Physiological significance of the microclimate in night refuges of the numbat (*Myrmecobius fasciatus*)

C.E. Cooper^{1,2} and P.C. Withers¹

¹ Zoology, School of Animal Biology M092, University of Western Australia, Crawley, Western Australia 6009.

² Present address: Department of Environmental Biology, Curtin University of Technology, PO Box U1987 Perth Western Australia 6845

e-mail: C.Cooper@curtin.edu.au

Address for correspondence:

Dr P. Withers

Zoology, School of Animal Biology M092

University of Western Australia

Crawley WA 6009

Ph 08 6488 2235

e-mail pwithers@cyllene.uwa.edu.au

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ABSTRACT

Numbats (*Myrmecobius fasciatus*) seek overnight refuge in hollow logs, tree hollows and burrows, which provide protection from predators. Occupied night refuges were on average 5°C warmer than ambient temperature, which would result in considerable energy savings (35 kJ over 12 h). Use of a nest within the refuge reduced calculated energy expenditure by a further 55 kJ over 12 h. Mean nightly temperature didn't differ with refuge type, but the nightly pattern of refuge temperature did. Burrows had higher insulation than logs or tree hollows, and had more constant night temperatures and higher minimum temperatures. Season had a significant influence on refuge temperature, with lower temperatures in winter than in other seasons for all refuge types. The gas composition of occupied night refuges was different to ambient, with refuge air differing in O₂ content by a maximum of 2.3%, and CO₂ by no more than 3.0% of ambient levels. The relative humidity in *M. fasciatus* refuges was extremely variable (23-100%), but was generally lower than ambient relative humidity. The overnight refuges of *M. fasciatus* (hollow logs, tree hollows and burrows) significantly buffer thermal conditions without major effects on the gaseous or hygric environment.

INTRODUCTION

The numbat (*Myrmecobius fasciatus*) is a small to medium-sized marsupial that inhabits areas of open woodland in the south-west of Western Australia. *Myrmecobius fasciatus* is exclusively diurnal and shelters at night in burrows, hollow logs, and tree hollows. Hollow logs are also used to escape from predators during the day. Single entrance hollows of approximately 7 cm diameter are preferred (Maisey and Bradbury 1983). *Myrmecobius fasciatus* also digs its own burrows, although it tends to use these less frequently than logs (Calaby 1960; Maisy and Bradbury 1983). Burrows generally consist of a straight, shallow shaft approximately 1 m long, with a terminal chamber 15 to 23 cm in diameter and 10 and 60 cm below ground level, in which a nest is constructed (Christensen *et al.* 1984; Friend 1993). *Myrmecobius fasciatus* uses a large number of hollows and burrows within its home range, some as refuges from predators and others as hollows or burrows with nests that are used overnight. Usually one or two night nests are frequented most (Friend 1993).

Refuges with favourable microclimates play a vital role in the survival of many mammals (Jackson *et al.* 2002). By behaviourally avoiding unfavourable climatic conditions, mammals may overcome physiological limitations and survive in habitats that otherwise have adverse climates (Hayward 1965). Burrows are of particular importance as they tend to buffer external environmental extremes and usually have relatively constant conditions of temperature and humidity (Baudinette 1974; Hayward 1965; Roper *et al.* 2001). However, air in mammalian refuges, particularly burrows, is often hypoxic and hypercapnic (Roper *et al.* 2001). The gaseous composition is determined by a range of factors including soil porosity, soil moisture content and the metabolic rate of the burrow occupant (Wilson and Kilgore 1978; Withers 1978) and there may be much variability both between and within species (Roper *et al.* 2001).

A lack of suitable hollow logs for shelter, due to land clearing and altered fire regimes, which in turn exacerbates predation by introduced predators, is one factor contributing to the drastic contraction in the distribution of *M. fasciatus* that has occurred since European settlement (Friend 1990). Clearly the availability of suitable refuges is an essential habitat component for *M. fasciatus*, and therefore influences the distribution and abundance of the species, despite their apparent lack of physiological specialisation for fossoriality (Cooper and Withers 2002). Here we investigate the temperature and gaseous composition of wild *M. fasciatus* hollows and burrows, and relate this to the physiology of the species.

