

Aardwolf adaptations: a review

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The aardwolf *Proteles cristatus* has developed a number of anatomical and morphological adaptations for feeding on its termite prey. These adaptations preclude the aardwolf from feeding on other, larger (vertebrate) prey, especially during the winter months, when the T_a drops below 9°C and when *Trinervitermes* termites are largely unavailable. Winter is therefore a stressful period for aardwolves, as evidenced by increased juvenile mortality, a 20% decline in body mass and depletion of subcutaneous fat reserves. The aardwolf uses both physiological and behavioural means to overcome this period of food stress. An increased period is spent underground in the thermally-stable environment of the den. Den sharing is more common in the winter months and social thermoregulation may result in energy savings. While inactive the aardwolf lowers its T_b (to an average of $34.1 \pm 1.6^\circ\text{C}$ during the middle of the inactive period during winter) and in some individuals this results in energy savings of up to 18%. Seasonal changes in pelage density and thermal conductance allow for more passive heat transfer during summer and improved heat retention during winter. Laboratory and field measurements of metabolic rate showed that the aardwolf has a low BMR and a low FMR (between 40 and 78% of that predicted by allometric equations). The aardwolf's metabolic rate is 11% lower during the winter months, resulting in reduced energy requirements during the period of limited food availability. Evaporative water loss rates are low, further reduced during the winter months, adaptations to survive in a desert environment and on a seasonally-unavailable food source. The aardwolf is therefore well adapted to feed on a diet of *Trinervitermes* termites, a food niche that has been largely unexploited by other animals, and it uses various ecological, behavioural and physiological adaptations to cope with this seasonally unavailable food source.

INTRODUCTION

The aardwolf *Proteles cristatus* is one of the world's most remarkable mammals. Despite its relatedness to the hyaenids, the aardwolf lives almost entirely on a diet of termites (Kruuk & Sands, 1972; Cooper & Skinner, 1979; Richardson, 1987a), making it one of the few true mammalian myrmecophages (Redford, 1987). This obligate myrmecophagous diet contrasts to the aardwolf's external characteristics (Anderson *et al.*, 1992). It does not possess the specialized morphological traits which characterize typical myrmecophages (Griffiths, 1968) and in contrast has features that are similar to its relatives, the hyaenids (Redford, 1987; Koehler & Richardson, 1990). The aardwolf is one of only 18 species of the 4060 living mammal species that feed exclusively on termites (Vaughan, 1986).

Throughout its range in Africa (Skinner & Smithers, 1990), the aardwolf principally feeds on termites of the genus *Trinervitermes* (Kruuk & Sands, 1972; Richardson, 1987a) and on *T. trinervoides* in southern Africa (Cooper & Skinner, 1979; Richardson, 1987a). These termites live in dome-shaped termite mounds and are common throughout the grassland areas of South Africa (Skaife, 1953). At night when conditions are favourable, these termites emerge in dense aggregations on the soil surface where they forage on grass stems (Anderson, 1987). The aardwolf feeds on these foraging termites, consuming as many as 300,000 on a warm summer night (Richardson, 1987b).

The soldier cast of *T. trinervoides* has a chemical defence system of noxious terpene-based secretions that are sprayed through an opening at the tip of the snout (of the head/frontal gland) at predators (Prestwich, 1983), thus protecting the worker termites while they harvest grass on the soil surface. This defence system is effective in limiting predation from most invertebrates and

vertebrates. It is thought that, as the aardwolf evolved from civet-like viverrids (Ewer, 1973; Savage, 1978), which are known to have the ability to feed on noxious foodstuffs, it was pre-adapted to feed on a diet of *Trinervitermes* termites.

