtained from De Wildt Cheetah Research Centre and one male aardwolf was loaned from the National Zoological Gardens (NZG), Pretoria. None of the female aardwolves were pregnant or lactating. The aardwolves were housed at the University of Pretoria for the duration of the experiments (March-December 1990). They were housed outside under a natural

diel regime, in separate enclosures (3 m x 4 m) (Figure 8.1). A wooden shelter (approximately 0,75 m^3), insulated with a 15 mm layer of polystyrene, was placed in the corner of each enclosure to serve as a den, and a sandpit was provided to serve as a midden (Figure 8.2). A maximum/minimum thermometer was placed in one of the enclosures and daily ambient temperature (T_a) measurements were taken. These T_as, for the duration of the experiments, were 6,4°C±0,4 and 24,6°C±0,7 during winter and 18,8°C±1,2 and 32,1°C±1,5 during summer.

The aardwolves were fed a mixture of Pronutro (Cerebos Food Corporation Ltd, Randburg, RSA) and ground, dry dogfood (Dogmor; S.A. Oil Mills, Universal Group Ltd., Randfontein, RSA). Experience showed that aardwolves in captivity consumed about 160 g of this mixture per day (pers. obs.). Hence in summer, the aardwolves were given this amount but to simulate the natural food restriction during winter I reduced the ration by 60%. A period of at least three weeks was allowed, prior to the commencement of the experiments, for the aardwolves to acclimate to the dietary regime. Water was provided *ad libitum*. The aardwolves were weighed daily.

Measurement of Oxygen Consumption and Evaporative Water Loss

I constructed a metabolism chamber from a 180 litre steel drum with a welded steel flange around the open end (Figure 8.3). A greased O-ring rendered the steel lid air-tight when bolted closed. The inner surface of the chamber was painted flat black. Because small air leaks can lead to serious errors in measurements, especially when a positive pressure system is used (Gessaman 1987), I tested the chamber extensively for air leaks. The chamber was tested manometrically before each set of experiments by sealing the outlet and placing the chamber under a vacuum. During each trial a solution of soapy water was applied around the lid, and at all the connections, to again check for leaks.

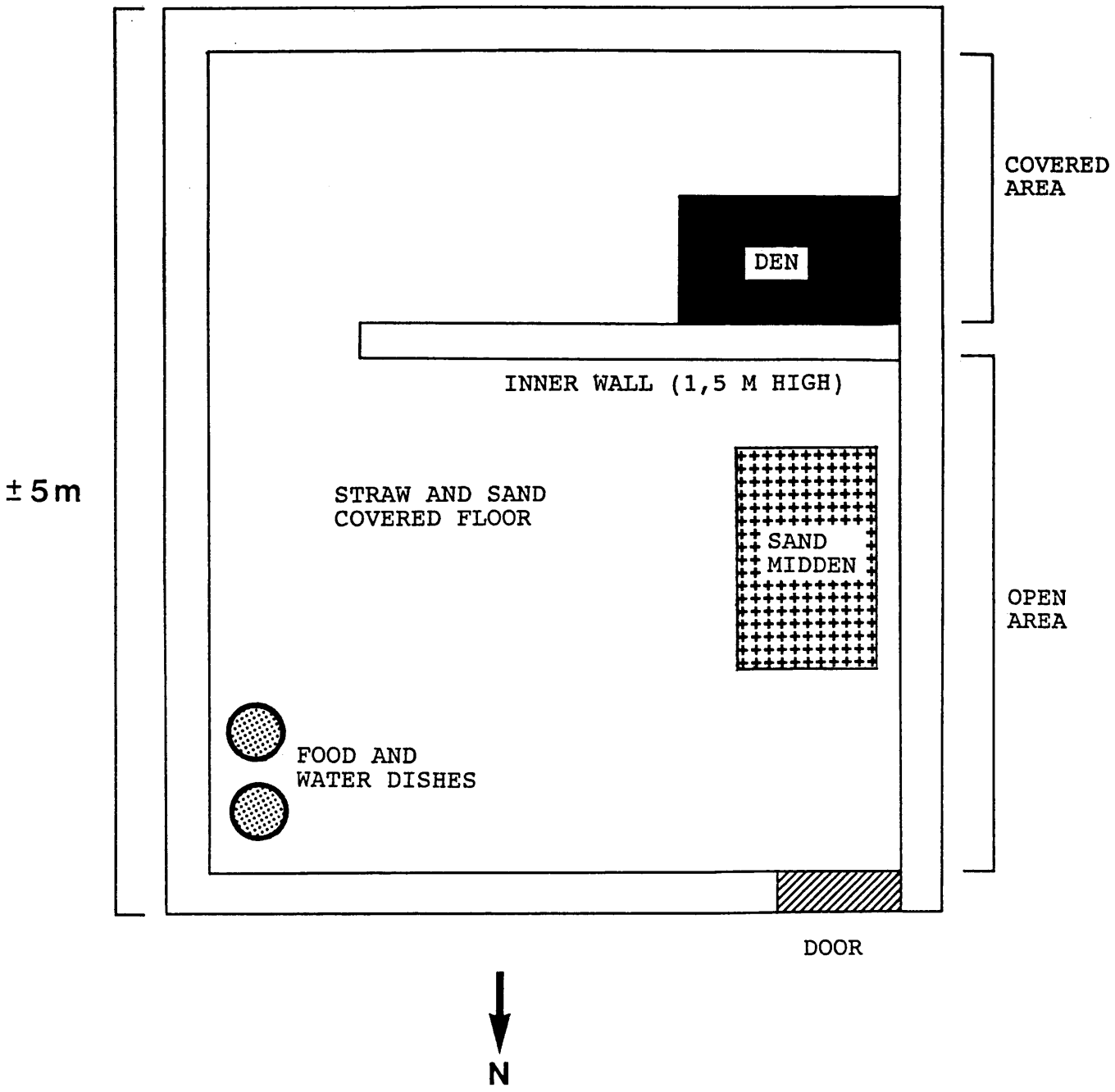


Figure 8.1 Schematic plan of one of the aardwolf enclosures at the experimental farm, University of Pretoria (not to scale).

Figure 8.2 An aardwolf in her enclosure at the experimental farm.

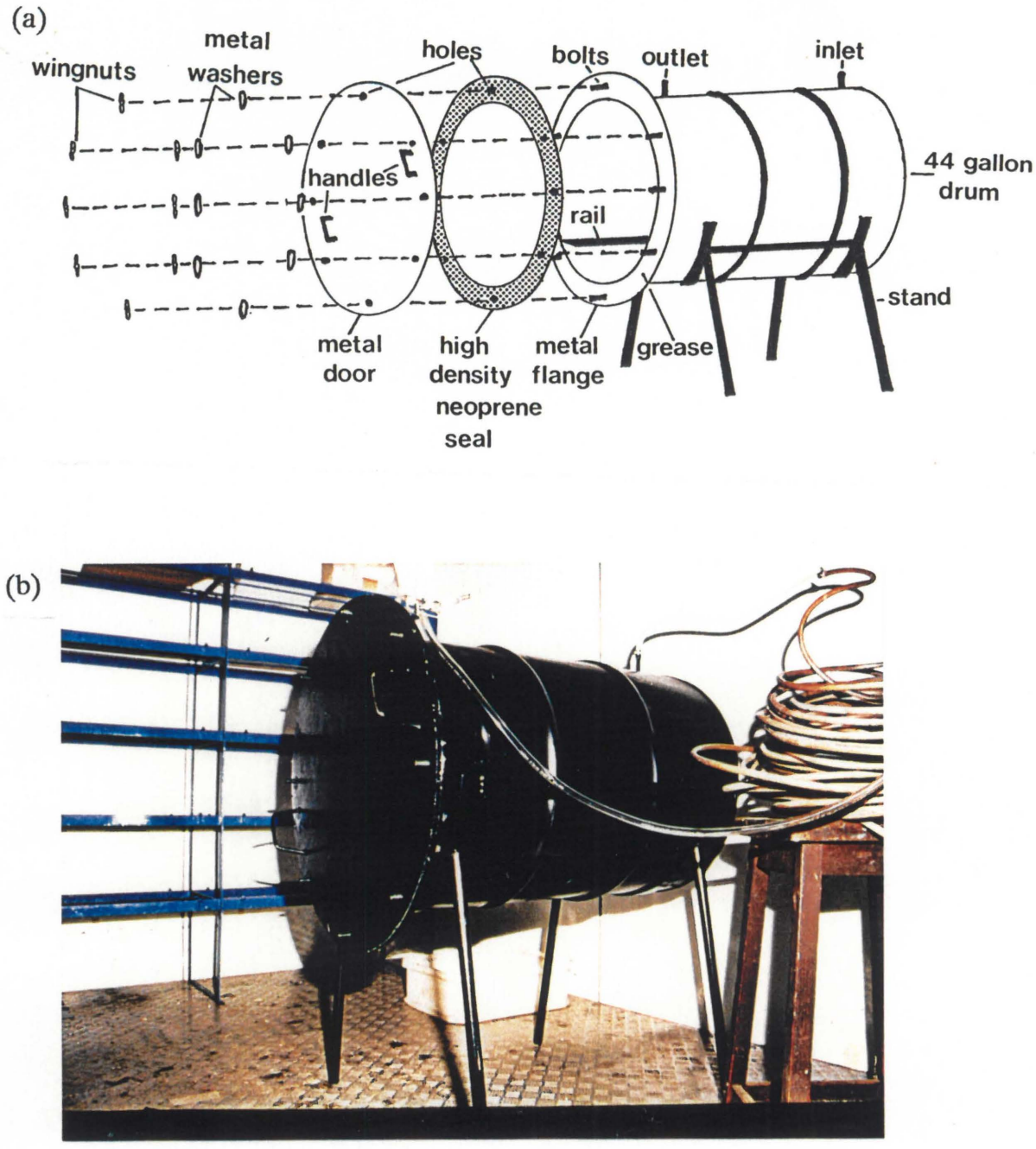


Figure 8.3 (a) The metabolism chamber used for the laboratory metabolism experiments. (b) The incoming airstream initially passed through a coil of copper tubing to equilibrate incurrent air with the temperature of the climate chamber.

Aardwolves were transported from their enclosures to the laboratory in a small wire cage (65 cm x 47 cm x 43 cm) which was covered with a blanket to limit unnecessary disturbance. The cage, which had a hardboard base, was specifically designed to fit neatly into the metabolism chamber. To prevent direct conduction with the walls, the cage was placed on two rails within the chamber, maintaining a distance of at least 4 cm between the cage and chamber walls. Although the aardwolves usually lay down, the cage was large enough for them to assume a standing posture. The cage and metabolism chamber were cleaned daily with soap and water. I eliminated experiments in which an aardwolf defecated or urinated during the trial or if I detected activity in the chamber.

Rates of oxygen consumption (VO_2) and total evaporative water loss (EWL) were determined for post-absorptive animals, during winter (August 1990) and summer (December 1990), during their inactive phase (07h00-17h00), by standard flow through respirometry and hygrometry methods using an open circuit system (Depocas and Hart 1957) (Figure 8.4). During each experiment the chamber containing the aardwolf was placed in a large temperature controlled environmental chamber (2,5 x 3 m; Specht Scientific, RSA) which held temperature constant to $\pm 0{,}1^{o}C$. Outside air flowed under positive pressure through a column of silica gel (Merck Chemicals, Midrand, RSA), removing H_2O from the air stream, through a rotameter (Fischer and Porter Ltd, Workington, England), through a copper coil, to equilibrate air with the chamber temperature, and into the chamber. Excurrent air passed through a thermohygrometer (Grant Instruments Ltd, Cambridge, England) to measure relative humidity, and finally into a large glass container. A subsample was routed from this container through a scrubbing column containing silica gel, soda lime (self indicating, 4 to 8 mm mesh; Saarchem Pty Ltd., Krugersdorp, RSA) and again silica gel, respectively, before entering an Amtek S-3A/1 paramagnetic oxygen analyzer (Thermox Instruments Division, Pittsburgh, USA) to determine the fractional concentration of oxygen in dry, CO_2-free air. The O_2 analyzer was calibrated with dry, CO_2-free air.

