The physical and thermal characteristics of aardwolf dens

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Received 12 January 2005. Accepted 24 August 2005

The aardwolf, *Proteles cristatus,* is an 8–12 kg, termite-eating member of the family Hyaenidae. Aardwolves are nocturnal and spend the daylight hours in an underground den. We investigated the physical and thermal characteristics of aardwolf dens. Aardwolf dens usually had only one entrance with a single, long tunnel. It appears as if aardwolves did not dig their own burrows but enlarged the burrows of springhares. Mean temperature of the burrows was 27.2 ± 02°C during summer and 12.2 ± 1.2°C during winter. Daily fluctuations in den temperature were reduced compared to surface ambient temperature. This favourable, thermally-stable environment is used by aardwolves to escape the external thermal extremes, as a refuge for the rearing of young, and to evade predation from black-backed jackals and other mammalian carnivores.

Key words: aardwolf, burrow, den, den characteristics, microclimate.

INTRODUCTION

The semi-arid environments of southern Africa are characterized by substantial daily and seasonal fluctuations in temperature (Tyson 1987). Small- and medium-sized mammals which inhabit these areas use behavioural and physiological means to escape the associated environmental stresses (Louw & Seely 1982). One such method is to escape the heat or cold by retreating into the thermally stable microclimate of a subterranean refuge, where conditions are normally more favourable (e.g. Downs & Perrin 1989; Ellison 1993).

The aardwolf, *Proteles cristatus,* is an 8–12 kg member of the Hyaenidae that specializes on a diet of termites. It occurs in the semi-arid areas of southern Africa (Smithers 1983; Koehler & Richardson 1990), with its distribution being determined primarily by the availability of *Trinervitermes* termites, which constitute its principal food source (Kruuk & Sands 1972; Cooper & Skinner 1979; Richardson l987a). In order to escape the thermal stresses of the environment it inhabits (see Anderson 2005), the aardwolf makes extensive use of subterranean dens during the inactive period (Smithers 1983; Richardson 1985; Richardson 1987a; Anderson 1994). During summer and winter aardwolves spend an average of 15 h 12 min (±1 h 26 min, n = 12) and 19 h 57 min (±2 h 19 min, n = 18) in the den, respectively (Anderson 1994).

Despite the aardwolf's dependence on these underground refugia, it is not well suited to digging (Anderson *et al.* 1992), unlike other ant-and termite-eating mammals (Redford 1987). It does not possess the well-developed claws and powerful limbs necessary to excavate a subterranean food source as it does not dig for its prey, but licks foraging termites off the soil surface (Anderson *et al.* 1992).

With its fairly limited ability to dig, the aardwolf cannot excavate termites from hypogeal or epigeal termitaria, particularly when they are absent from the soil surface during winter (Richardson 1987a,b). This results in severe nutritional stress for this myrmecophagous mammal at this time (Anderson 1994, 2005). During the winter months in the Kimberley area, when *Trinervitermes trinervoides* termites are unavailable, a greater proportion of time is consequently spent in the den (Richardson 1987b). During the colder months the aardwolf does become more diurnal, feeding on another termite species, *Hodotermes mossambicus,* during the late afternoon (Richardson 1987a). In the thermally stable den environment during winter, there is an increased period of inactivity, with huddling and temporal heterothermy (Anderson 1994, 2005; Anderson *et al.* 1997) and a concomitant reduction in daily energy expenditure (Williams *et al.* 1997). These contribute to the aardwolf's ability to survive during this energetically stressful period (Anderson 2005).

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Dens are also important for the rearing of young, and as a refuge for the cubs from black-backed jackals, *Canis mesomelas,* and possibly other mammalian predators (Richardson 1985). According to Richardson (1985), aardwolves frequently (as often as every 3–5 days) relocate to new dens (especially when they have cubs) and this is thought to be an anti-predatory strategy (Richardson 1985).

Despite the apparent important eco-physiological significance of aardwolf dens, little information is available about their physical and thermal characteristics (Smithers 1983; Richardson 1985). The purpose of this study, therefore, is to describe the physical and thermal characteristics of aardwolf dens and to elaborate on their significance to the life history strategy of this interesting mammal.

