

Refuge microclimates of rodents: a surface nesting *Otomys unisulcatus* and a burrowing *Parotomys brantsii*

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We investigated microclimates of the nest of *Otomys unisulcatus* Cuvier, 1829 and the warren of *Parotomys brantsii* (Smith, 1834) during two seasons and correlated these with the rodents' physiology. In both rodents' refuges, temperature varied less than ambient temperature (TA). In winter, temperatures in the *O. unisulcatus* nest at 40 cm below the nest apex, and in the *P. brantsii* warren 15 cm below the soil surface, were higher than nocturnal TA. In summer, during the hours of highest TA, refuges were cooler than TA. Vapour pressure (v.p.) in the refuges varied less and was higher than ambient v.p. In the humid refuges, heat loss by conduction rather than evaporative water loss is suggested. The nest of *O. unisulcatus*, with less temperature variation in winter and lower temperatures in summer, was less dependent of TA than *P. brantsii*'s warren. The use of these refuges therefore contributes to the survival of these mesic rodents in a semi-arid region.

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Introduction

Otomys unisulcatus (Cuvier, 1829) and *Parotomys brantsii* (Smith, 1834), rodents of the semi-arid Karoo, South Africa, are similar in body size, behaviour (diurnal and crepuscular) and diet (herbivory – Du Plessis 1989, Du Plessis *et al.* 1991), but have different refuge strategies. *O. unisulcatus* builds nests of sticks under shrubs (De Graaff 1981, Vermeulen and Nel 1988), whereas *P. brantsii* inhabits warrens. The nests of *O. unisulcatus* average 0.45 m in height and 1.27 × 1.10 m in diameter, with a mean of nine openings (n = 66; Du Plessis and Kerley 1991). Nest chambers, lined with dry grasses, occur at the base of the stick nest. All measurements in *O. unisulcatus* refuges refer to the stick nest and not the nest chamber itself. *P. brantsii* warrens extend over an average area of 7.3 × 7.2 m with a mean of 46 entrances (n = 22, Du Plessis and Kerley 1991).

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No studies have related refuge microclimates to physiological adaptations in these rodents (Du Plessis 1989). This paper aims to investigate to what extent the refuges of *O. unisulcatus* and *P. brantsii* contribute to their survival in a semi-arid environment.

Materials and methods

Study site

Field work was conducted at Tierberg in the southern Karoo (33°09'28"S, 22°15'48"E), South Africa. Mean annual rainfall is 167 mm per annum, largely during summer. Mean annual temperature is 17.5°C, but the climate is extreme with maxima exceeding 30°C on 90 days per annum and minima below 10°C on 10 days per annum (Milton *et al.* 1992). Representative active refuges, within 500 m of each other, were studied. The *O. unisulcatus* nest, typically located in taller vegetation (*Acacia karroo* and *Lycium* sp., 1–3 m in height), was 0.5 m in height with seven openings. The *P. brantsii* warren, with 12 openings, was on the open flats associated with dwarf (40–60 cm in height) shrubs e.g. *Pteronia pallens* and *Galenia fruticosa*.

Measurements

Refuge and ambient temperatures and humidity were recorded with a MCS-101 datalogger, using calibrated MCS-101 temperature sensors and a MCS-174 humidity sensor (MC Systems, Cape Town). Hourly averages were recorded for four to ten days in each refuge during summer (March–April 1988) and winter (July–August 1988). The periods sampled in each season, were representative of that season (Weather Bureau 1986).

Burrows in the *P. brantsii* warren and tunnels in the *O. unisulcatus* nest were located with an iron rod (Kennerly 1964). Probes, protected in PVC pipes, were introduced into the vertical opening created by the iron rod and sealed with soil and cotton wool. In the *P. brantsii* warren, temperatures were monitored in burrows at 10 cm (TW₁₀) and 15 cm (TW₁₅) depth below the soil surface, 15 cm being the maximum burrow depth found in an excavated warren near the study site. Tunnels in the nest of *O. unisulcatus* at 10 (TN₁₀) and 40 cm (TN₄₀) distance below the nest apex were monitored, where TN₄₀ was just above soil surface in the vicinity of the nest chamber. No microclimatic measurements were taken within the nest chamber itself as the chamber could not be located without destroying the refuge. The temperatures of the deep positions in the refuges (TN₄₀ and TW₁₅) are considered to be representative refuge temperatures.