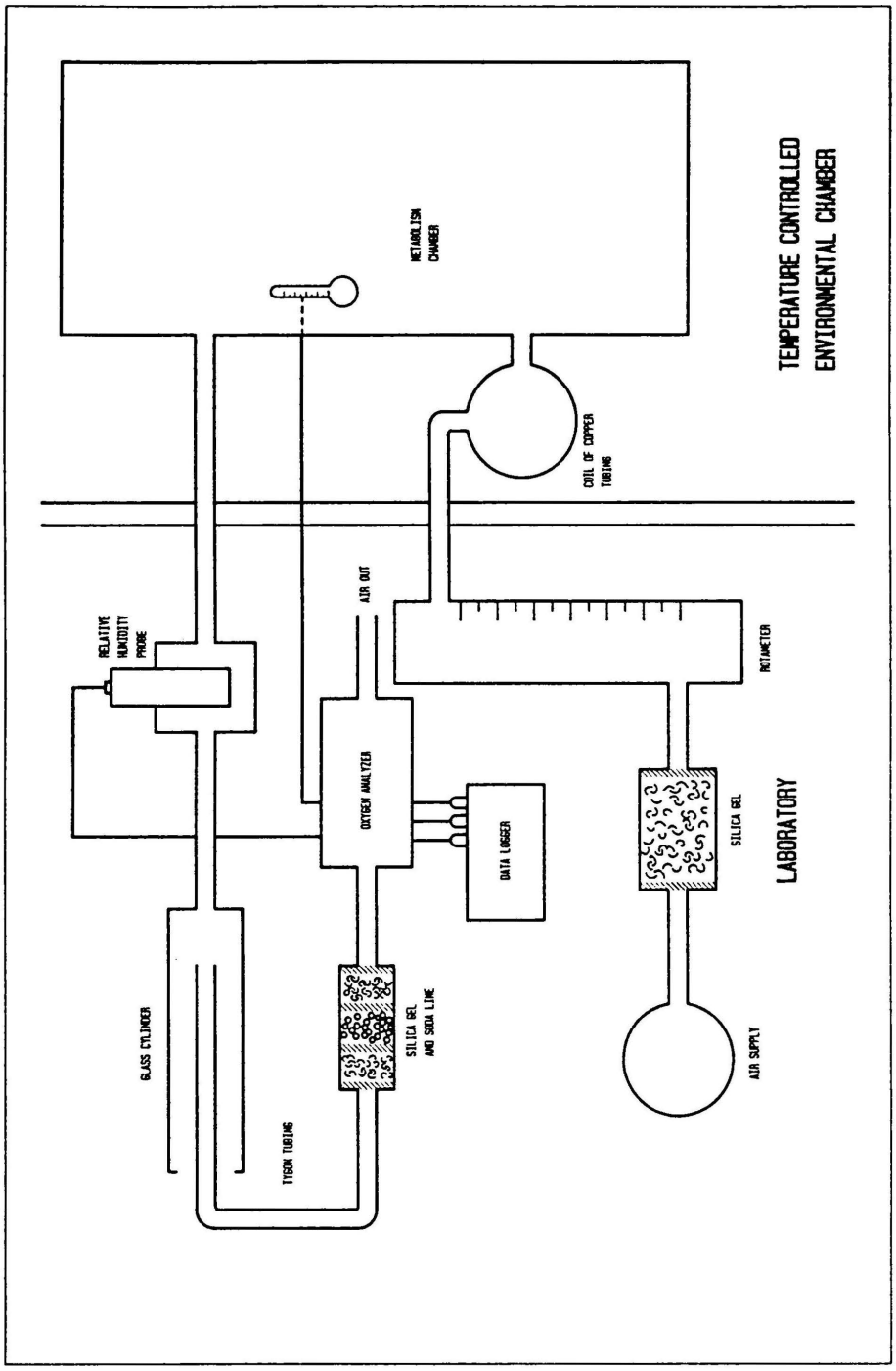


Figure 8.4 Schematic diagram of the experimental set-up used for the laboratory metabolism experiments.

Compressed air was metered through the chamber at a rate of approximately 12 000 ml/min (STPD). Flow rates were monitored continuously with the rotameter to assure constancy but were measured before and after each trial with a 2 000 ml glass bubble meter (Levy 1964) (Figure 8.5).

VO_2 was determined at 7.5; 10,0; 15,0; 17,5; 20,0; 25,0; 30,0; and 32,0^{o}C. I made 3-4 measurements of VO_2 and EWL each day with temperatures selected at random. The thermohygrometer was calibrated over LiCl and NaCl standards. Rates of EWL were calculated from air flow rates and measured values for relative humidity of the excurrent air stream.

Air temperature within the chamber was monitored with a Squirrel data logger (Grant Instruments). This temperature recorder was calibrated against a thermometer traceable to the South African Bureau of Standards, Pretoria.

At each T_a I allowed a minimum acclimation period of one hour before measurements commenced. The fractional concentration of oxygen in the airstream was recorded for at least 30 min, or until constant minimum readings were obtained. Equation 6 from Hill (1972) was used to calculate VO_2.

Thermal conductance

Thermal conductance (C) was calculated for aardwolves using the formula $C=(M/m)/(T_b-T_a)$ (M, metabolism = VO_2; m = body mass in g; T_b = body temperature) (McNab 1980).

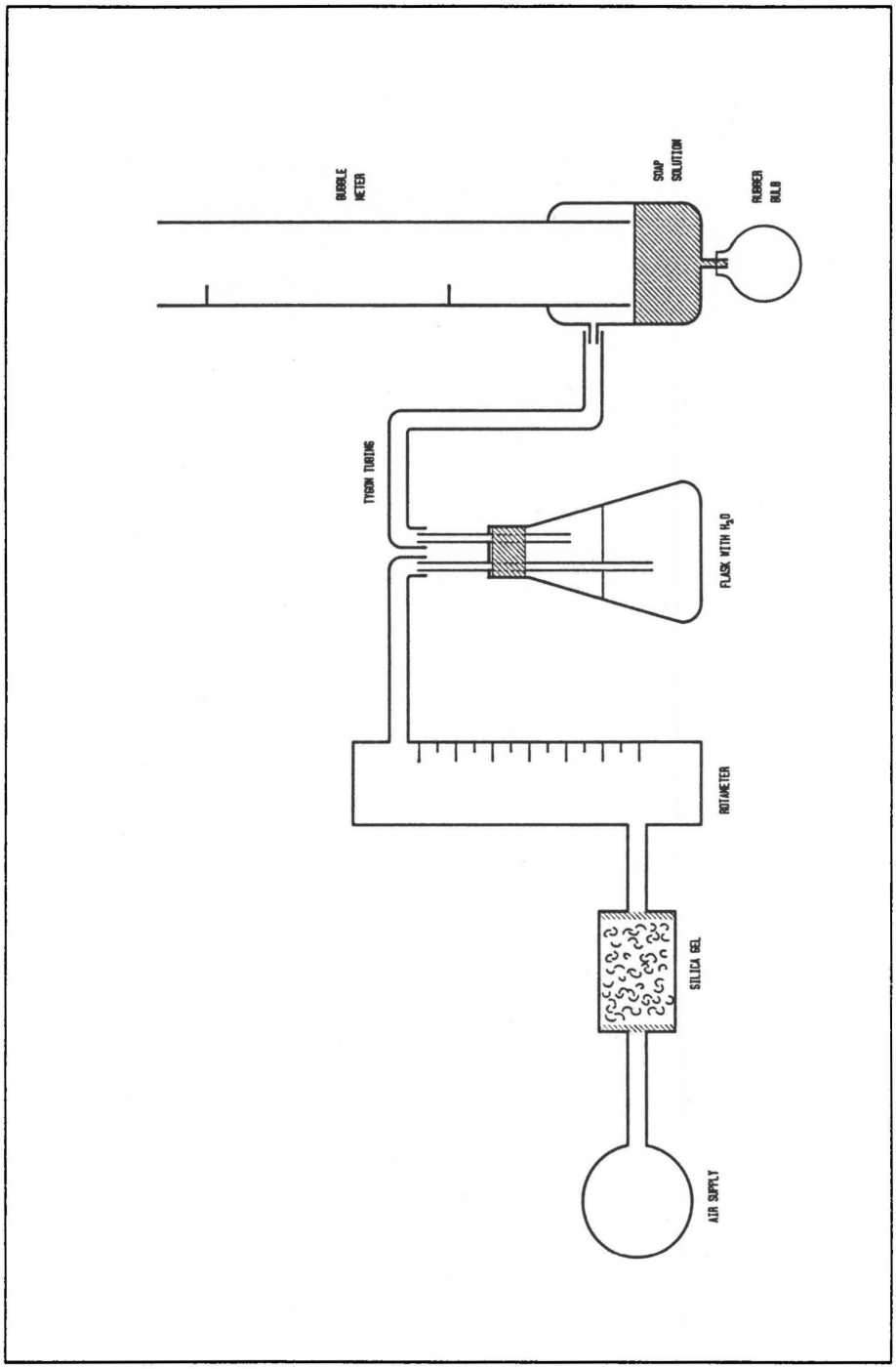


Figure 8.5 Schematic diagram of the equipment used to determine flow rates and calibrate the rotameter (after Levy (1964)).

Insulation

I measured the fur length of fifteen aardwolf museum study skins (winter: n = 7; summer: n = 8), at six body localities (upperback, lowerback, neck, foreleg, hindleg, and side - behind the forelimb), as an indicator of seasonal changes in insulative properties. Measurements were taken with calipers at each body locality and averaged. Along the back (upperback and lowerback) and neck the length of the general dense fur covering was measured and not the long mane hairs. In addition, as an index of seasonal changes in insulation, I shaved 3 cm^2 patches of hair (from the foreleg and hindleg) from six study skins, three individuals from late-summer (February/March) and three individuals from late-winter (August/September). These samples were dried to constant mass and weighed.

Body temperature

For three aardwolves during winter and two aardwolves during summer, while measuring VO_2 and EWL, I monitored T_b with abdominally implanted temperature telemeters (Telonics Inc, Arizona, USA; Van Urk transmitters, PU for CHE, Potchefstroom, RSA). The transmitters were calibrated before implantation, and after removal, in a constant temperature water bath. The transmitters were surgically implanted into the peritoneal cavity following the methods of Guynn, Davis & von Recum (1987) (see Chapter 7) at least one month prior to the experiments. Immobilization procedure followed that described by Anderson & Richardson (1992).

Statistical analyses

Regression equations were calculated by the method of least squares (Cass 1973). Differences between two regression lines were evaluated following Zar (1974). For the comparison of two samples the Students t-test was employed (Snedecor &

Cochran 1980). For measurements of VO_2 at T_as below thermoneutrality, I calculated regressions for each individual and tested for differences among individuals by analysis of covariance (Snedecor & Cochran 1980). The two-way anova was used to compare the summer and winter EWL data (Snedecor & Cochran 1980). Means are presented $\pm$1 SD.

RESULTS

Oxygen consumption

During the summer trials, aardwolves that weighed 8,1$\pm$0,7 kg consumed 2194,3 ml 0_2 h^{-1} (0,267 ml O_2 g^{-1} h^{-1}) in their thermoneutral zone (TNZ) (n=5) (Figure 8.6). Hence BMR was 1057,5 KJ/d, assuming a conversion factor of 20,08 J/ml O_2 (Schmidt-Nielsen 1985). Below 20^{o}C, there was no difference between the measurements for individual aardwolves (ANCOVAR; F=1,01; p>0,05) and these data were pooled. VO_2 between 7,5^{o}C and 20^{o}C is described by the equation VO_2=6070,0-167,1(T_a) (N=5 aardwolves; n=23 measurements; r=0,90; p<0,01). At zero metabolism this equation intercepts the abscissa at 36,3^{o}C. At the lowest T_a (7,5^{o}C) the aardwolves VO_2 translates to 2347,8 KJ/d.