T. trinervoides are very sensitive to unfavourable environmental conditions, thus limiting the period which they are available to the aardwolf. The termites lack cuticular pigmentation and consequently are not active during the day (Hewitt *et al.*, 1972). They are also inactive when the ambient temperature (T_a) declines below 9°C (Richardson, 1985; Richardson, 1987a; Anderson, 1987) and thus largely unavailable for the aardwolf during the winter months (Richardson, 1987a,b; Anderson, 1994). The aardwolf does feed on an alternative food source during winter, albeit to a much less extent (Richardson, 1987a). This species, *Hodotermes mossambicus*, is darkly-pigmented and therefore active by day and the aardwolf is thus active during the late-afternoon during the winter months when it feeds on these termites (Richardson, 1985).

This seasonal food unavailability is reminiscent of the ecological problems that are imposed on mammalian species of the temperate latitudes during winter (Lyman, 1963) and unusual for a carnivore in the Afrotropics. In South Africa, winter is thus a period of great stress for aardwolves as they have to endure four months with significantly less food (Richardson, 1985, 1987a,b), which results in a 20% decline in body mass (Richardson, 1985, 1987a). Richardson (1985) suggested that survival during winter can be attributed to the aardwolf's use of extensive subcutaneous fat reserves which are deposited during the summer months, as well as an increased period of inactivity in the den.

It was shown by McNab (1984) that the aardwolf, as with other myrmecophagous mammals, has a reduced basal meta-

bolic rate (BMR). He attributed this to their ant and termite diet that is nutritionally poor, seasonally unavailable, filled with chemical poisons and often ingested with grass and sand. A low BMR would allow the aardwolf to cope with a seasonally unavailable diet of termites.

The aim of this paper is to review how the aardwolf uses ecological, behavioural and physiological adaptations to allow its specialization on a diet of seasonally unavailable food. The field work for this study was conducted on De Beers' Benfontein Game Farm (28°50'S, 24°50'E), located c. 6 km south-east of Kimberley in the Northern Cape/Free State (Richardson, 1985; Anderson, 1994), and the laboratory work was done at the University of Pretoria.

ADAPTATIONS

Morphological and anatomical adaptations

Anderson *et al.* (1992) studied 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. It was found that the aardwolf possesses none of the obvious external physical features of a termite feeding style, characteristics that are typical of other myrmecophagous mammals (Griffiths, 1968). Behaviourally the aardwolf differs from the other typical myrmecophages 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 that are clear adaptations to this diet (Anderson *et al.*, 1992), which are summarized here.

The aardwolf has a large and hairless muzzle, which prevents the soldier termites' defensive secretions, and hence dirt, from adhering to the same extent as they would if the muzzle was haired (Kruuk & Sands, 1972).

The most noticeable features of the aardwolf skull are the widely spaced and small-peg-like teeth, the contrastingly large canines, and the broad and parallel-sided palate (Anderson *et al.*, 1992). Therefore, although the aardwolf probably has the ability to kill vertebrate prey with its large canines, because of a lack of developed molars and pre-molars, it would not be able to process the prey. The canines are used in territorial disputes against other aardwolves and in defence against predators (Richardson, 1985, 1987 a,b). The relatively well-developed incisors are almost certainly used for grooming.

An interesting aspect of the aardwolf's musculature is the relatively large digastric muscle, compared to that of a domestic dog (Turnbull, 1970). As the 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. Other features of the skull are the well-developed postorbital processes and the extra-ordinarily large tympanic bulla (Anderson *et al.*, 1992). As the aardwolf locates its prey using its senses of smell, sight, and particularly hearing, this explains, in particular, its well-developed tympanic bulla.

The aardwolf has a broad spatulate tongue (117–123 mm long, and 30–32 mm wide) covered with large, hardened papillae (one type, "incisiform" papillae may be unique to the aardwolf). This tongue is used to lick termites from the soil surface and the papillae are adaptations to protect the tongue against abrasion by sand. The broad palate accommodates the rapid licking movements of the broad tongue. It also has posteriorly-directed transverse ridges, which pre-

sumably act as a catchment area for termites as the tongue is again extruded.