METHODS

The study was conducted on Benfontein (28°50′S; 24°50′E), an 11 300 ha game farm located just south-east of Kimberley, on the border of the Northern Cape and Free State provinces. Fieldwork was conducted from 1989–1990.

Dens were located using radio telemetry (Richardson 1985; Anderson & Richardson 1992; Anderson 1994), by either following aardwolves until they retired to these refugia or by locating the position of inactive individuals.

The physical characteristics of burrow entrances were determined for 42 active aardwolf dens: (1) slope of the entrance measured using a clinometer (Suunto Co., Helsinki, Finland); (2) entrance orientation determined with a magnetic compass; (3) number of entrances; and (4) width, height and depth of entrance (measured from ground surface above the centre of the entrance to the roof of the entrance).

Two dens were completely excavated to determine burrow architecture. A larger number of dens were not excavated as the exercise is extremely laborious and we did not want to cause excessive disturbance to the aardwolves in the study area. Width, height and depth of these burrows were determined at the entrance and then at intervals along their length. The compass orientation of the entrances was determined and the orientation of the burrows were noted if there was a change in burrow direction relative to the entrance direction.

Burrow temperatures (T_d) of an unoccupied aardwolf den were determined during summer and winter study periods. Owing to time constraints the T_ds of additional dens were not measured. T_ds were measured using copper-constantan thermocouples inserted 2.5 m down the length of the burrow from the entrance and connected to a multi-channel temperature recorder (KM 1202, Kane May, Welwyn Garden City, U.K.). A thermocouple in a white ball measured ambient temperatures (T_a). An additional thermocouple was placed in a black ball on the ground surface outside the den to record the extreme changes in soil surface temperature. Thermocouples were allowed to equilibrate with soil temperature for 24 h before measurements began. All temperatures were determined hourly for five consecutive days in winter and three consecutive days in summer. Data are presented as the mean hourly temperatures. For purposes of graphic clarity, standard deviations are not presented, but were very small, seldom exceeding 2°C.

RESULTS AND DISCUSSION

Den characteristics

All 42 of the aardwolf dens examined in detail had only one entrance, with only two of a total of 197 dens located during this study and a study by Richardson (1985) having two entrances. This is in contrast to other burrowing mammals, such as the aardvark, *Orycteropus afer,* which has an extensive burrow system interconnected by many entrances and underground chambers (Melton 1976), and the springhare, *Pedetes capensis,* which often has a complex burrow system that sometimes includes several entrances (and escape holes) and chambers (Butynski & Mattingly 1979; Anderson 1996). The mean length of seven excavated springhare burrows was 17.2 m (Anderson 1996), considerably longer than the aardwolf dens we measured (Table 2, Richardson 1995).

Den entrances were randomly orientated, with the mean direction being 98.7 ± 106.1° (Z = 1.366; P = 0.256). Nine entrances faced south (135–225°, 170 ± 28°), 14 faced east (45–135°, 97 ± 25°), 11 faced north (315–360° and 0–45°, 197 ± 169°) and eight faced west (225–315°, 261 ± 28°) (Fig. 1). Dens were therefore not selected with the entrance facing away from the prevailing wind or to maximize solar radiation, as has been found in armadillos (Dasypodidae) (Carter & Encarnacao 1983) and the coyote, *Canis latrans* (Harrison & Gilbert 1985). Entrances of aardwolf dens were sufficiently below ground level with little direct exposure to the prevailing wind and therefore it is unlikely that wind affects the occupants.