During winter, VO_2 of aardwolves weighing 7,8$\pm$0,7 kg averaged 1869,5 ml 0_2 h^{-1} (0,240 ml O_2 g^{-1} h^{-1}) in their TNZ, which converts to 900,9 KJ/d (Figure 8.7). Below the TNZ, there were no differences between the individual aardwolves (ANCOVAR; F=0,92; p>0,05). VO_2 below the TNZ increased as T_a decreased and this is described by the equation VO_2=4434,8-129,1(T_a) (N=5 aardwolves; n=25 measurements; r=0,82; p<0,001). This equation intercepts the abscissa at 34,4^{o}C at zero metabolism. At 7,5^{o}C their VO_2 is equivalent to 1723 KJ/d.

The BMR of the aardwolves during summer was significantly higher than that determined during winter (t=2,34; p<0,03).

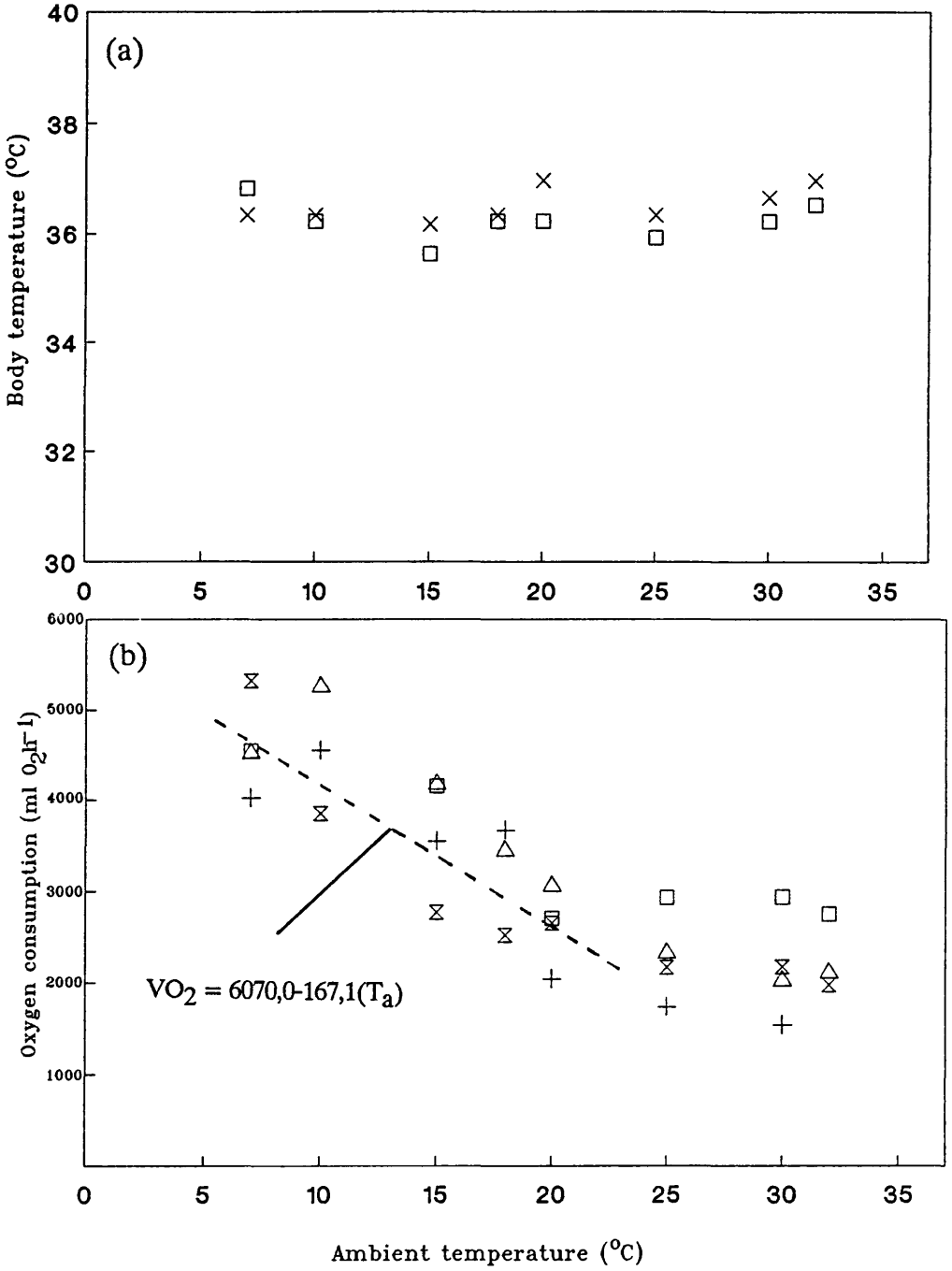


Figure 8.6 Relationship for the aardwolf between ambient temperature (°C) and (a) body temperature (°C) and (b) oxygen consumption (ml O_2 h^{-1}) during summer.

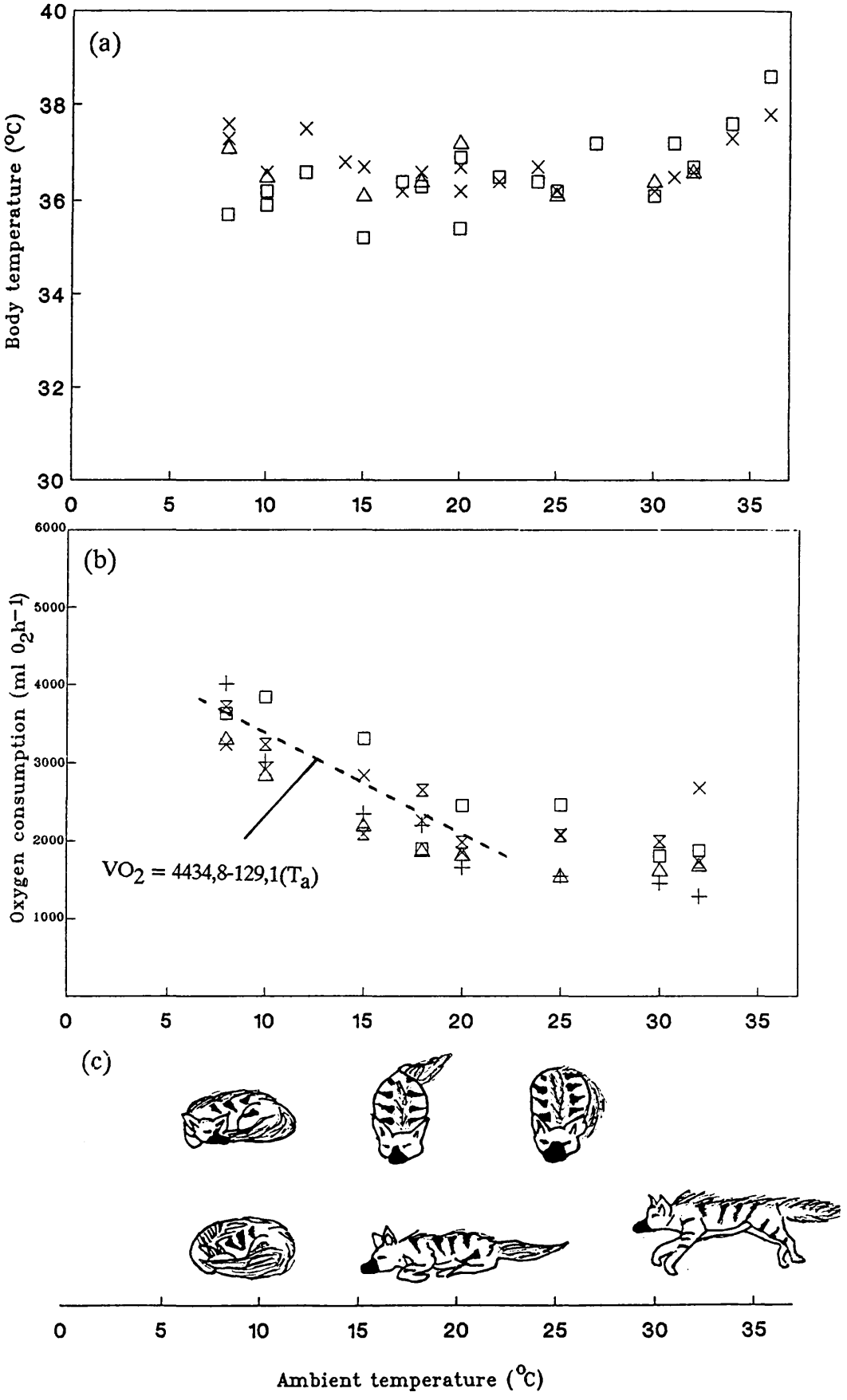


Figure 8.7 Relationship for the aardwolf between ambient temperature (°C) and (a) body temperature (°C), (b) oxygen consumption (ml O_2 h^{-1}) and (c) body postures during winter.

Thermal conductance and insulation

Thermal conductance was relatively constant at T_as below the TNZ for each season (Figure 8.8), averaging 0,022±0,001 ml O_2 g^{-1} h^{-1} $^oC^{-1}$ during summer and 0,015±0,001 ml O_2 g^{-1} h^{-1} $^oC^{-1}$ during winter. Conductances were significantly higher for the summer-acclimated aardwolves than for the winter-acclimated group ($t=8,99$; $p<0,001$).

The reciprocal of conductance, insulation, showed a similar seasonal trend (Table 8.1 & 8.2). The mean pelage length during summer (2,69±0,41 cm) increased by 1,0 cm to 3,68±0,47 cm during winter ($t=14,03$; $p<0,001$) (Table 8.1). The insulation indices (g/cm^2) were also significantly greater during winter for samples taken from the foreleg ($t=3,50$; $p<0,025$) and the hindleg ($t=3,47$; $p<0,05$) (Table 8.2).

Body temperature

T_b did not differ between the two aardwolves during summer ($t=1,79$; $p>0,05$) and, therefore, these data were pooled (Figure 8.6). At T_as between 7,5^{o}C and 32^{o}C, these two aardwolves regulated their core temperature well, maintaining an average T_b of 36,4^{o}C.

T_b did not differ between the three aardwolves during winter below T_as of 32^{o}C ($t=1,055$; $p>0,05$; $t=1,26$, $p>0,05$; $t=1,027$; $p>0,05$) and they maintained an average T_b of 36,5^{o}C (Figure 8.7). However, at T_as of 36^{o}C during winter the aardwolves were heat stressed, increasing their T_b to 38,2±0,4^{o}C.

There was no significant difference between the summer and winter T_bs ($F=0,102$; $p>0,5$).