METHODS

This study was conducted at Dryandra Woodland (31° 46' S, 117° 1' E), 170 km southeast of Perth, Western Australia. Five male and six female *M. fasciatus* that had previously been fitted with radio-telemetry collars (Biotrack TWS, 7g) were studied. Each held a territory within the main block (13000 ha) of Dryandra. Refuge conditions were examined for between one and five individuals for three nights in each of the four seasons (12 nights in total). The conditions in unoccupied burrows and hollows that had previously been used as night refuges were also examined. Temperature and gas composition were measured for five occupied burrows, 10 occupied logs (hollows in tree branches or trunks that were not free standing) and six occupied trees (hollows in the trunks or branches of trees that were free standing), as well as 10 unoccupied burrows, eight unoccupied logs and one unoccupied tree. Relative humidity was measured for five occupied burrows, seven occupied logs and five occupied trees, in addition to three unoccupied burrows, five unoccupied logs and one unoccupied tree.

The night refuge (burrow, log or tree) was located by radio-tracking after dark, once it was certain that the individual had ceased activity for the day. Air samples were extracted from the nest chamber by passing a length (2 m) of plastic tubing (attached to a piece of fencing wire for rigidity) through the burrow/hollow entrance. Air samples were extracted using a 50 ml syringe attached to the end of the tubing with a three way tap. Once sufficient syringes of extracted air had been discarded to eliminate the dead space in the tubing, 40 ml of refuge air was passed through a column of drierite to remove water vapour, then through a David Bishop 280 Combo O₂ and CO₂ gas analyser. The gas analyser was single-point calibrated immediately prior to sampling of burrow air using ambient air, which was assumed to be 20.95% O₂ and 0.03% CO₂ (Withers 1992).

A temperature and humidity logger (either Hobo-temp or Hobo-hum 18363, or Hobo R8 Temp/Hum logger) was taped to a 2 m long piece of fencing wire, and passed through the burrow/hollow entrance into the nest chamber. This was then left in place until 0930 h the following morning, to monitor refuge temperature (T_r) and relative humidity (RH_r) at 30 sec intervals. Ambient air temperature (T_a) and relative humidity (RH_a) were recorded by a separate set of data loggers placed in a permanently shaded position approximately 1 m above the ground. Data were downloaded to a PC daily, and analysed using Microsoft Excel. All temperature and humidity data were analysed for the same period each day (0100 - 0600 h). Loggers were placed into refuges at different times, as only one individual could be tracked at a time, so only data after the time of the last placement of a logger were used.

Five *M. fasciatus* nests, which had been removed intact from burrows, were obtained from the Department of Conservation and Land Management. The nests were placed

inside a wide-mesh plastic string bag (fruit bag) for mechanical rigidity, and placed inside a temperature-controlled cabinet at 10° C. A 500 ml plastic container of warm (40°C) water, containing a Hobo Hastings HTI data logger, was placed in the centre of the nest, and another identical water-filled container, also with a data logger, was placed in the cabinet. After 7.5 h, the dataloggers were removed from the water and cooling curves plotted from the resulting data. Cooling constants were calculated as the slope of the regression of $\ln(T_{water}-T_a)$ over time. These cooling constants were then converted to thermal conductance (assuming a specific heat for water of 4.18 J g⁻¹; Withers 1992).

Data are presented as mean \pm S.E. unless otherwise stated. One- and two-tailed t-tests (with a test and, if necessary, correction for equality of variances) were used to compare ambient conditions with the gas, temperature and humidity characteristics of M. fasciatus refuges. Seasonal differences were determined by ANOVA. Differences between refuge type and occupancy were determined by 2-way ANCOVA, with T_a as a covariate for T_r and RH, and one- and two-tailed t-tests for gas data. Statistical analyses were done using statistiXL v 1.1 (www.statistixl.com).