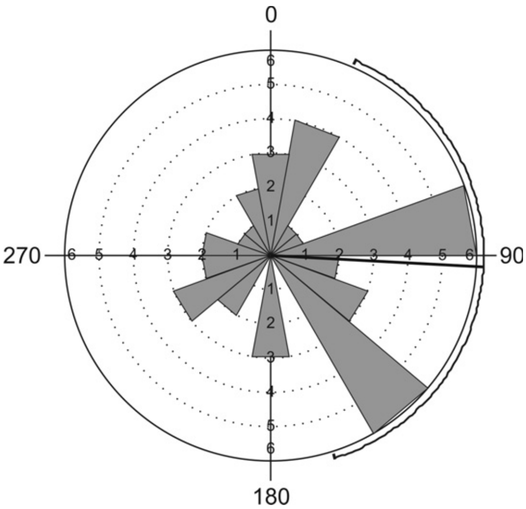

Fig. 1. A rose diagram indicating the direction of 42 aardwolf den entrances. The mean direction (98.7°) is indicated as the line running from the centre of the diagram to the outer edge, while the arc extending to either side represents the confidence limits of the mean.

The physical characteristics of the aardwolf den entrances are presented in Tables 1 and 2. Den entrances were semi-circular in shape and approximately 150% wider than high. They were easily distinguishable from the larger and rounder burrows of aardvark and the smaller burrows of springhare, which were the two other prominent burrowing species (although not of similar size) in the study area (see Richardson 1995). The slope of the den entrances were steep, averaging 19° (Table 2), whereas the slope of the ground into which the burrows were excavated was usually fairly flat or only gently sloped.

Tunnels of the two excavated aardwolf dens were narrow and well defined with no side tunnels (Table 1, Figs 2 & 3). The tunnels of the dens had no obvious enlargements at the end. In contrast, a den excavated by Richardson (1985) had a slight chamber enlargement at the end (approximately twice as wide as the tunnel). The two excavated burrows (Figs 2 & 3) narrowed into smaller burrows (presumed to be springhare burrows), with a tunnel height and width of approximately 10 cm and 15.5 cm, respectively. Although springhare burrow dimensions have apparently not been

Table 1. Tunnel dimensions (mean ± 1 S.D.) of two excavated aardwolf dens.

	Den A	Den B
Tunnel length (m)	6.5	5.1
Tunnel height (cm)	20.7 ± 1.8 (n = 7)	21.7 ± 2.7 (n = 6)
Tunnel width (cm)	34.8 ± 4.4 (n = 7)	36.8 ± 3.6 (n = 6)

determined, the internal diameter of 45 entrances measured 13.2 ± 4.9 cm (height) by 16.8 ± 5.3 cm (width) (Anderson 1996). We have no records of springhares using the enlarged aardwolf burrows. Richardson's (1985) excavated den did not narrow into a springhare burrow.

As aardwolves do not possess well-developed and powerful limbs to excavate a subterranean den (Anderson *et al.* 1992), we suggest that they may rather enlarge those dug by springhares. These rodents are prodigious diggers and their burrow structure, burrow utilization and fossorial ecology has been described by Butynski & Mattingly (1979), Anderson (1996) and Peinke & Brown (2005). Springhare burrows are probably of sufficient length to permit an aardwolf to enlarge the burrow before encountering any of the side tunnels. It is not known which specific springhare burrow entrance features are selected for by aardwolves, but it is possible that aardwolves may select more simple (recently excavated) springhare burrows (i.e. which do not have several tunnels, chambers, openings, etc.).

In the absence of existing, suitable holes it was suggested by Smithers (1983) that aardwolves may, however, be able to dig their own burrows. A burrow that he examined originated in a springbok, *Antidorcas marsupialis,* midden where the hard calcareous surface layer had been broken and churned up. The closely related and often sympatric hyaenas do not dig their own dens. Spotted hyaenas, *Crocuta crocuta,* sometimes take over porcupine, *Hystrix africaeaustralis,* dens, but, like brown hyaenas, *Hyaena brunnea,* regularly occupy abandoned aardvark dens (Mills 1990).

Aardwolf burrows are very narrow. This suggests that individual aardwolves do not require very

Table 2. The mean (± 1SD) depth, width, height (mm) and slope (°) of 42 aardwolf den entrances.