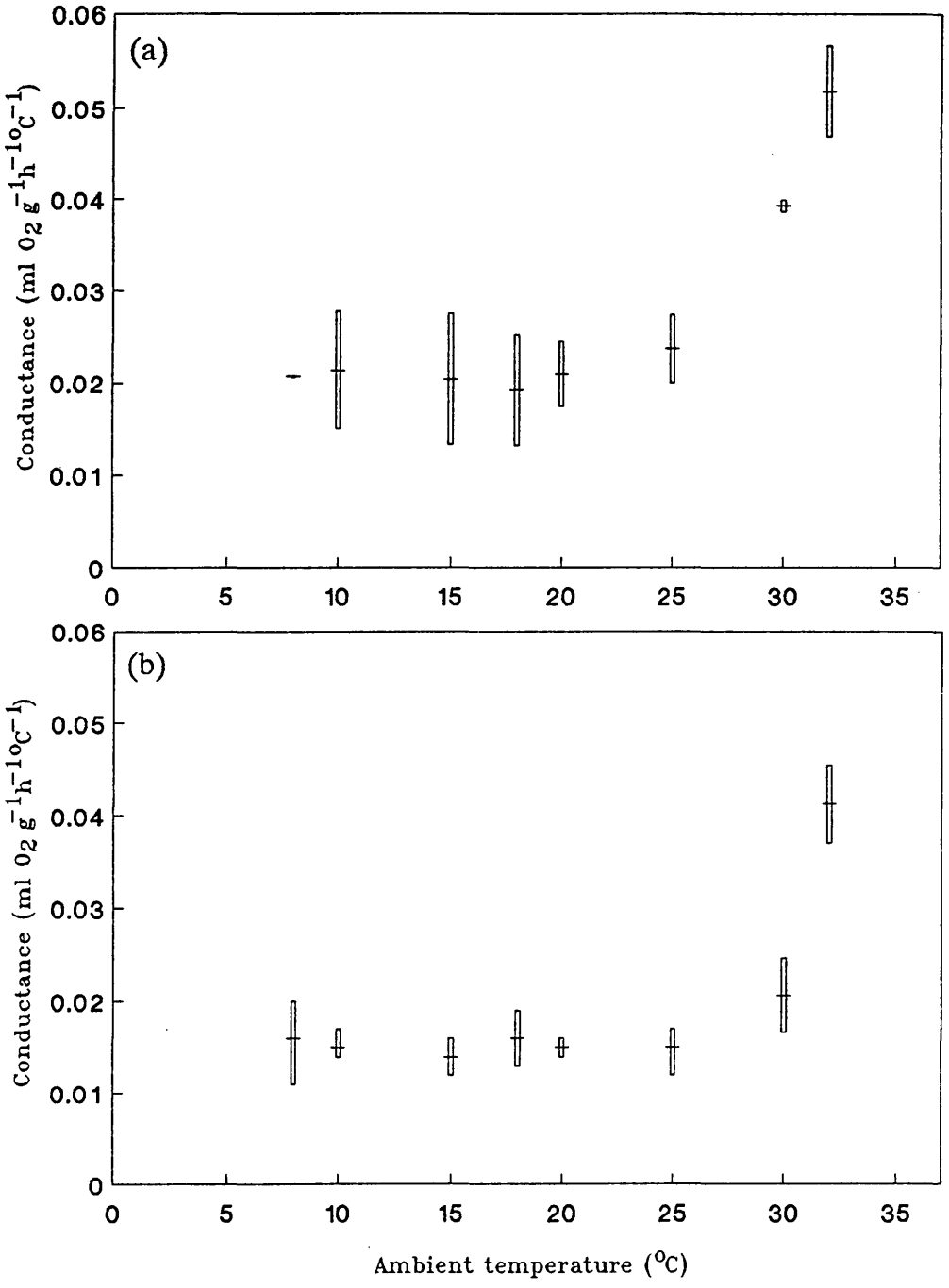


Figure 8.8 Overall thermal conductances of three aardwolves during (a) summer and (b) winter when exposed to different ambient temperature regimes.

Table 8.1 Pelage lengths (mm±SD) of 15 aardwolf museum study skins. The sample size refers to the number of skins for each month. Measurements were taken at six body localities

Month	Pelage length (mm)	SD	n	Season
January	(no skins available)			
February	27,8	2,2	2	summer
March	24,2	3,3	3	summer
April	(no skins available)			
May	37,2	4,6	1	winter
June	33,2	3,5	1	winter
July	38,0	4,4	1	winter
August	37,3	6,0	3	winter
September	35,8	3,1	1	winter
October	(no skins available)			
November	27,3	3,3	1	summer
December	30,0	4,8	2	summer

Table 8.2 Insulation indices (g/cm^2, and standard deviations) from the foreleg and hindleg of aardwolves collected during summer (n=3) and winter (n=3)

Summer		Winter	
Foreleg	Hindleg	Foreleg	Hindleg
0,099±0,013	0,090±0,034	0,162±0,028	0,214±0,063

Evaporative water loss

EWL during summer (Figure 8.9) showed a steady increase from 5,05±0,73 g H_2O h^{-1} at T_a=7,5°C to 9,66± 2,14 g H_2O h^{-1} at T_a = 32°C, and an exponential regression of these points is described by the equation $y=e^{0,058(Ta)-1,734}$ (N=5 aardwolves; n=33 measurements; r=0,98; p<0,001).

During winter EWL increased from 2,72±0,42 g H_2O h^{-1} at T_a=7,5°C to 6,64±1,13 g H_2O h^{-1} at T_a=32°C, and an exponential regression of these points can be described by the equation $y=e^{0,058(Ta)-1,736}$ (N=5 aardwolves; n=40 measurements; r=0,98; p<0,001) (Figure 8.9).

EWL of the five aardwolves during summer, over the range of T_as to which they were exposed, was significantly higher than that recorded during winter (Two-way analysis of variance; F=50,4; p<0,001).

Thermoregulatory behaviour

Aardwolves displayed postural changes associated with the degree of heat or cold stress they experienced (Figure 8.7). During exposure to mild heat stress (T_a>30°C) the animals lay on their sides with legs, head and tail outstretched, exposing their underparts; while, when exposed to cool or cold temperatures (T_a<15°C) they curled up into a ball-like posture, with head to rump, curling their tails against them, thus reducing their rate of heat loss. In addition, at low temperatures (T_a<15°C), shivering and piloerection were observed. At more favourable T_as (15-30°C) the aardwolves displayed intermediary postures, lying on their ventral surface, with head outstretched, and either with or without their tails against them.

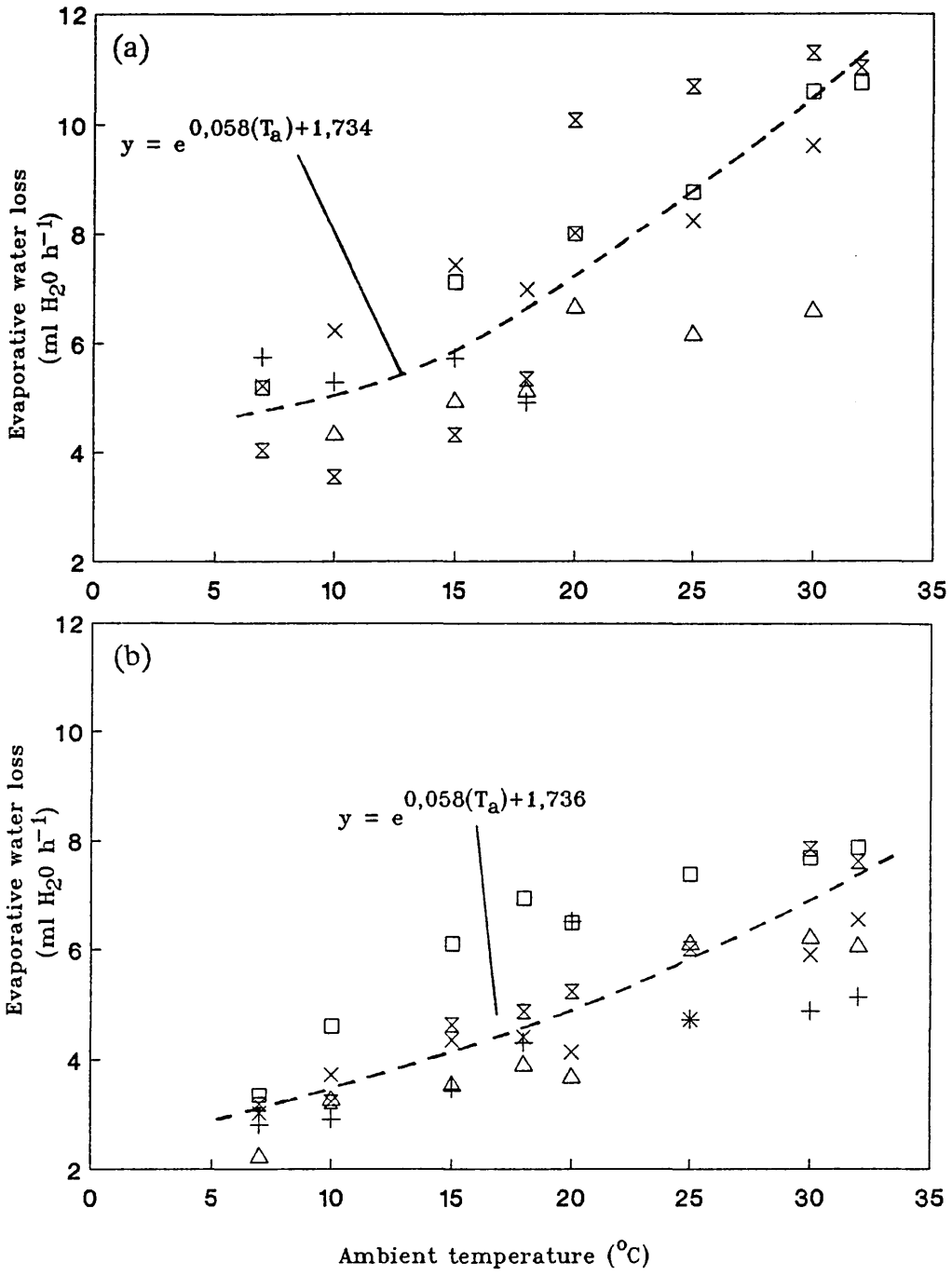


Figure 8.9 Relationship between ambient temperature (^{o}C) and evaporative water loss (ml H_2O h^{-1}) for the aardwolf during (a) summer and (b) winter.

DISCUSSION

The results of this study show that aardwolves have BMRs lower than that predicted by allometric equations (Kleiber 1961; Hayssen & Lacy 1985) (Table 8.3). These BMRs are also in agreement with the only previous study on aardwolf metabolism ($0{,}0254 \pm 0{,}013$ ml O_2 $g^{-1}h^{-1}$) and with the low rates of metabolism of other myrmecophages (McNab 1984). The BMR of the aardwolf is less than that of non-myrmecophagous carnivores, such as the 126%, 122% and 180% of predicted for coyotes *Canis latrans* (Shield 1972), red fox *Vulpes vulpes* (Golightly & Ohmart 1983), and African hunting dog (Taylor, Schmidt-Nielsen, Dmi'el & Fedak 1971), respectively. This variation may be attributed to the differences in the feeding habits of these species, and McNab (1984, 1986) has suggested that it is as a result of their diet of ants and termites that myrmecophages have these low BMRs. More recently, however, Elgar & Harvey (1987) and Harvey, Pagel & Rees (1991) have statistically demonstrated that there is no consistent variation between life-history variation (or ecological associations, such as myrmecophagy) and the BMR amongst eutherian mammals when body size effects are held constant. They concluded that many of the correlations between diet and relative metabolic rates can equally well be described by taxonomic associations and, thus, that phylogeny must be taken into account when seeking associations between metabolic rate, behaviour and ecology. For the purpose of this study, however, it is not important whether temperature (Bennett 1988), body mass (Kleiber 1961), phylogeny or taxonomic affiliation (Hulbert & Dawson 1974; Elgar & Harvey 1987; Crompton, Taylor & Jagger 1978; Harvey, Pagel & Rees 1991), climatic influences (McNab & Morrison 1963), burrowing habits (McNab 1966, 1979) or food habits (McNab 1984, 1986) are attributed to the low BMR of aardwolves. What is important is that a low BMR reduces the energy requirements of aardwolves.

Unlike the other myrmecophagous mammals which have a low BMR and which regulate their T_b at a low level (McNab 1984; Heath & Hammel 1986), the aardwolf has a 3-4^{o}C higher T_b. Only some of the smaller ant- and termite-eating Insectivora

weighing less than 100 g, such as *Elephantulus* spp, have T_bs comparable to that of aardwolves (McNab 1984). The higher T_b of aardwolves may, however, be promoted by their thick pelage and thus effective insulation.

Table 8.3 The percentage of the predicted metabolic rates, using Kleiber's (1961) and Hayssen & Lacy's (1985) formulae, from the BMR of aardwolves determined during summer and winter

	Summer	Winter
Kleiber (1961) (VO_2 (ml O_2 $g^{-1}h^{-1}$)=3,42M(g)$^{-0,25}$)	74,1%	66,0%
Hayssen & Lacy (1985) ($\log_{10}$ (VO_2)=0,630-0,262(log mass g))	67,1%	58,9%

An important advantage of having a low BMR is that it reduces food demand and thus enables aardwolves to inhabit regions where food is scarce, and/or seasonally unavailable (Richardson 1987a,b). As they are unable to feed on other more readily available prey items (Anderson, Richardson & Woodall 1992), aardwolves have to endure a period with limited food and a low BMR thus facilitates their survival through this period.