The mandibular salivary glands are very large (c. twice the size of the mandibular salivary glands of a similar-sized dog) and they are serous and mucous secreting, while the parotid, sublingual and zygomatic glands are serous or mixed. The mucous secretions 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, as has been speculated to be the case in myrmecophagous elephant shrews (Kratzing & Woodall, 1988). It is not known whether the saliva may play a role in the detoxification of the terpene secretions, i.e. similar to the tannin-binding proteins found in the saliva of browsing ruminants (Austin *et al.*, 1989).

The gastro-intestinal tract of the aardwolf follows the typical carnivore pattern and consists of a stomach, small intestine, caecum and colon (Anderson *et al.*, 1992). The smooth-walled pyloric region of the stomach has a few irregular folds and the walls are thick and muscular. As *Trinervitermes* termites are small and soft-bodied, chewing is unnecessary and the termites are probably pulverized by the muscular region of the stomach. A similar structure is found in the stomach of anteaters *Mirmecophagidae* spp. and pangolins *Manidae* (Chivers & Hladik, 1980). Chewing would not only limit the amount of termites that could be ingested, but also rupture the soldier termites' heads and thus release the terpene contents into the aardwolf's buccal cavity. The pulverization of termites in the stomach is probably aided by the sand and other debris that is incidentally ingested with the termites (up to 50% of the faeces contain sand; Cooper & Skinner, 1979).

The small intestine is short, a characteristic of animals that feed on soft, easily digestible material. Aardwolf digestion may be more geared to processing large volumes of material and the rapid digestion of the workers' abdomens, as opposed to the more efficient digestion of the whole termites. The small caecum may play a role in the absorption of water and electrolytes (Madge, 1975). The descending (distal) colon is characterized by thick walls with distinct longitudinal bands. This enables the distal colon to distend, allowing the accumulation of a large volume of faeces (over periods as long as 18 h). Soon after emergence from their den in the late-afternoon/early-evening, aardwolves walk to a nearby midden and defecate, with the first defecation of the evening weighing up to 1 kg (c. 10% of the mass of the animal!) (Kruuk & Sands, 1972; Richardson, 1987a). As aardwolves obtain most of their water from termites and thus very rarely drink (Richardson, 1985), the distal colon may play an important role in the absorption of water (Anderson *et al.*, 1992).

Body condition

In a study on the seasonal body condition of free-ranging aardwolves, Anderson (1994) collected data on body masses ($n = 137$), subcutaneous fat indices ($n = 29$ aardwolves) and 24 different blood variables (17 aardwolves during 49 captures; Anderson & Richardson, 1992).

Body mass

It was found that the body mass of aardwolves decreased significantly from late-summer to late-winter and during this period (April-August) aardwolves lost an average of 61 g body weight per month (Anderson, 1994). The body mass of individ-

uals during late-summer (9.6 ± 1.2 kg; $n = 33$; February, March and April) differed significantly from the body masses of individuals during mid-winter (8.4 ± 1.1 kg; $n = 55$; June, July and August) ($t = 4.85$; $p < 0.05$) (Anderson, 1994). These data are congruent with Richardson's (1987a) observation of a 20% decline of body mass in aardwolves during the winter months. Juvenile aardwolves suffer their highest mortality during the winter months (Richardson, 1985).

Subcutaneous fat fluctuations

Changes in the subcutaneous fat index, especially the measurements taken at the upperback, lowerback and waist, followed the same seasonal pattern as body mass with a general decline over winter, staying low during the first half of summer (Anderson, 1994). This seasonal pattern of declining body mass and subcutaneous fat reserves reflect the winter unavailability of termites (Richardson, 1987a; Anderson, 1994). Examination of aardwolf carcasses revealed that adult animals have a thick, yellow subcutaneous fat layer during mid/late-summer. This fat is mobilized during winter and is consequently almost totally absent from carcasses examined during late-winter/spring. The aardwolves' subcutaneous fat reserves are probably one of the keys to survival during the winter months (Richardson, 1985; Anderson, 1994). Subcutaneous fat is viewed as latent metabolic energy that 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).