Ambient temperatures (TA) were recorded in the shade 5 cm above soil surface. Black bulb temperatures were recorded in the sun 5 cm above soil surface, and used as an indication of maximum heat absorption. Relative humidities (RH) were measured at 40 cm below the nest apex for *O. unisulcatus* and in a burrow of the *P. brantsii* warren, at 10 cm depth. We converted relative humidity to partial vapour pressure (v.p. in mm Hg; Kleiber 1961). Standard meteorological data, including TA and RH, were obtained from an automated weather station within 500 m of the refuges (W. R. J. Dean, pers. comm.) and used to calculate ambient v.p. at 2 m above soil surface.

Data analysis

Comparisons were made between: ambient and refuge temperatures and vapour pressures. Student's *t*-test was used for differences between means (Zar 1984). Differences in coefficients of variance were used for comparisons of variation (as indicated by F ratio, Lewontin 1966 in Zar 1984).

Results

Refuge temperatures

Comparisons between nest and warren temperatures were possible because mean TA and variation in TA did not differ significantly within a season at the nest or warren ($p > 0.05$).

In both warren and nest, temperatures fluctuated daily and seasonally (Fig. 1), however these fluctuations were less than those of ambient temperatures. In winter, variation in T_{N40} (CV = 11%) and T_{W15} (CV = 20.3%) was significantly less than variation in TA (50.2%, $F = 19.6$, $p < 0.001$ and 52.2%, $F = 6.8$, $p < 0.001$, respectively). A smaller variation existed in T_{N40} in winter than in T_{W15} ($F = 3.75$, $p = 0.001$, d.f. = 24). Both refuge and ambient temperature varied less in summer than winter. In summer, the variation in T_{N40} (CV = 3.4%) and T_{W15} (CV = 2.5%) was also significantly lower than that of TA (21.8%, $F = 53.4$, $p < 0.001$ and 25.4%, $F = 99.2$, $p < 0.001$, respectively).

Refuge temperatures for both the nest and the warren were higher than TA at night ($p < 0.05$, Table 1). During summer nights, T_{N40} was not higher than the relatively moderate ambient temperatures, except at 7:00 (Table 1). Comparisons of refuge temperatures reveal that during summer and winter nights (20:00 – 7:00 and 19:00 – 8:00), T_{N40} did not differ from T_{W15} ($p > 0.05$).

Summer diurnal temperatures in both refuges were lower than TA (Table 1). In summer T_{W15} was lower than TA only during the hours of highest ambient temperatures (12:00 – 16:00, Table 1). In winter the refuge temperatures, T_{N40} and T_{W15} , differ only between 14:00 and 15:00, when T_{N40} was lower than T_{W15} ($p < 0.05$). However in summer the mean (over all hours for all days sampled)

Table 1. Ambient (TA) and refuge temperatures of *O. unisulcatus*'s nest (T_{N40} , measured 40 cm below nest apex) and *P. brentsi*'s warren (T_{W15} , measured 15 cm below soil surface). Time periods (hours) are indicated when refuge temperatures differ from TA, using Student's *t*-test (Zar 1984), where * indicates $p < 0.05$, and ** indicates $p < 0.001$.