	Depth	Width	Height	Slope
Mean (±1 S.D.)	49.6 ± 14.0	38.0 ± 6.9	25.5 ± 6.0	19 ± 15.7

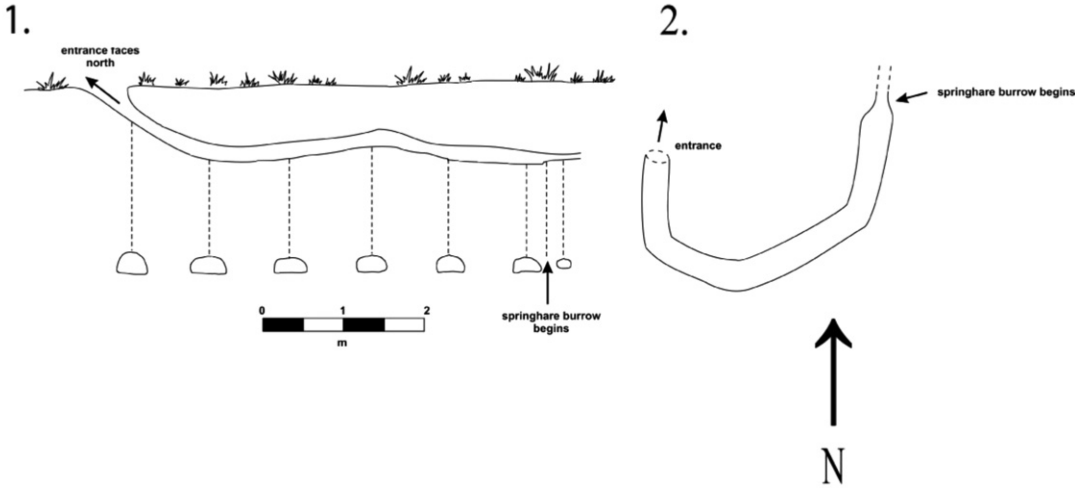

Fig. 2. Diagrammatic representation of an excavated aardwolf den (Den A): **1**, lateral view (with cross-section of burrows indicated at *c.* 2 m intervals); **2**, view from above.

much space inside their dens and keeping them as narrow as possible may offer protection against potential predators, especially in areas where large carnivores (such as leopards. *Panthera pardus,* and lions *Panthera leo*) still occur. Aardwolf burrow cross-sectional area does not differ significantly from that predicted by the allometric equation for semi-fossorial mammals (White 2005). A single entrance into the aardwolf den is also advantageous because it limits access by predators. This may however preclude the use of an alternative entrance/exit as an escape route should a predator enter the den. In an attempt to evade predation, aardwolves have been observed to block the burrow entrances with sand while they were being excavated from the burrow by humans (M.D.A. & P.R.K.R., pers. obs.). Furthermore, on one occasion, 4–5-week-old cubs attempted to evade being caught by humans while a den was being excavated by moving up the very narrow