Blood parameters

Anderson (1994) found that there were many differences between the sexes, ages and seasons with respect to the 24 different blood parameters. There were significantly higher levels of albumin, total plasma protein and creatinine during winter, while urea, cholesterol, triglycerides and phosphorous values were significantly greater during summer (Anderson, 1994). Seasonal variation in these variables reflects nutritional differences (food and water intake) between summer and winter.

Activity patterns and denning

The activity patterns of aardwolves were studied by following individual animals during their active period, recording the time they left the den and the time that they retired to these refuge (Richardson, 1985; Anderson, 1994). Richardson (1985) found that an average of 5.8 dens (range 2-9) were used by a pair of aardwolves in a territory each year, with each den being slept in for about 6-8 weeks before a different den was used. The time of departure from, and time of retirement to, dens was highly variable throughout the year but fairly consistent within a specific season (Richardson, 1987a; Anderson, 1994; Williams *et al.*, 1997), with aardwolves spending a greater proportion of time in their dens during winter. Denning times were 19.1 ± 1.2 h and 15.8 ± 1.72 h during winter and summer, respectively ($t = 6.04$; $P < 0.01$). The extended period spent in the den during winter, coupled with a reduced metabolic rate (see below), results in aardwolves conserving at least 639 kJ d^{-1} while in their winter dens (Anderson *et al.*, 1997). Aardwolf activity patterns and hence den usage are largely determined by the availability of termites. The den also has an important anti-predatory function, especially as it provides a safe refuge for the cubs from predators, such as black-backed jackals, *Canis mesomelas* (Richardson, 1985).

Anderson (1994) determined the characteristics of 42 aardwolf den entrances and two dens were excavated in order to study their internal structure. The 42 dens examined had only one entrance, with the entrances being randomly orientated ($Z = 1.366$, $p = 0.256$).

The two excavated aardwolf dens were narrow and well defined with no side tunnels and no obvious enlargements at the end. In contrast, a den excavated by Richardson (1985) had a slight chamber enlargement. The two excavated burrows narrowed into smaller springhare *Pedetes capensis* burrows, with a tunnel height and width of approximately 10 cm and 15.5 cm, respectively (Anderson, 1994). As aardwolves do not possess well-developed and powerful limbs to excavate a subterranean den (Anderson *et al.*, 1992), they apparently rather enlarge those dug by springhares.

Anderson (1994) recorded the temperature of an unoccupied aardwolf den (measurements made at a distance of 2.5 m into the burrow), as well as external T_a s, during mid-summer and mid-winter. The temperature of the aardwolf burrows (T_d) was relatively constant during summer and averaged $27.2 \pm 0.2^\circ\text{C}$, despite large daily fluctuations at the soil surface where temperatures ranged from a maximum of 39.5°C at 11h00 to a minimum of 15.0°C at 05h00 (Anderson, 1994). The T_d s during summer were high but still within the thermoneutral zone (TNZ) of the aardwolf (McNab, 1984; Anderson *et al.*, 1997). During winter, mean burrow temperatures were also constant, averaging $12.2 \pm 1.2^\circ\text{C}$, substantially lower than that recorded during summer (Anderson, 1994). Although the T_d during winter was below the TNZ of the aardwolf, it is still considerably warmer than the T_a s outside the den. It is likely that the relatively low T_d , together with a CO_2 build up in the den during winter (exacerbated by the extended period spent underground, and den sharing) (Anderson, 1994), may stimulate temporal heterothermy in the aardwolf (see Kuhnen 1986) (see below).