A low BMR means there is less body heat to lose through evaporative cooling, and therefore the animal conserves its body water. For small mammals, in the temperature range between 18 and 29°C, EWL is related to body mass by the equation EWL (g/hr) = 2,58M(kg)^{0,826} (Chew 1965). The EWL rates for

aardwolves are 39% and 55% of predicted (using this equation) for summer and winter, respectively. Thus, as in other arid-adapted mammals (Schmidt-Nielsen & Schmidt-Nielsen 1950; Noll-Banholzer 1979), aardwolves have a reduced rate of pulmocutaneous water loss. This is supported by the low water turnover rates of free-ranging aardwolves determined using $H_2{}^{18}O$ (Anderson, Williams & Richardson unpubl. data). Aardwolves rarely drink water and rely almost entirely on the water present in their termite diet (Richardson 1985; Anderson, Richardson & Woodall 1992).

The summer BMR of aardwolves is greater than the BMR determined during winter. Seasonal differences in BMR have also been reported for a number of other medium-sized mammals, for example: collared peccaries *Dicotyles tajacu* (Zervanos 1975), antelope jackrabbits *Lepus alleni* (Hinds 1977) and kit foxes *Vulpes macrotis* (Golightly & Ohmart 1983). The higher winter BMRs of the first two species were explained as an adaptation to winter cold, and the higher summer BMR of the latter species as a mechanism to maximize reproductive effort. The lower BMR of aardwolves during winter can be explained as an adaptation to minimize their energy requirements.

Aardwolf thermal conductances are greater than that predicted by body mass using three allometric equations (Table 8.4). A principle characteristic of burrowing mammals is a high conductance (McNab 1979). The high thermal conductance in aardwolves may also be an adaptation towards avoiding heat stress while excavating their burrows; while the lower thermal conductance and increased insulation (Heldmaier, Boeckler, Buchberger, Klaus, Puchalski, Steinlechner & Wiesinger 1985) observed during winter will improve their thermoregulation during this colder season. A reduced conductance during winter means that less body heat is lost to the environment and, therefore, less energy is needed to maintain a constant T_b.

Conductance is the reciprocal of insulation and it is unusual that the conductance of aardwolves is high considering that they have such a well developed and thick pelage (Smithers 1983). Heat loss probably takes place through the much more sparsely haired underparts. At high T_as in the metabolic chamber, aardwolves lay on their sides exposing these underparts, thus maximizing the surface area for passive heat loss and limiting the necessity for using evaporative cooling. The combination of a low BMR and a high thermal conductance is not uncommon amongst members of the Carnivora (Hennemann, Thompson & Konecny 1983).

Table 8.4 Predicted thermal conductances (ml O_2 $g^{-1}h^{-1}{}^{o}C$) (using three formulae) during summer and winter in relation to the observed minimum conductances determined during these seasons (0,0192 ml O_2 $g^{-1}h^{-1}{}^{o}C$ - summer; 0,0140 ml O_2 $g^{-1}h^{-1}{}^{o}C$ - winter)

Formula	Summer		Winter	
	Predicted	%	Predicted	%
$C=0,760W^{-0,426}$ (Bradley & Deavers 1980)	0,0164	117%	0,0167	84%
$C=1,00W^{-0,50}$ (McNab & Morrison 1963)	0,0111	173%	0,0113	124%
$C=1,02W^{-0,505}$ (Herreid & Kessel 1967)	0,0108	178%	0,0110	127%

W = body mass; summer - 8100 g; winter - 7800 g

At low T_as, insulation in aardwolves is improved by piloerection and by changes of the sleeping posture. By curling up into ball-like postures aardwolves reduce heat loss by minimizing their effective surface area. These behavioural cold defense responses are similar to those that have been observed in many other mammals, including the myrmecophagous pangolin (Heath & Hammel 1986). In the wild, during winter, aardwolf cubs return to share the den with their siblings and the adult female (Richardson 1985) and consequently this den sharing, or huddling, may contribute towards reducing the costs of thermoregulation. Henneman, Thompson & Konecny (1983) found that crab-eating foxes experienced 5-18% savings in energy expenditure when two animals huddled, and it is likely that aardwolves may exhibit similar savings.

Aardwolves are generally inactive, and below ground in the den, when the environmental conditions above ground are unfavourable (Richardson 1987a). Consequently they avoid the high summer diurnal T_as and the cold winter nocturnal T_as. The adaptations (low BMR and minimal EWL) of aardwolves to a semi-arid environment are energy and water conservative. Aardwolves have a BMR less than predicted, which reduces endogenous heat load and ultimately conserves water. Relatively high conductances, particularly during summer, result in minimal reliance on evaporation for heat dissipation, and this may also favour the aardwolves burrowing behaviour. Moreover, as a consequence of burrow dwelling and timing of activity to periods of low endogenous heat loads, aardwolves avoid the thermal stresses of a semi-arid environment.

CHAPTER 9. CONCLUSIONS

The aardwolf's *Proteles cristatus* specialization towards feeding on surface foraging termites proceeded simultaneously with the ability to tolerate *Trinervitermes* soldiers' terpene defence secretions, for which it was largely pre-adapted (Richardson 1987b). The most noteworthy morphological and anatomical features of aardwolves to their diet are the following: a hairless muzzle; a broad, spatulate tongue covered with many hardened papillae; a broad palate; large mandibular salivary glands; a muscular pyloric region in the stomach; and a distensible distal colon (Anderson, Richardson & Woodall 1992). These specializations, however, appear to be non-adaptive, given the seasonal fluctuations in *Trinervitermes* availability, as during winter aardwolves are unable to procure "inactive" termites from their nests using the same method of feeding which is employed during the summer months. Aardwolves do not have the powerful limbs and strong claws of typical "anteaters" but instead are similar in appearance and external morphology to their extant carnivorous, hyaenid relatives.

T. trinervoides are similar to other termites and other invertebrates in that they have a low nutritional quality (Redford & Dorea 1984). Ancestral aardwolves, therefore, probably selected this food source not on the basis of its nutritional quality but for its accessibility, its local abundant availability and the absence of competitors feeding on it. The consumption of these termites off the soil surface also means that large quantities of indigestible materials such as sand and grass litter enter the digestive system. Aardwolves compensate for this nutritionally poor diet by eating vast quantities of termites. They cope with this enormous quantity of ingested material by having a rapid passage rate and a thick, muscular and distensible distal colon. The first defaecation of the night often weighs up to 1,2 kg and this volume of material is probably accumulated in the distal part of the colon.

Even on this nutritionally poor diet aardwolves deposit a thick, yellow subcutaneous layer of fat during summer. By late winter these supplies are depleted and this

reflects the importance of these stores in facilitating survival during winter (Young 1976). Between late-summer and mid-winter there is a 25% reduction in the body mass of aardwolves. Adults are more likely than juveniles to survive through the winter months because by this time they would have reached a suitable mass with an adequate supply of fat (Hanks 1981). However, the fast growth rate recorded in juvenile aardwolves (Van Jaarsveld, Richardson & Anderson unpubl. data) reflects their need to obtain a suitable body mass to enable them to survive their first winter, but, nevertheless, winter is a period of the greatest mortality of aardwolf cubs (Richardson 1985). Blood parameters are also indicative of the seasonal availability of food. There was a significant seasonal variation of albumin, total plasma proteins, creatinine, urea, cholesterol and triglycerides; with the latter two parameters being the most reliable indicators of nutritional status.

During winter aardwolves spend approximately 25% more time in their dens than during summer. Inactivity during winter is an important behavioural adaptation to reduce energy expenditure when food is unavailable. During winter aardwolves usually retreat to their dens as soon as termites are no longer available. They do not spend time searching for food that has a limited availability because the metabolic requirements for thermoregulation during winter are high. One of the predictions of optimal foraging theory is that animals should be sensitive to patchily distributed food resources and allocate foraging efforts that maximize the rate of energy intake (Stephens & Krebs 1987). This is because the energetic costs of movement and prey capture need to be balanced by adequate food intake. During winter the foraging efficiency of aardwolves is constrained by the availability of termites.

The den has a thermally stable microclimate with very limited daily fluctuations in temperature, in contrast to the ambient temperatures above-ground. Seasonally, however, there is a marked difference in the temperatures of aardwolves dens. Aardwolves appear to not dig their own dens but usually modify and occupy those dug by other mammals. Two of the dens excavated in this study narrowed into

springhare *Pedetes capensis* burrows. It appears as if aardwolves enlarge the burrows of *P. capensis* to suit their requirements. An advantage of the narrow tunnel at the distal end of the burrow is that it may serve as an emergency refuge for young aardwolves while attempting to evade predators.

While inactive in the den, aardwolves probably adopt a suitable body posture depending on the degree of cold or heat stress they are experiencing, consequently resulting in significant energy savings. Additional thermoregulatory behaviour may include huddling which will result in a further reduction in heat loss. Huddling will reduce their effective surface area and thus limit excessive heat loss and consequently allow for more effective energy conservation. At low T_as, piloerection and shivering are adaptations to increase insulation and produce heat, respectively.

It is likely that aardwolves, as with other myrmecophages such as echidnas *Tachyglossus aculeatus* (Abensperg-Traun & De Boer 1992), are able to maintain a positive water balance throughout the year with only limited additional water uptake (Richardson 1985; Anderson, Richardson & Woodall 1992). The aardwolves H_2O requirements are met almost entirely by moisture obtained from their food source (*T. trinervoides* = $\pm$70% water). In the laboratory aardwolves exhibited minimal evaporative water loss rates, only 39-55% of that predicted by an allometric equation. In the field, water turnover rates are also very low (Anderson, Williams & Richardson unpubl. data) and aardwolves conserve water to maintain their body water homeostasis. Conductance appears to be a more important avenue for heat loss than pulmucutaneous cooling. The thick, muscular distal colon may also be important in the re-absorption of water.

Insulation in aardwolves increased significantly during winter. This was also manifested by a concomitant decrease in thermal conductance in captive aardwolves during winter. Thermal conductances were greater than expected, as predicted by the appropriate allometric equations, and this may be important in water conservation

and also to prevent overheating while resting in the burrow, or during excessive periods of exercise.

During summer aardwolves maintain a relatively constant euthermic body temperature (T_b) while inactive in the den. During winter, however, aardwolves gradually decrease their T_b, after retreating to their den, until mid-morning (the middle of their inactive period) when their T_b was between 3-6^{o}C less than euthermic values. This daily decrease in T_b (hypothermy) during winter contributes to significant energy savings of up to 17,7%. Surprisingly not every individual exhibits hypothermy, and the intraspecific variation observed may result in differential survival during periods of extreme energy stress.

Aardwolves have a basal metabolic rate (BMR) which is less than that predicted by the appropriate allometric equations, and in accordance with the low BMRs of other myrmecophages (McNab 1984). McNab (1984) implies a cause and effect relationship and he has suggested that all mammals which feed on a diet of ants and termites have low BMRs. Many other studies have shown that there is no consistent relationship between life-history variation and BMR amongst eutherian mammals (for example, Bennett 1988; Harvey, Pagel & Rees 1991) and for the purpose of this study it is not important whether body mass (Kleiber 1961), phylogeny and taxonomic affiliation (Hulbert & Dawson 1974; Crompton, Taylor & Jagger 1978; Elgar & Harvey 1987; Harvey, Pagel & Rees 1991), climatic influences (McNab & Morrison 1963), burrowing habits (McNab 1966, 1979) or food habits (McNab 1984, 1986) are attributed to the low BMR observed in aardwolves and other myrmecophages. What is important however is that a low BMR reduces the energy requirements of aardwolves. This may be fortuitous for aardwolves as it decidedly plays a role in ensuring survival during the period of low unavailability.