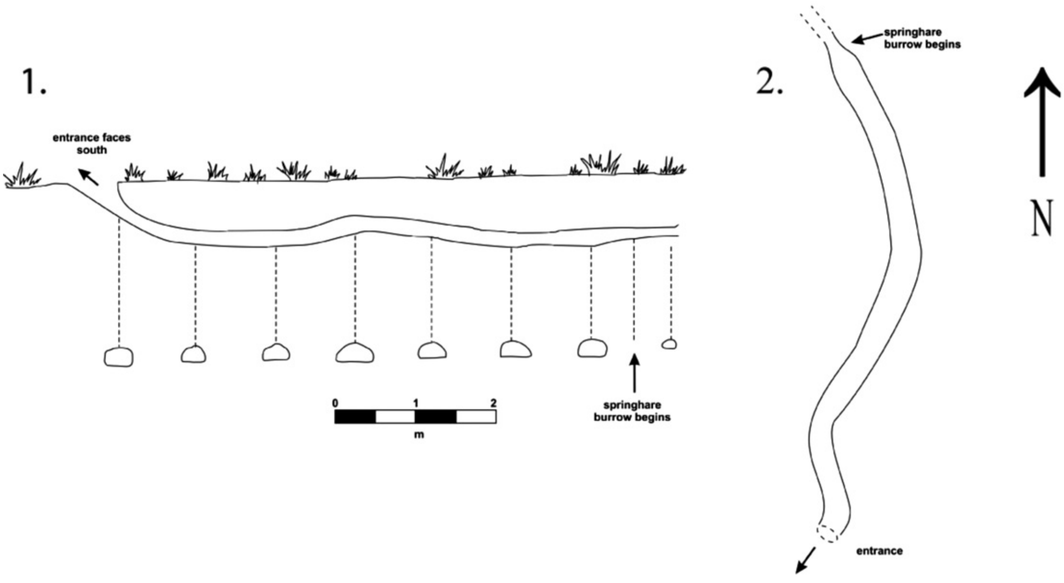

Fig. 3. Diagrammatic representation of an excavated aardwolf den (Den B): **1**, lateral view (with cross-section of the burrow indicated at *c.* 2 m intervals); **2**, view from above.

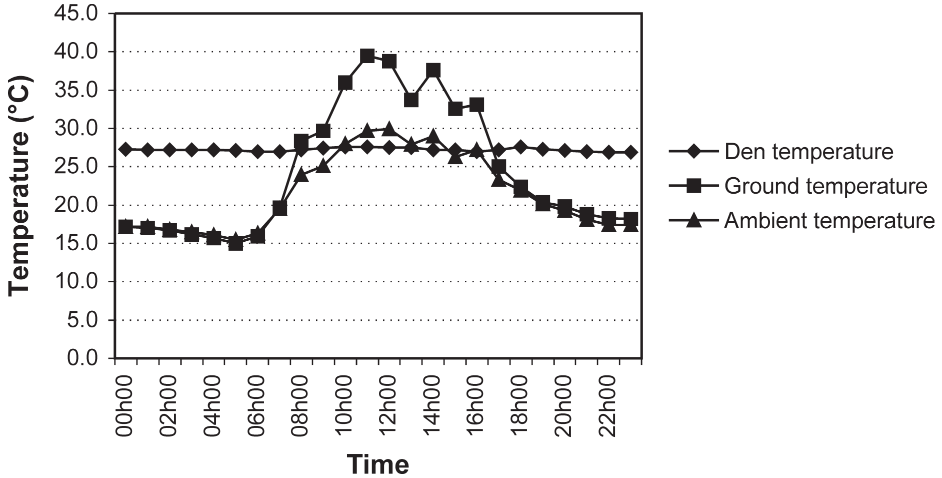

Fig. 4. Temperatures of an aardwolf den, soil surface in the vicinity of the den, and ambient temperature from the weather station at the Kimberley airport during summer.

springhare burrow extension, filling in this passage with soil behind them. This is an advantage of utilizing springhare burrows, and this digging behaviour recorded in the aardwolf cubs may explain why they have well developed claws at a young age. The prime function of brown and spotted hyaena dens is also to provide protection for the cubs (Mills 1990). Entrances of hyaena dens are large but they narrow down to small, oval-shaped tunnels, which are large enough only for the cubs but not large enough for adult hyaenas or other large carnivores, such as lions, 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.

Thermal environment of the den

The temperature of aardwolf burrows at 2.5 m into the burrow was relatively constant during summer and averaged 27.2 ± 0.2°C, despite large daily fluctuations at the soil surface where temperatures ranged from a maximum of 39.5°C at 11:00 to a minimum of 15.0°C at 05:00 (Fig. 4). The T_ds during summer are 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 ± 1.2°C, substantially lower than that recorded during summer (Fig. 5). Although the T_d during winter is below the TNZ of the aardwolf, it is still considerably warmer