It was found that during winter young aardwolves frequently shared their dens with siblings or one of their parents (Richardson, 1985; Anderson, 1994). Huddling reduces their effective surface area, resulting in a reduction in heat loss (Anderson, 1994, Anderson *et al.*, 1997). Owing to the small size of the den chamber, heat produced by the occupant(s) will also raise the T_d to some extent, so the T_d of the aardwolf chamber may therefore rise above the lower critical temperature of the TNZ. The three dens examined in Anderson's (1994) and Richardson's (1985) studies were not lined with insulative materials (such as grass, litter or fur) as has been found in the dens of other animals, and in particular hibernating mammals, such as the black bear *Ursus americanus* (Tietje & Ruff, 1980).

Body temperature

Anderson (1994) measured the body temperatures (T_b) of six aardwolves during summer and winter using temperature-sensitive radio transmitters. In this study it was found that aardwolves demonstrated a daily T_b cycle that was evident during both summer and winter (similar to the typical activity-rest cycle, or circadian rhythm, of endotherms; Stanier *et al.*, 1984), but the pattern was more exaggerated during winter (Anderson, 1994). During winter active aardwolves maintained an average T_b of approximately 37.3°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 $34.1 \pm 1.6^\circ\text{C}$. The lowest T_b recorded during winter was 31.2°C in one female at 09h00. There was

considerable variation between individuals in the extent of hypothermia during the inactive period (Anderson, 1994). Although the mean T_b s of active aardwolves was greater than the mean T_b s of inactive animals during summer, the variation in T_b was not as great as that during winter.

The most obvious effect of hypothermia on the biology of endotherms is a reduction of their energy requirements for the maintenance of T_b . Using Wunder's (1975) model for estimating metabolic rate (MR), it was determined that hypothermia in the aardwolf during winter translates to a *c.* 18% energy saving (Anderson, 1994). The estimated reduction in metabolism is at the lower end of the 18–31% saving observed in most small mammalian species that exhibit daily hypothermia (Vogt & Lynch, 1982; Wang & Wolowyk, 1988). This suggests that the aardwolf does 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 avoidance. More importantly, however, the aardwolf's size may preclude it from lowering its T_b below 31–33°C. Although a number of medium- to large-sized mammals undergo hypothermia (e.g. Heldmaier & Steinlechner, 1981; Bakko & Nahorniak, 1986; Wang & Holowyk, 1988), this physiological adaptation is typical of small mammals where the size limit to hypothermia is set by the costs of rewarming which is directly proportional to body mass, so the larger the animal the greater the costs (Prothero & Jurgens, 1986; Geiser, 1988).

Lowered T_b also has adaptive potential for water conservation by a reduction of evaporative water loss. If the effective temperature of the evaporative surface is lowered the vapour pressure that drives evaporative water loss also decreases (Thornwaite, 1940; Weast, 1985). Previous studies have found that aardwolves only drink water during mid-winter (Richardson, 1985; Anderson, *et al.* 1992), when they feed very little, and during the rest of the year their water requirements are met by moisture derived from termites.

Laboratory metabolism

Measurements of the BMR of five captive aardwolves showed that aardwolves have a reduced metabolic rate and evaporative water loss, further reduced during winter (when the aardwolves were fed a reduced daily ration during winter (90 g d⁻¹), thus simulating their natural food restriction during this time of year), thus reducing energy requirements during the stressful winter months. During summer the VO_2 of five aardwolves was 2194±443 mL O₂ h⁻¹ or 1058 kJ d⁻¹. VO_2 was lower during winter ($F = 23.1$, $df = 2.8$, $P < 0.005$), with a BMR of 1844±224 mL O₂ h⁻¹ or 889 kJ d⁻¹ (Anderson, 1994; Anderson *et al.*, 1997). These summer and winter estimates of BMR were 77.6% and 60.0% of the prediction made by the Kleiber (1961) equation, and 67.1% and 58.0% of that predicted by Hayssen & Lacy's (1985) equation for carnivores. Aardwolves therefore have a reduced BMR compared to other species of mammals and it is hypothesized that this translates to a reduced field metabolic rate (FMR) in the wild (Anderson *et al.*, 1997). McNab (1984) suggested that ant- and termite-eating mammals have evolved a low BMR in order to survive on a diet of termites, which are not only nutritionally poor (Phelps *et al.*, 1975; Redford & Dorea, 1984; Anderson, 1994), but also have a patchy distribution in both space and time (*cf* Richardson, 1985; Anderson, 1994). Aardwolves reduce their rates of energy expenditure to levels