During the period of food stress in winter aardwolves show a variety of adaptations which can be grouped into two broad categories: (1) avoidance (mechanisms for

reducing the magnitude of the stress; e.g. insulation, microclimate usage) and (2) resistance (mechanisms for combating the stress; e.g. low BMR, hypothermy, shivering). Aardwolves are thus metabolically capable of tolerating the low energy conditions during winter. Most importantly they spend less metabolic energy than other placental mammals because of their low BMRs and their food demands are thus lower. They also lower their T_b and are thus capable of reducing metabolic requirements should energy conditions fall below a critical level.

OPSOMMING

Die aardwolf *Proteles cristatus* is oor 'n periode van twee jaar, van Desember 1988 tot Januarie 1991, bestudeer op die wildplaas Benfontein in die noordelike Kaapprovinisie, Suid-Afrika. Die grasdraertermiete, *Trinervitermes trinervoides*, wat die aardwolf se hoof voedselbron in hierdie area is, is grootliks onaktief gedurende die winter en gevolglik onbeskikbaar vir die aardwolf. Hierdie seisoenale voedselbeperking plaas 'n ernstige voedingsdruk op *P. cristatus*.

Anders as by tipiese "miervreters", grawe aardwolwe nie vir hulle prooi nie, maar lek grasdraertermiete van die grondoppervlakte af op. Gevolglik beskik aardwolwe nie oor die fisiese eienskappe wat kenmerkend is van tipiese mier- en termietvretende soogdiere nie. Aardwolwe het egter 'n aantal anatomiese eienskappe wat duidelike aanpassings by hulle dieët en voedingstyl is. Die mees opvallendste eienskappe is 'n spatelvormige tong wat bedek is met groot, verharde papillae, 'n breë verhemelte, groot mandibulere speekselkliere en 'n gespierde piloriese gebied in die maag. Die aardwolf is afhanklik van 'n dieët van oppervlakvoedende termiete en is vanwee 'n verminderde aantal tande nie in staat om op alternatiewe, groter prooispesies te voed nie.

Soos by ander invertebrata, is die voedingswaarde van *T. trinervoides* laag. Aardwolwe vergoed hiervoor deurdat groot hoeveelhede termiete gevreet word. Tot soveel as 300 000 termiete kan per nag per dier gedurende die warm somermaande gevreet word wat die neerlegging van onderhuidse vet moontlik maak. Gedurende die wintermaande (April - Augustus), het die liggaamsmassa van die aardwolwe met 25% afgeneem van ongeveer 10 kg tot 7,5 kg. Onderhuidse vetreserwes (gemeet by ses liggaamslokaliteite) het 'n aansienlike afname gedurende die winter getoon. Bloedmonsters, geanaliseer gedurende die somer en winter ten opsigte van 16 biochemiese en agt hematalogiese parameters, het ook betekenisvolle verskille ten

opsigte van geslag, ouderdomsklas en seisoen getoon. Die mees betroubare aanduiders van voedingstatus was trigliseried en cholesterol waardes.

Gedurende onaktiewe tye is skuiling gesoek in ondergrondse gate wat gewoonlik gewysigde springhaas (*Pedetes capensis*) gate was. Gedurende die winter is ongeveer 20 uur per dag in die gate deurgebring in vergelyking met 'n korter 15 uur 20 min gedurende die somer. Die gate is termies stabiel en skep dus 'n gunstige mikro-habitat wat help om die warm uiterstes van die Noord-Kaap te ontduik. In vergelyking met die uiterste variasie in omgewings temperature bo-op die grondoppervlakte buitekant die gate, was die gattemperature konstant, naamlik 12^{o}C en 27^{o}C gedurende die winter en somer, onderskeidelik.

Dit word voorgestel dat liggaamshouding en sosiale saamgroepering in die gate as belangrike energiebesparende meganismes dien. 'n Aansienlike toename in insolasie, gepaardgaande met 'n afname in termiese geleibaarheid gedurende die winter, was belangrike faktore in die beperking van hitteverlies. Waterbewaring deur die beperking van waterverdampingsverleis is belangrik om waterhomeostase in die liggaam tydens winter te onderhou.

Aktiewe aardwolwe het relatief konstante liggaamstemperature (T_b) van 37,0 - 37,5^{o}C gehandhaaf. Waneer die dier onaktief is, en veral in die winter, is 'n betekenisvolle afname in T_b waargeneem. T_bs so laag as 31,2^{o}C is in die middel van die onaktiewe periode gedurende die winter aangeteken. Die waargenome afname in T_b lei tot energiebesparing van tot 17,7%, en dra gevolglik by tot die aardwolf se vermoë om die periodieke beperkings ten opsigte van energiebronne gedurende winter te hanteer.

Die gemiddelde basale metaboliese tempo (BMR) van aardwolwe in gevangenskap was 1869,5 ml O_2 h^{-1} en 2194,3 ml O_2 h^{-1} in winter en somer, onderskeidelik. Hierdie metaboliese tempos is aansienlike laer (58,9% - winter; 67,1 % - somer) as

wat deur allometriese gelykstellings voorspel word. 'n Lae BMR, wat in die winter nog meer afneem, verlaag die oorhoofse energiebenodighede van die aardwolf.

Die aardwolf voed op 'n voedselbron wat, vanweë hul skadelike chemiese verdedigingsisteem, grootliks deur ander soogdiere vermy word. Hierdie voedselbron is nie in die winter beskikbaar nie en as gevolg van fisiese aanpassings is die aardwolf nie in staat om alternatiewe voedselbronne te benut nie. Oorlewing gedurende die winter word egter moontlik gemaak deur 'n kombinasie van 'n aantal fisiologiese en gedragsaanpassings. As gevolg van die aardwolf se spesialisasie op hierdie unieke dieët, en die vermoe om met die afwesigheid van termiete gedurende winter klaar te kom, het die dier 'n voedingsnis binnegedring wat feitlik heeltemal sonder mededingers is.

REFERENCES

Abensperg-Traun, M. 1991. Survival strategies of the echidna *Tachyglossus aculeatus* Shaw 1792 (Monotremata: Tachyglossidae). *Biol. Cons.* 58: 317-328.

Abensperg-Traun, M. & De Boer, E.S. 1992. The foraging ecology of the termite- and ant-eating specialist, the echidna *Tachyglossus aculeatus* (Monotremata: Tachyglossidae). *J. Zool., Lond.* 226: 243-257.

Acocks, J.P.H. 1975. Veld types of South Africa. (2nd Edn.). *Mem. Bot Surv. sth. Afr.* No. 42.

Allen, C.S., Grimshaw, H.M., Parkinson J.A. & Quarmby, C. 1974. *Chemical analyses of ecological materials*. Blackwells, Oxford.

Anderson, M.D. 1987. *The foraging behaviour of the snouted harvester termite Trinervitermes trinervoides in relation to different environmental factors.* Unpubl. BSc. (Hons) thesis, University of Pretoria.

Anderson, M.D. 1988. The aardwolf: harmless ant-eater. *Farmers Weekly*. August 19: 34-36.

Anderson, M.D. 1992. Anteating chats feeding in association with aardwolves. *Ostrich* 63: 186.

Anderson, M.D. & Jordaan, A. 1991. Aardwolf g'n lammervanger. *Landbouweekblad* 711: 44-47.

Anderson, M.D. & Richardson, P.R.K. 1992. Remote immobilization of the aardwolf. *S. Afr. J. Wildl. Res.* 22: 26-28.

Anderson, M.D., Richardson, P.R.K. & Woodall, P.F. 1992. A functional analysis of the feeding apparatus and digestive tract anatomy of the aardwolf, *Proteles cristatus*. *J. Zool., Lond.* 228: 423-434.

A.O.A.C. 1975. *Official methods of the Association of Analytical Chemists*. (12th Edn). (Ed.) W. Horwitz. Association of Analytical Chemists, Washington.

Arnold, W. 1988. Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *J. Comp. Physiol.* 158: 151-156.

Austin, P.J., Suchar, L.A., Robbins, C.T. & Hagerman, A.E. 1989. Tannin-binding proteins in saliva of deer and their absence in saliva of sheep and cattle. *J. Chem. Ecol.* 15: 1335-1347.

Bailey, E.D. & Davis, D.E. 1965. The utilization of body fat during hibernation in woodchucks. *Can. J. Zool.* 43: 701-707.

Bakko, E.B. & Nahorniak, J. 1986. Torpor patterns in captive white-tailed prairie dog *Cynomys leucurus*. *J. Mamm.* 67: 576-578.

Bakko, E.B., Porter, W.P. & Wunder, B.A. 1988. Body temperature patterns in black-tailed prairie dogs in the field. *Can. J. Zool.* 66: 1783-1789.

Bartholomew, G.A. 1972. Body temperature and energy metabolism. In: *Animal physiology*. (Ed.) M.S. Gordon. New York, Macmillan.

Bennett, A.F. 1988. Structural and functional determinates of metabolic rate. *Amer. Zool.* 28: 699-708.

Benton Jones, J. & Steyn, W.J.H. 1973. Sampling, handling and analysing plant tissue samples. In: *Soil testing and plant analysis*. (Eds) L.M. Walsh & J.D. Beaton. Soil Sci. Soc. of Am. Madison, Wisconsin.

Best, R.C. & Harada, A.Y. 1985. Food habits of the silky anteater (*Cyclopes didactylus*) in the Central Amazon. *J. Mamm.* 66: 780-781.

Bothma, J. du P. 1965. Random observations of the food habits of certain Carnivora (Mammalia) in Southern Africa. *Fauna and Flora* 16: 16-22.

Bothma, J. du P. & Nel, J.A.J. 1980. Winter food and foraging behaviour of the aardwolf *Proteles cristatus* in the Namib-Naukluft Park. *Madoqua* 12: 141-149.

Bothma, J. du P., Nel J.A.J. & Macdonald, A. 1984. Food niche separation between four sympatric Namib Desert carnivores. *J. Zool., Lond.* 202: 327-340.

Bradley, S.R. & Deavers, D.R. 1980. A re-examination of the relationships between thermal conductance and body weight in mammals. *Comp. Biochem. Physiol.* 65: 465-476.

Carter, T.S. Encarnacao, C.D. 1983. Characteristics and use of burrows by four species of armadillos in Brazil. *J. Mamm.* 64: 103-108.

Cass, T. 1973. *Statistical methods in management*. Cassell, London.

Chaplin, S.B., Diesel D.A., & Kasparie, J.A. 1984. Body temperature regulation in red-tailed hawks and great horned owls: responses to air temperature and food deprivation. *Condor* 86: 175-181.

Chew, R.M. 1965. Water metabolism of mammals. In *Physiological Mammalogy*. (Vol. 2). (Eds) W. Mayer & R.G. Van Gelder. Academic Press, New York.

Chivers, D.J. & Hladick, C.M. 1980. Morphology of the gastrointestinal tract in Primates: comparisons with other mammals in relation to diet. *J. Morph.* 166: 337-386.

Coaton, W.G.H. 1963. Survey of the termites (Isoptera) of the Kalahari thornveld and shrub bushveld of the R.S.A. *Koedoe* 6: 38-68

Coblentz, B.E. 1975. Serum cholesterol changes in George reserve deer. *J. Wildl. Manage.* 39: 432-435.

Coles, E.H. 1974. *Veterinary Clinical Pathology*. (2nd Ed.). W.B. Saunders CO., Philadelphia.

Cooper, R.L. 1977. *The importance of termites (Isoptera) as a food source to mammals.* BSc. (Hons) thesis. University of Pretoria, Pretoria.

Cooper, R.L. & Skinner, J.D. 1979. Importance of termites in the diet of the aardwolf *Proteles cristatus* in southern Africa. *S. Afr. J. Zool.* 14: 5-8.

Cornelius, C. Dandrifosse, G. & Jeuniaux, C. 1976. Chitinolytic enzymes of the gastric mucosa of *Perodicticus potto* (Primate Prosimian): purification and enzyme specificity. *Int. J. Biochem.* 7: 445-448.