RESULTS

Refuge Temperature

Minimum T_a ranged from 1.7 (winter) to 13.2°C (summer) during the study, while average nightly T_a ranged from 3.7 (winter) to 15.5°C (summer). The lowest minimum temperature recorded for an occupied refuge (T_r) was 9.7°C for a hollow log during summer (minimum $T_a = 7.7$ °C), while the highest minimum T_r was 23.2°C for a tree hollow on the same night. The lowest average refuge night time temperature experienced by *M. fasciatus* (11.7°C) was for a log during winter (average $T_a = 3.4$ °C), while the highest was 25.7°C for a tree hollow in summer (average $T_a = 10.3$ °C).

Season had a highly significant effect on both minimum and average nightly T_r , $(F_{3,32}=10.6,\ p<0.001;\ F_{3,32}=14.13,\ p<0.001;\ Fig.\ 1)$, with T_r lower in winter than other seasons (Table 1). Refuges had significantly higher minimum and mean nightly temperatures than ambient $(t_{39}=12.9,\ p<0.001;\ t_{39}=14.9,\ p<0.001)$. There was no significant difference in T_r of occupied and unoccupied refuges $(F_{1,33}=0.096,\ p=0.758;\ F_{1,33}=0.06,\ p=0.808$ for minimum and average nightly T_r respectively; T_a as a covariate). The minimum night time T_r varied between logs, burrows and trees, but the average night T_r did not vary with refuge type $(F_{2,33}=4.6,\ p=0.018;\ F_{2,33}=0.442,\ p=0.647$ for minimum and average T_r respectively; T_a as a covariate; see Fig. 1 and Table 1). The difference between minimum and mean nightly T_r differed with the type of refuge $(F_{2,33}=15.31,\ p<0.001;\ T_a$ as a covariate), with burrows having a much more constant T_r (e.g. Fig 1, Table 1). The slope of the regression line relating T_r and T_a varied significantly between refuge type $(F_{2,37}=18.30,\ p<0.001)$, with the slope for burrows (0.061) being lower than that for either logs $(0.828;\ p=0.003)$ or trees $(0.641;\ p<0.001)$.

Fig. 1 and Table 1 hereabouts

Nest Conductance

The five *M. fasciatus* nests consisted of interwoven bark, dried grass and dried leaves. The cooling constant for the nests ranged from 0.20 to 0.37° C min⁻¹ (mean 0.30 ± 0.090 °C min⁻¹). This was equivalent to a mean thermal conductance of 1.2 ± 0.08 J g⁻¹ h⁻¹ °C⁻¹.

Refuge Gas Composition

Refuge gas composition was extremely variable (Table 2). Oxygen concentrations ranged from ambient (20.95%) to 18.39%, and CO_2 ranged from ambient (0.03%) to 3.06% for occupied and unoccupied refuges. The O_2 concentration was significantly lower than ambient air for both occupied and unoccupied burrows ($t_6 = 3.01$, p = 0.012; $t_7 = 2.42$, p = 0.023) and occupied logs ($t_9 = 2.03$, p = 0.037), but not unoccupied logs ($t_8 = 1.00$, p = 0.173) or occupied tree hollows ($t_4 = 1.63$, p = 0.089). Occupied burrows were more hypoxic than unoccupied burrows ($t_6 = 2.86$, p = 0.029) but this was not significant for logs ($t_9 = 2.02$, p = 0.056). There was a significant difference in O_2 concentration between occupied refuge type ($F_{2,19} = 3.53$, p = 0.050), with burrows having a significantly lower O_2 than tree hollows (and logs were intermediate, but not significantly different from either). There was a significant negative correlation between % O_2 and % CO_2 in refuges (r = -0.5, p = 0.001).

Table 2 hereabouts.