that permit them to balance their energy budgets when termites are least available. During summer, BMRs exceed winter values by *c.* 11%. Summer is a time of abundant food supply for aardwolves and their set point for metabolic rate is apparently higher and their pelage is less insulative, perhaps to allow more passive heat transfer during this season (Anderson, 1994; Anderson *et al.*, 1997). During winter, when subjected to periods of fasting, they respond physiologically by lowering their BMRs, an adjustment that likely lowers their food requirement at a time when food availability is low.

The evaporative water loss rates for aardwolves were 39% and 55% of those predicted by Chew's (1965) allometric equation for summer and winter respectively (Anderson *et al.*, 1997). Thus, as in other arid-adapted mammals (Schmidt-Nielsen & Schmidt-Nielsen, 1950; Noll-Banholzer, 1979), the aardwolf has a reduced rate of pulmo-cutaneous water loss. This translates into a reduced water turnover rate in the field, which is advantageous to an animal living under desert conditions.

Field metabolism

Estimates of daily energy expenditure and water flux were obtained by means of the doubly-labeled water technique (Lifson & McClintock, 1966; Nagy, 1980). The methodology and detailed results of the field metabolism research are reported in Williams *et al.* (1997). In summary, during summer aardwolves had a CO₂ production of 112.5 l CO₂/d, equivalent to an energy expenditure of 2891.2 kJ/d. During winter CO₂ production averaged 71.8 l CO₂/d, equivalent to an energy expenditure of 1844.8 kJ/d, statistically lower than the summer values ($f = 9.9$, $df = 1, 15$, $p < 0.006$). These results support the hypothesis that a reduced BMR results in a low FMR. Based on doubly labeled water studies of 46 eutherian species, the equation of Nagy (1987) predicts a FMR of 4873.3 kJ/d for aardwolves in summer and 5265.0 kJ/day in winter. The aardwolf therefore has a FMR that deviates -40.6% and -65.0%, respectively, from the summer and winter predictions (Williams *et al.*, 1997). Besides a reduced BMR, other components of the aardwolf's energy budget are also reduced, thus accounting for their very frugal total energy expenditure, especially relative to other carnivores (Williams *et al.*, 1997). The largest amount of energy (36.6%) of the aardwolf's daily energy expenditure during summer is used on territory maintenance. In contrast, during winter, when aardwolves occupy a den that has a thermal environment that is below their thermo-neutral-zone, 57.3% of their energy costs are incurred on energy expenditure for BMR, heat increment of feeding, and thermoregulation (Williams *et al.*, 1997).

Water flux during winter (292 ml/d) was also statistically lower than during summer (615 ml/d) ($f = 11.9$, $df = 1$, $P < 0.001$), a decrease of 53.1%. These rates of water influx are 64.3% and 17.7% lower, respectively, during summer and winter than one would expect from an eutherian mammal living in an arid environment (Williams *et al.*, 1997).

CONCLUSIONS

This review shows that the aardwolf is very well adapted to surviving on a diet of *Trinervitermes* termites, even though this food source is seasonally unavailable. With the development of a number of anatomical and morphological adaptations, the aardwolf is unable to feed on other prey, especially during the winter months when *Trinervitermes* are unavailable. Despite a decline in body mass and a depletion of subcutaneous fat

reserves, the aardwolf survives through the stressful period by using various ecological, behavioural and physiological adaptations. The aardwolf is therefore well adapted to feed on a diet of *Trinervitermes* termites, a food niche that has been largely unexploited by other animals.