		Temperature range (°C)		Time	<i>p</i>
		Refuge	TA		
Night temperatures					
Winter:	T_{N40}	10.5 – 12.1	6.1 – 9.9	22.00 – 8.00	*
	T_{W15}	8.4 – 14.5	3.4 – 9.9	19.00 – 8.00	*
Summer:	T_{N40}	19.7 – 21.4	17.5 – 24.4	7.00	*
	T_{W15}	22.7 – 23.8	15.9 – 22.8	21.00 – 8.00	*
Day temperatures					
Winter:	T_{N40}	10.2 – 15.2	8.1 – 23.8	9.00 – 17.00	**
	T_{W15}	9.2 – 16.6	10.9 – 23.2	9.00 – 17.00	**
Summer:	T_{N40}	19.7 – 21.5	17.7 – 35.5	9.00 – 19.00	**
	T_{W15}	22.0 – 24.6	21.4 – 33.5	12.00 – 16.00	*

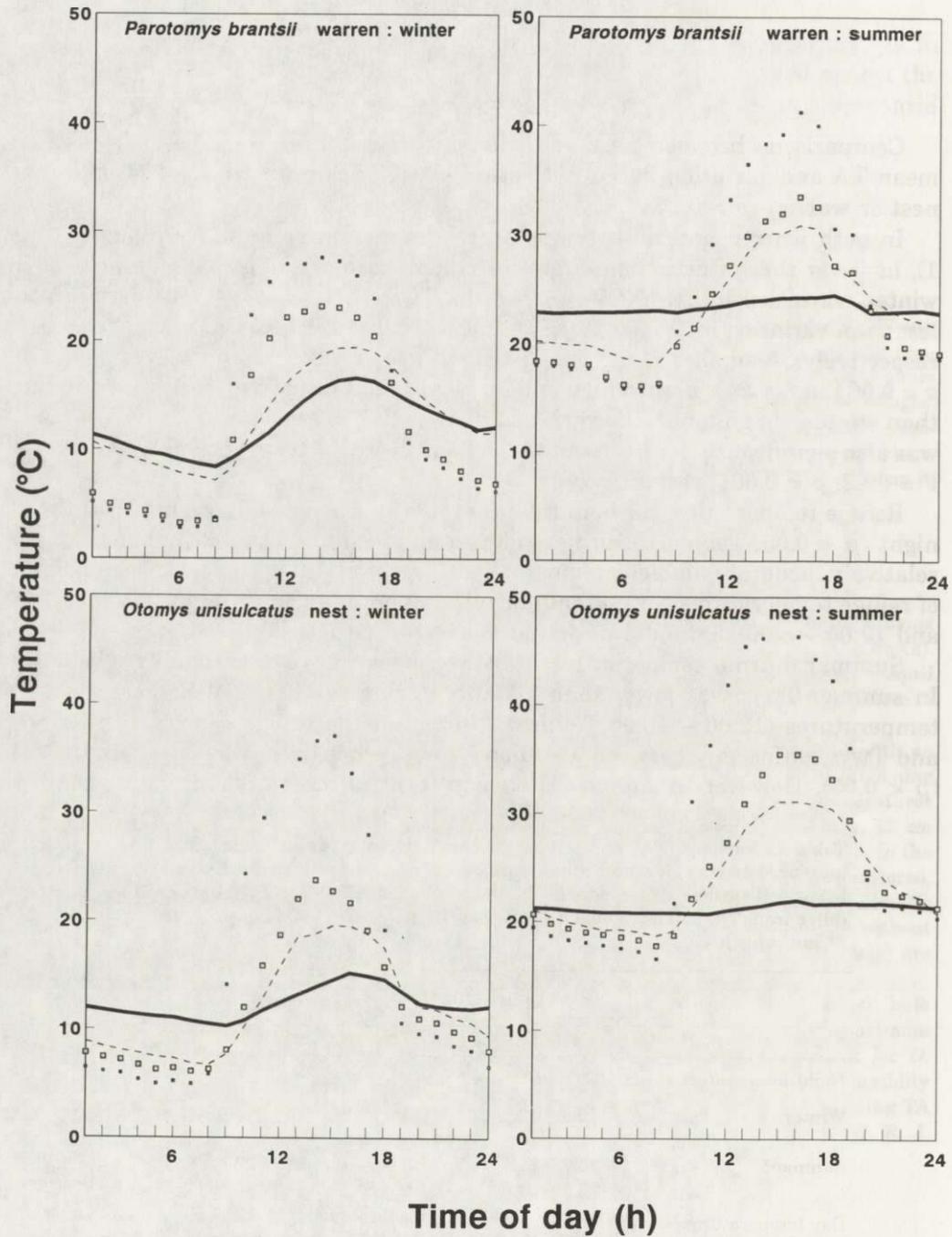


Fig. 1. Daily temperature profiles in *P. brantsii*'s warren and *O. unisulcatus*'s nest in winter and summer. Means ($n = 5$) are indicated, where large points are ambient temperature at warren or nest and small points are black bulb temperatures. Broken lines indicate superficial refuge temperatures (T_{N10} or T_{W10}) and solid lines indicate interior temperatures (T_{N40} or T_{W15}).

T_{N40} was lower than mean T_{W15} ($t = -8.49$, $p < 0.001$, d.f. = 24). In summer the mean hourly T_{N40} was lower than the mean hourly T_{W15} after sunrise (8:00 – 10:00) and at sunset (19:00, $p < 0.05$).

The amplitude of temperature change decreased with depth in the refuge. In the *O. unisulcatus* nest variation in T_{N10} was larger than variation in T_{N40} and in the *P. brantsii* warren variation in T_{W10} was larger than variation in T_{W15} (Fig. 1).

The maximum differences between refuge temperatures and TA were recorded in the *O. unisulcatus* nest: in summer (mean temperature difference at 14:00 = 11°C cooler in nest, $n = 5$) and in winter (mean at 14:00 = 9.9°C warmer in nest, $n = 5$). By comparison, the *P. brantsii* warren was 9.2°C cooler in summer (at 15:00, $n = 5$) and 8.4°C warmer in winter (at 12:00, $n = 5$).