Refuge Humidity

Ambient RH (RH_a) varied significantly with season ($F_{3,13} = 4.5$, p = 0.022), being higher in autumn and winter than in spring and summer, but there was no significant seasonal effect for maximum RH_a. Average and minimum RH_r were significantly lower than ambient RH ($t_{25} = 3.3$, p = 0.002; $t_{25} = 2.4$, p = 0.026; $t_{25} = 3.4$, p = 0.003 respectively). Maximum RH_r ranged from 24.1% (unoccupied log in spring) to 100% (occupied and unoccupied burrows in autumn and winter; occupied and unoccupied logs in spring and winter; Table 3). Mean RH_r ranged from 23.3% (for an occupied tree in summer) to 100% (for an unoccupied burrow in winter; Table 3). The lowest RH experienced by *M. fasciatus* in a refuge during the measurement period was 21% (a log in spring), the highest 100% (a log in spring and a burrow in autumn). RH_r was

extremely variable, and there were no significant effects of season, refuge occupancy or refuge type.

Table 3 hereabouts.

DISCUSSION

Hollow logs, burrows and tree hollows not only provide diurnally active *M. fasciatus* with a refuge that offers protection from nocturnal predators, but also buffer the climatic conditions to which they are exposed at night, as the microclimate of *M. fasciatus* night refuges differs from that of the external environment.

Refuge Temperature

 T_r differed with refuge type. The more stable T_r of burrows than of logs or trees (Fig. 1) is typical of animal burrows (Hayward 1965; Roper *et al.* 2001; Brice *et al.* 2002; Jackson *et al.* 2002). Burrows also had a higher minimum temperature than logs and trees, although the average nightly T_r of burrows did not differ from tree hollows. The slope of the regression line relating T_a and T_r is an index of refuge insulation. It indicates that burrows are better insulated (lower slope) than either logs or trees, with the T_r of burrows being almost independent of T_a . The less insulated logs and trees were warmer than burrows early in the night, but colder than burrow temperatures later (Fig. 1). There was a lag in the temperature change of logs compared to T_a , with the minimum T_r for logs often reached after T_a had begun to rise in the morning (Fig. 1). Although the minimum T_a of burrows was higher than that of logs, the similar mean T_r suggests that logs and trees provide an equivalent overall thermal benefit to burrows. However, retreating to burrows rather than logs or trees would be particularly advantageous in avoiding very low minimal T_a s.

As expected, night refuges were considerably warmer than ambient conditions due to the insulating properties of wooden logs and the soil in which the burrows were dug. By using these warmer refuges, M. fasciatus would reduce resting metabolic requirements. The mean night time T_r is on average 5°C warmer than T_a . For a normothermic individual with a thermal conductance below thermoneutrality of 1.6 J g⁻¹ h⁻¹ °C⁻¹ (at T_a = 10°C; Cooper and Withers 2002) this reduces resting metabolic rate by 0.3 ml O_2 g⁻¹ h⁻¹. For a 550g numbat that spends 12 h in its night refuge (Friend and Burrows 1983), the nightly energy saving is 35 kJ (assuming a respiratory exchange ratio of 0.75; Cooper and Withers 2002).

Despite being warmer than T_a , the mean nightly temperatures within refuges during all seasons were well below 30°C, which is the lower limit of thermoneutrality for M. fasciatus (Cooper and Withers 2002). Therefore refuges reduce but don't eliminate the energetic cost of thermoregulation. For example, the mean average T_r for numbat logs (over all seasons between 0100 and 0600 h) was 16.5 ± 0.83 °C, at which the RMR of a numbat would be 1.12 ml O_2 g⁻¹ h⁻¹, or 61.1 kJ per night (calculated for a 550 g numbat over 5 h, with a respiratory exchange ratio of 0.76; Cooper and Withers 2002). This represents an energetic cost of thermoregulation of 40.3 kJ in 5 h (*i.e.* the increment above nightly basal energy requirements of 20.8 kJ if M. fasciatus is to maintain a normothermic T_b of 34.1°C).