Crompton, A.W., Taylor, C.R. & Jagger, J.A. 1978. Evolution of homeothermy in mammals. *Nature* 272: 33-336.

Delgiudice, G.D., Seal, U.S. & Mech, L.D. 1987. Effects of feeding and fasting on wolf blood and urine characteristics. *J. Wildl. Manage.* 51: 1-10.

Depocas, F. & Hart, J.S. 1957. Use of the Pauling oxygen analyser for measurements of oxygen consumption of animals in open-circuit system and in short-lag, closed-circuit apparatus. *J. Appl. Physiol.* 10: 388-392.

Eagle, T.C., Choromanski-Norris, J. & Kuechle, V.B. 1984. Implanting radio transmitters in mink and Franklin's ground squirrels. *Wildl. Soc. Bull.* 12: 180-184.

Elgar, M.A. & Harvey, P.H. 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Funct. Ecol.* 1: 25-36.

Evans, H.E. & Christensen, G.C. 1979. *Miller's anatomy of the dog.* (2nd Edn.). W.B. Saunders Co, Philadelphia.

Ewer, R.F. 1973. *The carnivores.* Weidenfeld and Nicolson, London.

Ferguson, J.W.H. 1988. Dietary overlap in plocepasserine weavers (Aves: Ploceidae). *S. Afr. J. Zool.* 23: 266-271.

Flower, W.H. 1869. On the anatomy of *Proteles cristatus* (Sparmann). *Proc. Zool. Soc. Lond.* 474-496.

Franzmann, A.W. & Schwartz, C.C. 1988. Evaluating condition of Alaskan black bears with blood profiles. *J. Wildl. Manage.* 52: 63-70.

Geffen, E., Hefner, R., Macdonald, D.W. & Ucko, M. 1992. Morphological adaptations and seasonal weight changes in Blanford's fox, *Vulpes cana*. *J. Arid. Env.* 23: 287-292.

Geiser, F. 1988. Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? *J. Comp. Physiol.* 158: 25-37.

Geiser, F. & Kenagy, G.J. 1987. Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. *Am. J. Physiol.* 252: 897-901.

Gessaman, J.A. 1987. Energetics. In: *Raptor management technique manual.* (Eds) B.A. Giron Pendleton, B.A. Millsap, K.W. Cline & D.M. Bird. National Wildlife Federation, Washington.

Goering, H.K. & Van Soest, P.J. 1970. *Forage fibre analysis*. Agricultural Research Services. Washington D.L.

Golightly, R.T. & Omart, R.D. 1983. Metabolism and body temperature of two desert canids: coyotes and kit foxes. *J. Mamm.* 64: 624-635.

Gordon, M.S. 1982. *Animal physiology: principles and adaptations.* Macmillan, New York.

Green, B., Griffiths, M. & Newgrain, K. 1992. Seasonal patterns in water, sodium and energy turnover in free-living echidnas, *Tachyglossus aculeatus* (Mammalia: Monotremata). *J. Zool., Lond.* 227: 351-365.

Griffiths, M. 1968. *Echidnas*. Pergamon Press, Oxford.

Guynn, D.C., Davis, J.R. & von Recum, A.F. 1987. Pathological potential of intraperitoneal transmitter implants in beavers. *J. Wildl. Manage.* 51: 605-606.

Halloran, D.W. & Pearson, A.M. 1972. Blood chemistry of the brown bear (*Ursus arctus*) from southwestern Yukon Territory, Canada. *Can. J. Zool.* 50: 827-833.

Hanks, J. 1981. Characterization of population condition. In: *Dynamics of large animal populations*. (Eds) C.W. Fowler & T.D. Smith. John Wiley and Sons, New York.

Harrison, D.J. & Gilbert, J.R. 1985. Denning ecology and movements of coyotes in Maine during pup rearing. *J. Mamm.* 66: 712-719.

Harvey, P.H., Pagel, M.D. & Rees, J.A. 1991. Mammalian metabolism and life history strategies. *Amer. Nat.* 137: 556-566.

Hayssen, V. & Lacy, R.C. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol.* 81: 741-754.

Heath, M.E. & Hammel, H.T. 1986. Body temperature and rate of O_2 consumption in Chinese pangolins. *Am. J. Physiol.* 250: 377-382.

Heldmaier, G. & Steinlechner, S. 1981. Seasonal pattern and energetics of shallow daily torpor in the Djungarian hamster, *Phodopus sungorus*. *Oecologia* 48: 265-270.

Heldmaier, G. Bockler, H., Buchberger, A., Lynch, G.R., Punchalski, W., Steinlechner, S. & Weisinger, H. 1985. Seasonal acclimation and thermogenesis. In: *Circulation, respiration, and metabolism*. (Ed.) R. Gilles. Springer, Berlin.

Hellgren, E.C., Vaughan, M.R. & KirkPatrick, R.L. 1989. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia - North Carolina. *Can. J. Zool.* 67: 1837-1850.

Henneman, III, W.W., Thompson, S.D. & Konecny, M.J. 1983. Metabolism of crab-eating foxes, *Cerdocyon thous*: ecological influences on the energetics of canids. *Physiol. Zool.* 56: 319-324.

Herreid, C.F. & Kessel, B. 1967. Thermal conductance in birds and mammals. *Comp. Biochem. Physiol.* 21: 405-414.

Hewitt, P.H., Nel, J.J.C. & Schoeman, I. 1972. The solar and ultraviolet radiation tolerances of several termite species. *J. ent. Soc. S. Afr.* 35: 119-121.

Hill, R.W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyser. *J. Appl. Physiol.* 33: 261-263.

Hill, R.W. 1975. Daily torpor in *Peromyscus leucopus* on an adequate diet. *Comp. Biochem. Physiol.* 51A: 413-423.

Hinds, D.S. 1977. Acclimatization of thermoregulation in desert-inhabiting jackrabbits (*Lepus alleni* and *Lepus californicus*). *Ecology* 58: 246-264.

Hubert, B., Gillon, D. & Adam, F. 1981. Cycle annuel du regime alimentaire des trois principlaes especes de rongeurs (Rodentia; Gerbillidae et Muridae) de Bandia (Senegal). *Mammalia* 45: 1-20.

Hudson, J.W. 1974. Torpidity in mammals. In: *Comparative physiology of thermoregulation*. (Vol. III). (Ed.) G.C. Whittow. Academic Press, New York.

Hulbert, A.J. & Dawson, T.J. 1974. Standard metabolism and body temperature of perameloid marsupials from different environments. *Comp. Biochem. Physiol.* 47A: 583-590.

Kay, R.N.B. 1987. Weights of salivary glands in some ruminant animals. *J. Zool., Lond.* 211: 431-436.

Kingdon, J. 1971. *East African mammals.* (Vol. I). Academic Press, London.

Kingdon, J. 1977. *East African Mammals.* (Vol III). Academic Press, London,.

Kleiber, M. 1961. *The fire of life.* Wiley, New York.

Koehler, C.E. & Richardson, P.R.K. 1990. *Proteles cristatus.* Mammalian Species No. 363: 1-6.

Kratzing, J.E. & Woodall, P.F. 1988. The rostral nasal anatomy of two elephant shrews. *J. Anat.* 157: 135-143.

Kruuk, H. 1972. *The spotted hyaena.* University of Chicago Press, Chicago.

Kruuk, H. & Sands, W.A. 1972. The aardwolf (*Proteles cristatus* Sparmann 1783) as a predator of termites. *E. Afr. Wildl. J.* 10: 211-227.

Kruuk, H. & Parish, T. 1983. Seasonal and local differences in the weight of European badgers (*Meles meles* L.) in relation to food supply. *Z. Saugetierk.* 48: 45-50.

Kuhnen, G. 1986. O_2 and CO_2 concentrations in burrows of euthermic and hibernating golden hamsters. *Comp. Biochem. Physiol.* 84A: 517-522.

Levy, A. 1964. The accuracy of the bubble meter method for gas flow measurements. *J. Sci. Instrum.* 41: 449-453.

Lindeque, M. & Skinner, J.D. 1984. Size frequency analysis of tooth wear in spotted hyaenas *Crocuta crocuta*. *S. Afr. J. Zool.* 19: 291-294.

Longhurst, C., Johnson, R.A. & Wood, T.G. 1978. Predation by *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae) on termites in Southern Guinea Savanna. *Oecologia* 32: 101-107.

Longhurst, C., Johnson R.A. & Wood, T.G. 1979. Foraging, recruitment and predation by *Decamonium uelense* (Sanstchi) (Formicidae: Myrmicinae) on termites in Southern Guinea Savanna, Nigeria. *Oecologia* 38: 83-91.

Louw, G.N. & Seely, M.K. 1982. *Ecology of desert organisms*. Longman, London & New York.

Lubin, Y.D. & Montgomery, G.G. 1981. Defenses of *Nasutitermes* termites (Isoptera, Termitidae) against *Tamandua* Anteaters (Edentata, Myrmecophagidae). *Biotropica* 13: 66-76.

Lyman, C.P. 1963. Hibernation in mammals and birds. *Am. Sci.* 51: 127-138.

Maberly, C.T.A. 1962. *Animals of East Africa*. Howard Timmins, Cape Town.

MacDonald, D.W. & Amlaner Jr, C.J. 1980. A practical guide to radio tracking. In: *A handbook on biotelemetry and radio tracking*. (Eds) Amlaner jr, C.J. & MacDonald, D.W. Pergamon Press, Oxford.

Madge, D.S. 1975. *The mammalian alimentary system: a functional approach*. Crane, Russak & Company, Inc, New York.

Matsumoto, T. 1976. The role of termites in an equatorial rain forest ecosystem of West Malaysia. *Oecologia* 22: 153-178.

McClure, P.A. & Porter, W.P. 1983. Development of insulation in neonatal cotton rats (*Sigmodon hispidus*). *Physiol. Zool.* 56: 18-32.

McKenzie, A.A. 1989. Increasing the rate of recovery of projectile syringes and of animals darted at night. *S. Afr. J. Wild. Res.* 19: 85-86.

McKenzie, A.A., Meltzer, D.G.A., le Roux, P.G. & Goss, R.A. 1990. Use of implantable radio transmitters in large African carnivores. *S. Afr. J. Wild. Res.* 20: 33-35.

McNab, B.K. 1966. The metabolism of fossorial rodents: A study of convergence. *Ecology* 47: 712-733.

McNab, B.K. 1979. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. *Ecology* 60: 1010-1021.

McNab, B.K. 1980. On estimating thermal conductance in endotherms. *Physiol. Zool.* 53: 145-156.

McNab, B.K. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *J. Zool., (Lond.)* 302: 485-510.

McNab, B.K. 1986. The influence of food habits on the energetics of eutherian mammals. *Ecol. Mono.* 56: 1-19.

McNab, B.K. 1989. Basal rate of metabolism, body size and food habits in the order Carnivora. In: *Carnivore behaviour, ecology and evolution*. (Ed.) J.L. Gittleman. Cornell University Press, Ithaca.

McNab, B.K. & Morrison, P.R. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecol. Mono.* 33: 63-82.

Menansho, H., Hagerman, A.E., Clements, S., Butler, L., Rogler, J. & Carlson, D.M. 1983. Modulation of proline-rich protein biosynthesis in rat parotid glands by sorghums with high tannin levels. *Proc. Natl. Acad. Sci. U.S.A.* 80: 3948-3952.

Melton, D.A. 1976. The biology of the aardvark (Tubulidentata - Orycteropodidae). *Mammal. Rev.* 6: 75-88.

Mills, M.G.L. 1981. *The socio-ecology and social behaviour of the brown hyaena, Hyaena hyaena Thunberg, 1820, in the southern Kalahari.* Unpubl. DSc. thesis, University of Pretoria, Pretoria.

Mills, M.G.L. 1990. *Kalahari Hyaenas: comparative ecology of two species*. Unwin Hyman, London.