The highest hourly maximum TA was recorded during summer at the *O. unisulcatus* nest (mean = 35°C, $n = 10$ at 14:00) and it was significantly lower than the black bulb temperature measured at 14:00 (mean = 46.6°C, $n = 10$, $t = 9.20$, $p < 0.001$), at this time mean T_{N40} averaged 21.47°C ($n = 9$). In winter the lowest mean minimum TA was recorded at the *P. brantsii* warren, (mean = 3.3°C, $n = 10$ at 6:00) and did not differ from the black bulb temperature (2.8°C, $n = 10$, $t = -0.286$, $p > 0.05$), at this time T_{W15} averaged 9.0°C ($n = 10$).

Vapour pressure

Vapour pressure in the refuges was higher than ambient v.p. for both seasons ($p < 0.05$, Table 2). Refuge v.p. varied less than ambient v.p., except in the warren in summer (Table 2). This high variability may have been due to the shallowness of the burrow. Ambient and refuge v.p. were lower during winter than summer (Table 2). Within a season, ambient v.p. at the nest and warren differed ($p < 0.05$), limiting comparisons between refuges. Relative humidities inside the *O. unisulcatus* nest ranged between 64 – 74% in summer and 56 – 83% in winter. In the *P. brantsii* warren, RH ranged between 51 – 60% in summer and 56 – 98% in winter.

Table 2. Comparison between ambient vapour pressure (v.p.a, mm Hg) and vapour pressure in *O. unisulcatus*'s nest and *P. brantsii*'s warren. Coefficients of Variation (CV) indicate variation in vapour pressure using F ratio where Ho: CV refuge = CV v.p.a (Zar 1984). Student's *t*-test was used for differences between means (calculated over all days and all hours), where * indicates $p < 0.05$ and ** indicates $p < 0.001$.