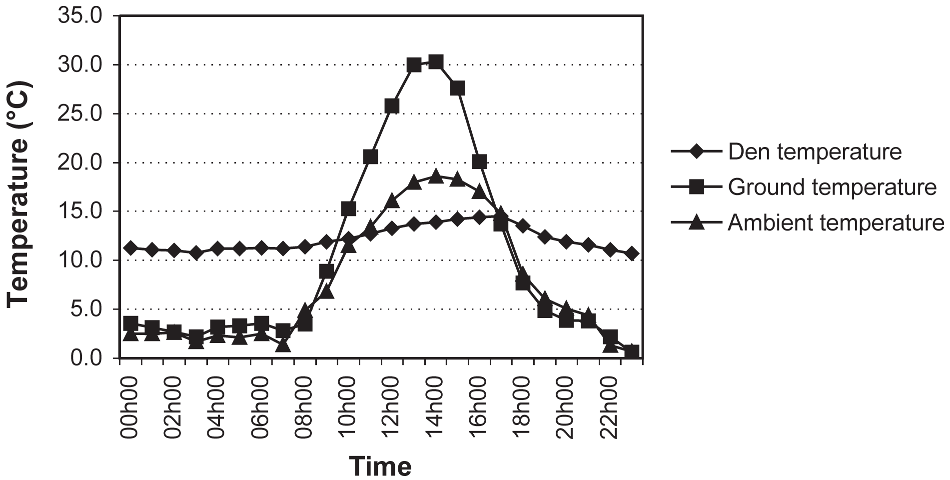

Fig. 5. Temperatures of an aardwolf den, soil surface in the vicinity of the den, and ambient temperature from the weather station at the Kimberley airport during winter.

than the T_as outside the den, which averaged 7.6 ± 6.4°C. It is likely that the relatively low T_d, together with a CO_2 build up in the den during winter (Anderson 1994) (exacerbated by the extended period spent underground, and den sharing; see below), may stimulate temporal heterothermy in this species (see Kuhnen 1986). Aardwolves lower their body temperature (T_b) by an average of 4.2°C while inactive in their dens during winter (Anderson 1994). This is presumably an adaptation to reduce energy expenditure when food is scarce (Anderson 1994). The den, therefore, may provide not only the cues necessary for lowering metabolism and a drop in T_b (hypercapnic and hypothermic conditions) but probably also provides a protective environment in which to enter a hypothermic state (Anderson 1994).

Aardwolf cubs share the den with their parents after they are born (early-October) until February; they then, until the winter months, often use their own den. During the colder months the young aardwolves frequently share their dens with siblings or one of their parents. Huddling reduces their effective surface area, resulting in a reduction in heat loss (Anderson 1994; Anderson *et al.* 1997). The ameliorating effects due to huddling may be critical in maintaining the aardwolves T_b within the TNZ. Owing to the small diameter of the den tunnel (and chamber, if one is present; see Richardson 1985), heat produced by the occupant(s) will also raise the T_d to some extent. Several studies have indicated that small mammals warm up their chambers by 8–21°C when they are inside (Sealander 1952; Stark 1963), so the T_d of the aardwolf chamber may therefore rise above the lower critical temperature of the TNZ. The T_d of occupied aardwolf dens was not measured in order to limit disturbance to the study animals while field metabolic rates were being determined (Williams *et al.* 1997). Only one of three excavated aardwolf dens had end chambers (this study and Richardson (1985)). Although a large den chamber would be advantageous in that it would facilitate movement, it would contribute to excessive heat loss during winter.

The three excavated aardwolf dens (this study and Richardson (1985)) 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 (Tietje & Ruff 1980).

In conclusion, aardwolves make obligatory use of subterranean dens during their resting period. The den provides a safe refuge from predators, and is particularly important for the shelter, protection and rearing of cubs. In the den refugia, aardwolves are able to lower their metabolism and T_b and consequently reduce their energy expenditure (Anderson *et al.* 1997; Williams *et al.* 1997). Use of these thermally-stable and protected refugia probably increases the chances of survival of aardwolves, particularly during the winter months when termites, their principal food, are generally not available.

ACKNOWLEDGEMENTS

This research was conducted while M.D.A. was an M.Sc. student at the University of Pretoria. Logistic support was provided by Hatfield Ford, Pretoria, and the McGregor Museum, Kimberley. The project was supported financially by the University of Pretoria, the National Research Foundation (Foundation for Research Development), the Wildlife & Environment Society (Northern Cape Region), and the Bob Blundell and Charles Astley Maberly post-graduate scholarship to M.D.A. We are grateful to De Beers Consolidated Mines Ltd for allowing us to study aardwolves on Benfontein. Christopher Willis and George Ellison provided advice, and Tania Anderson assisted in the field. Colleen Downs, Alexander Sliwa, Guy Castley and Chris Brown commented on drafts of the manuscript.

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