Within the refuge, nests provide considerable further insulation. The thermal conductance of five nests $(1.2 \pm 0.08 \text{ J g}^{-1} \text{ h}^{-1} \text{ °C}^{-1})$ was similar to the whole-body thermal conductance $(1.6 \text{ J g}^{-1} \text{ h}^{-1} \text{ °C}^{-1})$; Cooper and Withers 2002), and so a nest effectively doubles the thermal resistance of M. fasciatus. The calculated energy

savings of a nest when in a burrow in winter (*i.e* $T_r = 11.7$ °C) is 0.4 ml O_2 g⁻¹ h⁻¹ (difference between VO_2 calculated for *M. fasciatus* with and without a nest; see Cooper and Withers 2002 for data). This is a saving of 55 kJ, compared with 35 kJ savings from use of a burrow with no nest.

Refuge Gas Composition

The gas composition of occupied M. fasciatus burrows was significantly different from ambient. However, as for many other mammal burrows (Roper et~al.~2001), these differences were generally small and (especially for CO_2) extremely variable. Burrows had a significantly lower O_2 concentration than tree hollows and ambient air, and logs were intermediate (Table 2). This presumably reflects the relative openness of these refuges. The variability of gas concentrations could also reflect how close the occupant was to the sampling tube, and its metabolic rate (e.g.) whether euthermic or torpid). Differences in burrow depth, the position of hollows in logs, and soil porosity and moisture content would also contribute to this variation (Withers 1978). CO_2 was too variable to detect any statistical differences between refuges, and may be more variable than O_2 due to its high solubility in soil water. Despite this, the correlation between % O_2 and % CO_2 , although weak ($R^2 = 0.5$), was highly significant (p = 0.001).

Unoccupied burrows had O_2 and CO_2 concentrations that were different from ambient, and this presumably reflects the metabolic activity of soil flora and fauna. Roper *et al.* (2001) also found that unoccupied mole-rat burrows had gas concentrations intermediate between occupied burrows and ambient conditions.

Mammal burrows may sometimes have extreme concentrations of O_2 and CO_2 , although often they are similar to ambient conditions. Most animal refuges (like M. fasciatus

burrows and logs) differ by only 1-2% from ambient conditions (Roper *et al.* 2001). O₂ was not sufficiently low in any refuge type to suggest that *M. fasciatus* required any particular tolerance to hypoxia. CO₂ within refuges was generally also insufficient to have any physiological effects (*i.e.*< 1%). However, the two highest levels measured (1.26 and 3.06%), although not extreme by comparison with some other burrowing mammals (up to 10-15% CO₂; Hayward 1965), suggest that *M. fasciatus* may need to tolerate at least occasional mild hypercapnia.

Refuge Relative Humidity

Generally, animal burrows have a high RH, often approaching 100% (Baudinette 1974; McNab 1966). However *M. fasciatus* refuges, including burrows, had an extremely variable RH, with mean nightly RH_r ranging from 23.3 to 100%. This variability presumably results from varying T_r, and differences in the openness of the various refuges. There were no differences in RH_r due to season, refuge occupancy or refuge type.

The evaporative water loss (EWL) of M. fasciatus at a T_a of 17.4°C (average for occupied refuges across all types and all seasons) is approximately 0.6 mg H_2O g⁻¹ h⁻¹ at a RH of \leq 16% (chamber RH for EWL measurements; Cooper and Withers 2002). At a refuge RH of 23.3% (the lowest measured), EWL would be about 0.17 mg H_2O g⁻¹ h⁻¹ or, for a 550 g numbat over the 5 hour measurement period, 0.46 ml H_2O . This is only 0.5% of the total daily field water turnover of M. fasciatus (84.1 ml H_2O day⁻¹; Cooper et al. 2003). Therefore EWL in these refuges (over the range of 23.3 to 100% RH) comprises such a small portion of their daily water turnover that variation in RH_r probably has little impact on the water budget of M. fasciatus.

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Fig. 1: Examples of temperature ($^{\circ}$ C) in numbat night refuges and ambient air (T_a) on a summer and winter night.