	CV %				Mean			
	Refuge	v.p.a.	F	<i>p</i>	Refuge	v.p.a.	<i>t</i>	<i>p</i>
Winter								
Nest	14.3	19.7	2.13	**	7.4	5.8	10.5	*
Warren	13.7	35.5	3.14	**	8.8	4.8	30.7	*
Summer								
Nest	15.8	19.2	1.75	*	14.1	10.9	7.7	*
Warren	49.4	8.7	23.4	**	15.0	11.4	3.1	*

Discussion

Refuge microclimate and rodent physiology

Du Plessis *et al.* (1989) showed that these rodents' physiology was not characteristic of desert rodents. Thus lower critical temperatures of 22.5°C and 25°C were recorded for winter acclimated *O. unisulcatus* and *P. brantsii*, respectively. Similarly, they exhibited symptoms of heat stress at 31°C. Du Plessis *et al.* (1989) concluded that behaviour must play an important role in these species survival in the semi-arid Karoo, where ambient temperatures would frequently be beyond their thermoneutral zone. It was hypothesized that the use of the refuge was the most important behavioural adaptation.

Results presented here supported this hypothesis with temperatures in the refuges being significantly dampened from the extremes of ambient heat or cold. Conditions within the refuges were, however not always within the thermoneutral zone for these species, particularly during cold periods. It is unfortunate that conditions could not be recorded in the actual nesting chambers during the present study. We hypothesize that the use of nest material to reduce heat loss (e.g. Hart 1971, Gettinger 1975) may be important. Furthermore, both these species are relatively social and may be able to reduce heat loss through huddling. In winter the use of shallower (warmer) burrows or tunnels during the day would enhance exposure to higher temperatures.

Refuge v.p. in this study was high compared to ambient v.p. (Table 2) and is the result of reduced ventilation in the refuges (Kennerly 1964, Lee 1964). Respiratory evaporation may also contribute to the vapour pressure in the refuges. In winter the refuge v.p. is low compared to summer, possibly the result of lower ambient v.p.

The high summer refuge v.p. decreases the effectiveness of evaporation for heat loss and water is thereby conserved (Schmidt-Nielsen and Schmidt-Nielsen 1950, Baudinette 1972, Gettinger 1975). Other avenues for heat loss, e.g. conduction, are therefore more effective. High conduction, as observed for *O. unisulcatus* and *P. brantsii* (Du Plessis *et al.* 1989), would then be advantageous. Furthermore, the low evaporative water loss, demonstrated for *O. unisulcatus* and *P. brantsii*, is comparable with that of rodents inhabiting relatively humid environments (Du Plessis *et al.* 1989).

Comparison of refuge microclimates

Temperatures in the *O. unisulcatus* nest are more independent of TA than warren temperatures, with winter nest temperatures varying less and summer nest temperatures being cooler than those of the warren. This is possibly the result of the structure. Nest building is dependent on the availability of plant cover and dense foliage for material, which is characteristic of *O. unisulcatus*'s habitat compared to *P. brantsii*'s habitat (Du Plessis and Kerley 1991). Shading by tall dense foliage, as in *O. unisulcatus*'s habitat, reduces radiation to and from the

sky, providing higher insulation, thereby creating a more stable environment than areas with lower plant cover (Kohnke 1968, Dawson and Denny 1969).

The temperature and relative humidity values in refuges of *O. unisulcatus* and *P. brantsii* were comparable with microclimates in burrows of other rodents under similar ambient extremes for summer (Cotton and Griffiths 1967) and winter (Carpenter 1966). Vapour pressure in both refuges investigated here were lower than reported in burrows of other rodents (Kennerly 1964, McNab 1966).

The *O. unisulcatus* refuge varied less in temperature and humidity than the less structured (G. I. H. Kerley, pers. obs.) stick nest of the North American wood rat, *Neotoma* sp. (Lee 1964). Higher ventilation in the nest of *Neotoma* sp. probably results in the low v.p. compared to *O. unisulcatus*'s nest.

In conclusion, the refuges of *O. unisulcatus* and *P. brantsii* create a favourable microclimate compared to their semi-arid environment and contribute to the survival of these two physiologically mesic rodents (Du Plessis *et al.* 1989). In summer the nest was cooler and in winter less variable than the warren and it is suggested that energy expenditure for thermoregulation may be lower in the nest than in the warren.

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