Morhardt, J.E. 1970. Body temperature of white-footed mice (*Peromyscus* sp.) during daily torpor. *Comp. Biochem. Physiol.* 6: 57-68.

Morris, J.G. 1980. Assessment of sodium requirements of grazing beef cattle: A review. *J. anim. Sci.* 50: 145-152.

Nel, J.A.J. 1978. Notes on the food and foraging behavior of the bat-eared fox *Otocyon megalotis*. *Bull. Carneg. Mus. Nat. Hist.* 6: 132-137.

Noll-Banholzer, U. 1979. Body temperature, oxygen consumption, evaporative water loss, and heart rate in the fennec. *Comp. Biochem. Physiol.* 62A: 585-592.

Phelps, R.J., Struthers, J.K. & Moho, S.J.L. 1975. Investigations into the nutritive value of *Macrotermes falciger* (Isoptera: Termitidae) *Zool. Afr.* 10: 123-132.

Philo, L.M., Wolfe, D.L. & Fassig, S.M. 1979. Treatment of an acquired abdominal hernia in a polar bear. *J. Wildl. Dis.* 15: 121-123.

Philo, L.M., Follman, E.H. & Reynolds, H.V. 1981. Field surgical techniques for implanting temperature-sensitive radio transmitters in grizzly bears. *J. Wildl. Manage.* 45: 772-775.

Pocock, R.I. 1916. On some external characters of the striped hyaena (*Hyaena hyaena*) and related genera and species. *Ann. Mag. Nat. Hist.* 17: 330-343.

Prestwich, G.D. 1983. The chemical defenses of termites. *Sci. Am.* 249: 68-75.

Prothero, J. & Jurgens, K.D. 1986. An energetic model of daily torpor in endotherms. *J. theor. Biol.* 121: 403-415.

Redford, K.H. 1985. Feeding and food preference in captive and wild Giant anteaters (*Myrmecophaga tridactyla*). *J. Zool., Lond.* 205: 559-572.

Redford, K.H. 1987. Ants and termites as food. Patterns of mammalian myrmecophagy. In *Current Mammalogy.* (Vol. I). (Ed.) H.H. Genoways. Plenum Press, New York.

Redford, K.H. & Dorea, J.G. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. *J. Zool., Lond.* 203: 385-395.

Richardson, P.R.K. 1983. An improved darting system for immobilizing smaller mammals in the wild. *S. Afr. J. Wildl. Res.* 19: 67-70.

Richardson, P.R.K. 1985. *The social behaviour and ecology of the aardwolf, Proteles cristatus (Sparrman, 1783) in relation to its food resources*. Unpubl. D. Phil. thesis, University of Oxford, Oxford.

Richardson, P.R.K. 1987a. Food consumption and seasonal variation in the diet of the aardwolf *Proteles cristatus* in southern Africa. *Z. Saugetierk.* 52: 307-325.

Richardson, P.R.K. 1987b. Aardwolf: the most highly specialized myrmecophagous mammal? *S. Afr. J. Sci.* 83: 405-410.

Richardson, P.R.K. 1987c. Aardwolf mating system: overt cuckoldry in an apparently monogamous mating system. *S. Afr. J. Sci.* 63: 405-410.

Richardson, P.R.K. 1991a. Territorial significance of scent marking during the non-mating season in the aardwolf *Proteles cristatus* (Carnivora: Protelidae). *Ethology* 87: 9-27.

Richardson, P.R.K. 1991b. Scent marking and territoriality in the aardwolf. In: *Chemical signals in vertebrates*. (Eds) D.W. Macdonald, D. Muller-Schwarze & S. Natynczuk. Oxford University Press, Oxford.

Richardson, P.R.K. & Anderson, M.D. 1993a. Physical capture of the aardwolf *Proteles cristatus*. In: *The capture and care manual: capture, care, accommodation and transportation of wild African mammals.* (Ed.) A.A. McKenzie. Wildlife Decision Support Services, and South African Veterinary Foundation, South Africa.

Richardson, P.R.K. & Anderson, M.D. 1993b. Chemical capture of the aardwolf *Proteles cristatus*. In: *The capture and care manual: capture, care, accommodation and transportation of wild African mammals.* (Ed.) A.A. McKenzie. Wildlife Decision Support Services, and South African Veterinary Foundation, South Africa.

Riney, T. 1982. *A study and management of large mammals*. John Wiley & Sons, New York.

Robbins, C.T. 1983. *Wildlife feeding and nutrition*. Academic Press, New York.

Rock, P. & Williams, O. 1979. Change in lipid content of the montane vole. *Acta Theriol.* 24: 237-247.

Savage, R.J.G. 1978. Carnivora. In *Evolution of African Mammals*: 249-267. (Eds) V.J. Maglio & H.B.S. Cooke. Harvard University Press, Cambridge.

Sawicka-Kapusta, K. 1975. Fat extraction in the Soxhlet apparatus. In: *Methods of ecological bioenergetics.* (Eds) W. Grodzinski, R.Z. Klekkowski & A. Duncan. Blackwells, Oxford.

Schmidt-Nielsen, K. 1964. *Desert animals, physiological problems of heat and water.* Oxford University Press, London.

Schmidt-Nielsen, K. 1985. *Animal physiology: adaptation and natural environment.* Cambridge University Press, London.

Schmidt-Nielsen, B. & Schmidt-Nielsen, K. 1950. Pulmonary water loss in desert rodents. *Am. J. Physiol.* 162: 31-36.

Schulze, R.E. & McGee, O.S. 1978. Climatic indices and classifications in relation to the biogeography of southern Africa. In: *Biogeography and Ecology of South Africa*. (Ed.) M.J.A. Werger. W. Junk, The Hague.

Seal, U.S. & Hoskinson, R.L. 1978. Metabolic indicators of habitat condition and capture stress in pronghorns. *J. Wildl. Manage.* 42: 755-763.

Seal, U.S. & Mech, L.D. 1983. Blood indicators of seasonal metabolic patterns in captive adult gray wolves. *J. Wildl. Manage.* 47: 704-715.

Seal, U.S., Mech, L.D. & Van Ballenberghe, V. 1975. Blood analyses of wolf pups and their ecological and metabolic interpretation. *J. Mamm.* 56: 64-75.

Searcy, R.L. 1969. *Diagnostic Biochemistry.* McGraw-Hill Co., New York.

Shield, J. 1972. Acclimation and energy metabolism of the dingo, *Canis dingo*, and coyote, *Canis latrans. J. Zool., Lond.* 168: 483-501.

Shortridge, G.C. 1934. *The mammals of South West Africa.* William Heineman, London.

Siegel, S. 1956. *Nonparametric statistics for the behavioural sciences*. McGraw-Hill, Tokyo.

Skaife, S.H. 1953. *African insect life*. Longmans, Green and Co., Cape Town and New York.

Skinner, J.D. & van Aarde, R.J. 1985. The use of space by the aardwolf *Proteles cristatus. J. Zool., Lond.* 209: 299-301.

Smith, G.J. & Rongstad, O.J. 1980. Serological and hematological values of wild coyotes in Wisconsin. *J. Wildl. Dis.* 16: 491-497.

Smith, D.W., Peterson, R.O., Drummer, T.D. & Sheputis, D.S. 1991. Over-winter activity and body temperature patterns in northern beavers. *Can. J. Zool.* 69: 2178-2182.

Smithers, R.H.N. 1983. *The Mammals of the southern African subregion.* University of Pretoria, Pretoria.

Smithers, R.H.N. 1986. *South African red data book - terrestrial mammals.* South African National Science Progress Report, Pretoria.

Snedecor, G.W. & Cochran, W.G. 1967. *Statistical methods.* (6th Edn). Iowa State University Press, Iowa.

Snyder, G.K. & Nestler, J.R. 1990. Relationships between body temperature, thermal conductance, Q_{10} and energy metabolism during daily torpor and hibernation in rodents. *J. Comp. Physiol.* 159: 667-675.

Stanier, M.W. Mount, L.E. & Bligh, J. 1984. *Energy balance and temperature regulation.* Cambridge University Press, Cambridge.

Stark, R., Roper, T.J., MacLarnon, A.M., & Chivers, D.J. 1987. Gastrointestinal anatomy of the European badger *Meles meles* L. A comparative study. *Z. Saugetierk.* 52: 88-96.

Stephens, D.W. & Krebs, J.R. 1987. *Foraging theory.* Princeton University Press, Princeton.

Studier, E.H. & Proctor, J.W. 1971. Respiratory gases in burrows of *Spermophilus tridecemlineatus*. *J. Mamm.* 52: 631-633.

Tannenbaum, M.G. & Pivorum, E.B. 1984. Differences in daily torpor patterns among three southeastern species of *Peromyscus*. *J. Comp. Physiol.* 154: 233-236.

Taylor, C.R., Schmidt-Nielsen, K., Dmi'el, R. & Fedak, M. 1971. Effect of hyperthermia on heat balance during running in the African hunting dog. *Amer. J. Physiol.* 220: 823-827.

Thenius, E. 1966. Zur stammesgeschichte der hyanen (Carnivora, Mammalia) . *Z. Saugetierk.* 31: 293-300.

Thornwaite, C.W. 1940. Atmospheric moisture in relation to ecological problems. *Ecology* 21: 17-28.

Tietje, W.D. & Ruff, R.L. 1980. Denning behaviour of black bears in boreal forest of Alberta. *J. Wildl. Manage.* 44: 858-870.

Tucker, V.A. 1965. Oxygen consumption, thermal conductance and torpor in the Californian pocket mouse *Perognathus californicus*. *J. Cell. Comp. Physiol.* 65: 393-404.

Turnbull, W.D. 1970. Mammalian masticatory apparatus. *Fieldiana (Geology)* 18: 147-356.

Tyson, P.D. 1986. *Climatic change and variability in southern Africa.* University of Witwatersrand, Johannesburg.

Vogt, F.D. & Lynch, G.R. 1982. Influence of ambient temperature, nest availability, huddling, and daily torpor on energy expenditure in the white-footed mouse, *Peromyscus leucopus*. *Physiol. Zool.* 55: 56-63.

Walther, H. 1963. The water supply of desert plants. In: *The water relations of plants*. (Eds) A.J. Putter & F.H. Whitehead. John Wiley, New York.

Wang, L.C.H. & Wolowk, M.W. 1988. Torpor in mammals and birds. *Can. J. Zool.* 66: 133-137.

Weast, R.C. 1985. *The CRC handbook of chemistry and physics*. CRC Press, Boca Raton.

Wells, M.E. 1968. A comparison of the reproductive tracts of *Crocuta crocuta*, *Hyaena hyaena* and *Proteles cristatus*. *E. Afr. Wildl. J.* 6: 63-70.

Williams, D.D. & Rausch, R.L. 1973. Seasonal carbon dioxide and oxygen concentrations in the dens of hibernating mammals (Sciuridae). *Comp. Biochem. Physiol.* 44A: 1227-1235.

Willis, C.K. & Anderson, M.D. 1990. The hole truth: the story behind those mammals of the underground. *Custos* 19: 20-24.

Willis, C.K., Skinner, J.D. & Robertson, H.G. 1992. Relative importance of ants and termites in the diet of the aardvark *Orycteropus afer*. *Afr. J. Ecol.* 30: 322-334.

Wood, D.H. & Lee, A.K. 1985. An examination of sodium, potassium and osmotic concentrations in blood and urine of arid-zone rabbits in seasonal field conditions and in the laboratory. *Aust. Wildl. Res.* 12: 173-182.

Wunder, B.A. 1975. A model for estimating metabolic rate of active and resting mammals. *J. theor. biol.* 49: 345-354.

Young, R.A. 1976. Fat, energy, and mammalian survival. *Am. Zool.* 16: 699-710.

Zar, J.H. 1974. *Biostatistical analysis*. Prentice Hall, New Jersey.

Zervanos, S.M. 1975. Seasonal effects of temperature on the respiratory metabolism of the collared peccary (*Tayassu tajacu*). *Comp. Biochem. Physiol.* 50: 365-371.