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REFERENCES

- ANDERSON, M.D. 1987. The foraging behaviour of the snouted harvester termite *Trinervitermes trinervoides* in relation to different environmental factors. Unpublished B.Sc. Honours Dissertation, University of Pretoria, Pretoria.
- ANDERSON, M.D. 1994. The influence of seasonality and quality of diet on the metabolism of the aardwolf, *Proteles cristatus* (Sparman 1783). Unpublished M.Sc. Dissertation, University of Pretoria, Pretoria.
- ANDERSON, M.D. & RICHARDSON, P.R.K. 1992. Remote immobilization of the aardwolf. *South African Journal of Science* 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*. *Journal of Zoology, London* 228: 423-434.
- ANDERSON, M.D., WILLIAMS, J.B. & RICHARDSON, P.R.K. 1997. Laboratory metabolism and evaporative water loss of the aardwolf. *Physiological Zoology* 70: 464-469.
- 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. *Journal of Chemical Ecology* 15: 1335-1347.
- BAKKO, E.B. & NAHORNIK, J. 1986. Torpor patterns in captive white-tailed prairie dog *Cynomys leucurus*. *Journal of Mammalogy* 67: 576-578.
- CHEW, R.M. 1965. Water metabolism of mammals. In W. Mayer & R.G. van Gelder (Eds) *Physiological Mammalogy*. Vol. 2. New York, Academic Press. pp 43-155.
- CHIVERS, D.J. & HLADICK, C.M. 1980. Morphology of the gastrointestinal tract in Primates: Comparisons with other mammals in relation to diet. *Journal of Morphology* 166: 337-386.
- COOPER, R.L. & SKINNER, J.D. 1979. Importance of termites in the diet of the aardwolf *Proteles cristatus* in southern Africa. *South African Journal of Zoology* 14: 5-8.
- EWER, R.F. 1973. *The carnivores*. London, Weidenfeld and Nicolson. 494 pp.
- GEISER, F. 1988. Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? *Journal of Comparative Physiology* 158: 25-37.
- GRIFFITHS, M. 1968. *Echidnas*. Oxford, Pergamon Press. 282 pp.
- HAYSEN, V. & LACY, R.C. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comparative Biochemistry and Physiology* 81: 741-754.
- HELDMAIER, G. & STEINLECHNER, S. 1981. Seasonal pattern and energetics of shallow daily torpor in the Djungarian hamster, *Phodopus sungorus*. *Oecologia* 48: 265-270.
- HEWITT, P.H., NEL, J.J.C. & SCHOEMAN, I. 1972. The solar and ultraviolet radiation tolerances of several termite species. *Journal of the Entomological Society of South Africa* 35: 119-121.
- KLEIBER, M. 1961. *The fire of life*. New York, Wiley. 454 pp.
- 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. *Journal of Anatomy* 157: 135-143.
- KRUUK, H. & SANDS, W.A. 1972. The aardwolf (*Proteles cristatus* Sparmann 1783) as a predator of termites. *East African Wildlife Journal* 10: 211-227.
- KUHNEN, G. 1986. O₂ and CO₂ concentrations in burrows of euthermic and hibernating golden hamsters. *Comparative Biochemistry and Physiology* 84A: 517-522.
- LIFSON, N.M. & MCCLINTOCK, R. 1966. Theory of use of turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology* 12: 46-74.
- LYMAN, C.P. 1963. Hibernation in mammals and birds. *American Scientist* 51: 127-138.
- MADGE, D.S. 1975. *The mammalian alimentary system: a functional approach*. New York, Crane, Russak & Company, Inc. 195 pp.
- MCNAB, B.K. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *Journal of Zoology, London* 302: 485-510.