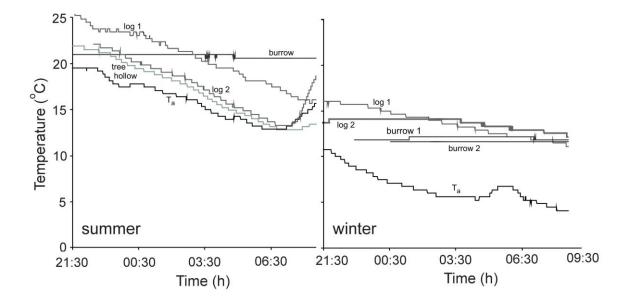


Table 1: Minimum and average ambient temperatures (°C) and night refuge temperatures (burrows, hollow logs, tree hollows) for *Myrmecobius fasciatus*; values are mean \pm S.E. (n).

Refuge		Summer	Autumn	Winter	Spring
Ta	Minimum	8.0 ± 1.26 (3)	8.6 ± 0.6 (3)	2.8 ± 0.69 (3)	11.4 ± 1.81 (3)
	Average	10.2 ± 0.50 (3)	12.0 ± 0.79 (3)	4.6 ± 1.01 (3)	14.0 ± 1.77 (3)
Burrow	Minimum	21.1 ± 0.87 (2)	18.9 ± 0.32 (5)	10.9 ± 0.27 (4)	16.8 ± 0.22 (4)
	Average	21.1 ± 0.87 (2)	19.0 ± 0.31 (5)	11.7 ± 0.41 (4)	17.0 ± 0.20 (4)
Log	Minimum	$14.7 \pm 1.60 (7)$	13.7 ± 1.57 (3)	10.5 ± 0.76 (4)	16.0 ± 1.05 (4)
	Average	17.6 ± 1.67 (7)	16.5 ± 0.94 (3)	11.8 ± 0.60 (4)	18.0 ± 0.68 (4)
Tree	Minimum	17.1 ± 3.15 (3)	-	-	14.3 ± 1.16 (4)
	Average	21.3 ± 2.01 (3)	-	-	16.4 ± 0.99 (4)

 $\textbf{Table 2:} \ Concentrations \ of \ O_2 \ and \ CO_2 \ in \ \textit{Myrmecobius fasciatus} \ night \ refuges; \ values \ are \ mean \pm S.E.$

(n).

Refuge		% O ₂	% CO ₂
Ambient		20.95	0.03
Burrow	Occupied	19.69 ± 0.429 (7)	0.88 ± 0.418 (7)
	Unoccupied	20.89 ± 0.024 (8)	0.16 ± 0.049 (8)
Log	Occupied	$20.43 \pm 0.271 \ (10)$	0.86 ± 0.412 (10)
	Unoccupied	20.95 ± 0.002 (8)	0.04 ± 0.009 (8)
Tree	Occupied	20.91 ± 0.022 (6)	0.09 ± 0.045 (6)
	Unoccupied	20.95 (1)	0.08 (1)

Table 3: Average and maximum relative humidities (%) for *M. fasciatus* night refuges (burrows, hollow logs and tree hollows); values are mean \pm S.E.

Refuge		Summer	Autumn	Winter	Spring
RHa	Maximum	50.3 ± 15.27 (3)	96.4 ± 2.02 (3)	100 ± 0 (3)	83.6 ± 16.43 (3)
	Average	48.1 ± 10.41 (3)	8.8 ± 1.54 (3)	90.9 ± 2.36 (3)	65.7 ± 8.46 (3)
Burrow	Maximum	-	96.7± 1.85 (4)	75.1 ± 16.43 (3)	80.6 (1)
	Average	-	89.6 ± 4.75 (4)	63.3 ± 19.84 (3)	59.8 (1)
Log	Maximum	32.3 ± 5.64 (3)	61.8 (1)	97.8 ± 1.47 (4)	43.1 ± 18.96 (4)
	Average	30.3 ± 4.17 (3)	48.4 (1)	71.7 ± 16.73 (4)	37.8 ± 13.88 (4)
Tree	Maximum	45.8 ± 21.55 (3)	-	-	58.4 ± 9.02 (3)
	Average	34.7 ± 11.09 (3)	-	-	51.9 ± 5.5 (3)