- NAGY, K.A. 1980. CO₂ production in animals: an analysis of potential errors in the doubly-labeled water method. *American Journal of Physiology* 238: R466-R473.
- NAGY, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57: 111-128.
- NOLL-BANHOLZER, U. 1979. Body temperature, oxygen consumption, evaporative water loss, and heart rate in the fennec. *Comparative Biochemistry and Physiology* 62A: 585-592.
- PHHELPS, R.J., STRUTHERS, J.K. & MOHO, S.J.L. 1975. Investigations into the nutritive value of *Macrotermes falciger* (Isoptera: Termitidae). *Zoologica Africana* 10: 123-132.
- PRESTWICH, G.D. 1983. The chemical defenses of termites. *Scientific American* 249: 68-75.
- PROTHERO, J. & JURGENS, K.D. 1986. An energetic model of daily torpor in endotherms. *Journal of Theoretical Biology* 121: 403-415.
- REDFORD, K.H. 1987. Ants and termites as food. Patterns of mammalian myrmecophagy. In H.H. Genoways (Ed) *Current Mammalogy* Vol. 1. New York, Plenum Press. pp. 349-399.
- REDFORD, K.H. & DOREA, J.G. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. *Journal of Zoology, London* 203: 385-395.
- RICHARDSON, P.R.K. 1985. The social behaviour and ecology of the aardwolf, *Proteles cristatus* (Sparman, 1783) in relation to its food resources. Unpublished 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. *Zeitschrift für Säugetierkunde* 52: 307-325.
- RICHARDSON, P.R.K. 1987b. Aardwolf: the most highly specialized myrmecophagous mammal? *South African Journal of Science* 83: 405-410.
- ROCK, P. & WILLIAMS, O. 1979. Change in lipid content of the montane vole. *Acta Theriologica* 24: 237-247.
- SAVAGE, R.J.G. 1978. Carnivora. In Maglio, V.J. & Cooke, H.B.S. (Eds) *Evolution of African Mammals*. Cambridge, Harvard University Press pp. 249-267.
- SCHMIDT-NIELSEN, K. 1985. *Animal physiology: adaptation and natural environment*. London, Cambridge University Press. 619 pp.
- SCHMIDT-NIELSEN, B. & SCHMIDT-NIELSEN, K. 1950. Pulmonary water loss in desert rodents. *American Journal of Physiology* 162: 31-36.
- SKAIFE, S.H. 1953. *African insect life*. Longmans, Cape Town and New York, Green and Co. 387 pp.
- SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The mammals of the southern African subregion* 2nd edn. Pretoria, University of Pretoria. 770 pp.
- STANIER, M.W. MOUNT, L.E. & BLIGH, J. 1984. *Energy balance and temperature regulation*. Cambridge, Cambridge University Press. 152 pp.
- 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. *Journal of Wildlife Management* 44: 858-870.

- TURNBULL, W.D. 1970. Mammalian masticatory apparatus. *Fieldiana (Geology)* 18: 147-356.
- VAUGHAN, T.A. 1986. *Mammalogy*. Philadelphia, CBS College Publishing. pp. 159-164.
- 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*. *Physiological Zoology* 55: 56-63.
- WANG, L.C.H. & WOLOWYK, M.W. 1988. Torpor in mammals and birds. *Canadian Journal of Zoology* 66: 133-137.
- WEAST, R.C. 1985. *The CRC handbook of chemistry and physics*. Boca Raton, CRC Press. 2362 pp.
- WILLIAMS, J.B., ANDERSON, M.D. & RICHARDSON, P.R.K. 1997. Seasonal differences in field metabolism, water requirements, and foraging behaviour of free-living aardwolves in South Africa. *Ecology* 78: 2588-2602.
- WUNDER, B.A. 1975. A model for estimating metabolic rate of active and resting mammals. *Journal of Theoretical Biology* 49: