

Influence of season and weather on activity patterns of the numbat
(*Myrmecobius fasciatus*) in captivity

C.E. Cooper^{1,2} and P.C. Withers¹

¹ Zoology, School of Animal Biology M092, University of Western
Australia, Stirling Highway, Crawley W.A. 6009

²Present address: Centre for Behavioural and Physiological Ecology,
Zoology, University of New England, Armidale N.S.W. 2351.

Address for correspondence:

Dr Christine Cooper

Centre for Behavioural and Physiological Ecology

Zoology

University of New England

Armidale N.S.W. 2351

Ph (02) 6773 2262

Fax (02) 6773 3814

e-mail ccooper9@pobox.une.edu.au

Abstract

The influence of season and weather on activity was examined for captive numbats, to separate the influence of weather from predation pressure and food availability, since these confound the interpretation of activity data for wild numbats. Unlike other Australian marsupials, numbats are exclusively diurnal, being active for an average of 21.2 % of the 24 h day. However, activity duration varied seasonally, with numbats being active for longer periods in summer (39-65 % of the available daylight) than winter (17-59 %). Captive numbats were active for shorter periods than wild numbats in winter (presumably as captive numbats don't have to forage for food) but did not cease activity in the middle of the day in summer (suggesting that summer midday inactivity of wild numbats is a response to food availability rather than a thermoregulatory response). Captive numbats were more active in summer than in winter, which may reflect their summer breeding season. Environmental conditions significantly affected daily activity, with low levels on days of low light intensity and high relative humidity. The majority of numbat activity occurred at ambient temperatures below thermoneutrality (< 30 °C). The associated costs of thermoregulation for active numbats were calculated, from activity time, to be higher in winter (0.586 ml O₂ g⁻¹ h⁻¹) than in summer (0.274 ml O₂ g⁻¹ h⁻¹).

Introduction

Numbats are small to medium sized (550 g) marsupials that belong to the monospecific family Myrmecobiidae. Morphological features and serological and albumin systematics indicate that the numbat is most closely related to the family Dasyuridae within the marsupial order Dasyuromorphia (Kirsch 1968; Archer and Kirsch 1977; Archer 1984; Baverstock *et al.* 1990; Wroe *et al.* 2000). Numbats are unique amongst Australian marsupials with respect to their diet, being exclusively termitivorous, and their diurnal activity pattern. Marsupials show a variety of activity patterns, which are related to factors including body size, diet, habitat and season, although the vast majority are nocturnal, *i.e.* predominantly active during the dark phase of the photoperiod (Russell *et al.* 1993). Dasyurid marsupials are generally nocturnal, although some have crepuscular or arrhythmic activity patterns (Fleay 1949; Hall 1980; Woolley *et al.* 1991). The strictly diurnal activity rhythm of the numbat (Calaby 1960a,b; Maisey and Bradbury 1983; Christensen *et al.* 1984; Friend 1986) is therefore unusual amongst marsupials in general, and the closely-related dasyurids in particular.

The endogenous circadian rhythmicity of an animal's activity may be further influenced on a day-to-day basis by an array of factors including predation, food availability and weather (Russell *et al.* 1993). Numbats feed on termites by exposing sub-surface soil galleries or by turning over small pieces of wood on the soil surface, and their diurnal activity pattern has been correlated with increased activity of termites close to the soil surface during the day (Maisey and Bradbury 1983; Christensen *et al.* 1984; Friend 1986). Seasonal variation in numbat foraging timing, duration and methods has also been attributed to seasonal changes in termite abundance close to the soil surface (Christensen *et al.* 1984), which in turn are influenced by ambient temperature (T_a) and soil moisture (Evans and Gleeson 2001).

Weather conditions such as T_a , rainfall, relative humidity, wind speed, cloud cover and light intensity may have a strong effect on animal activity (Martin 1973; Vickery and Bider 1978, 1981; Wells 1978; Roxburgh and Perrin 1994; McDonough and Loughry 1997). By avoiding inclement and utilising favourable weather conditions, animals may reduce predation pressure, increase foraging success, and reduce the energetic costs of thermoregulation (Vickery and Bider 1981). Radiotracking of wild numbats suggests that they avoid rain (Maisey and Bradbury 1983), but their response to other weather conditions is unknown. This study investigates the influence of season and weather on daily activity for captive male numbats. The activity pattern of numbats in captivity excludes possible effects of predation pressure and food availability (that would presumably influence wild numbat activity) and allows us to focus on seasonal effects of weather on activity patterns.

Methods

The numbats used for this study were part of a captive breeding program at Perth Zoo, Western Australia (South Perth 31° 58' S 115° 51' E). They were housed individually in outdoor wire cages measuring 10 x 2.5 x 2.5 m, and experienced natural conditions of weather and photoperiod. Two nest boxes were provided for each numbat, with one at either end of each cage. Cages had a natural substrate and contained logs and vegetation for environmental enrichment and shelter. During daylight hours, each cage had areas of both full sunlight and shade. The numbats were fed by staff at 0900 and 1300 h daily, and fresh water was available at all times.

Nine passive infrared detectors (PID) were positioned at 1 m intervals along a metal beam that ran the length of the roof of a numbat cage. Each PID covered an area of the

ground surface of the cage 2.5 m (*i.e.* the entire width of the cage) by approximately 0.5 m, providing a series of ten bands of detectable area along the length of the cage. The detectors were individually wired to a PC, which provided the power source to operate the detectors (12 V) and received the signal from each detector via the printer and soundcard-joystick ports. A signal was produced whenever a numbat made some movement within the range of the detectors. Signals were recorded and saved with a custom QBasic program. Light intensity (LI; relative units; Pasco CI-6504A light sensor), ambient air temperature (T_a ; °C; Wescor TH-65 digital TC thermometer) and relative humidity (RH; %; Vaisala HMP 31 UT humidity probe) were monitored within 50 m of the numbat cage, simultaneously with numbat activity, and recorded (via a Pasco ScienceWorkshop 300 interface) by the same PC, using ScienceWorkshop.

The detection of numbat movement by the PIDs was tested by directly observing numbat activity for several days, and comparing the actual activity and positions of the numbats with the activity patterns recorded by the detection system. Zoo staff maintained a log of entry and exit from the numbat cages, and movements attributed to staff were excluded from the data. The detection system was positioned above an empty numbat cage for several weeks at the conclusion of the study to confirm that no movements were recorded in empty cages.

Numbats remained in their own cages, and the detectors were moved above a different cage weekly over the period from August 2000 to December 2001. Five adult male numbats were available for the study. No female numbats were available due to the zoo's husbandry procedures (females were moved indoors during winter to maximise their reproductive success). Each numbat's activity (and ambient LI, T_a and RH) was monitored for at least five (usually seven) consecutive days in summer, autumn, winter

and spring. The effects of season and weather on numbat activity were examined by repeated measures ANOVA, where numbat and season were considered as factors, and LI, T_a and RH as covariates. A priori contrasts were used to examine seasonal patterns. Seasonal variation in weather was examined using ANOVA with post hoc Student-Newman-Keuls tests. SPSS version 10 and *statistiXL* version 1.1 were used for all statistical tests. Values are presented as mean \pm standard error. Times for sunrise and sunset were obtained from the Australian Bureau of Meteorology. All times of day refer to Australian Western Standard Time, which is Coordinated Universal Time + 8 h.

Results

The PIDs accurately detected numbat movements, within the general limitation of the detector circuitry that introduced a few second time delay to detection, and about a 20 second “on” period during which further movements were not detected. No movements that could be confused with numbat activity were detected in the empty “control” numbat cage. The log of entry and exit from the cage maintained by zoo staff accounted for any movements recorded in this cage.

Mean daytime (sunrise to sunset) LI, T_a and RH differed significantly between season ($F_{3,140} = 16.3$, $p < 0.001$; $F_{3, 140} = 4.7$, $p = 0.003$; $F_{3, 140} = 12.3$, $p < 0.001$ respectively). LI was higher in summer and spring than in autumn and winter (Table 1). Daytime T_a was higher in summer and autumn than in winter and spring. In summer, RH was lower than in all other seasons ($p < 0.05$). Daytime LI and RH, and T_a and RH, were significantly negatively correlated ($r = 0.65$, $p < 0.001$; $R = 0.49$, $p = 0.003$ respectively). Summer was characterised by higher T_a and LI, and lower RH than other seasons, while winter had lower T_a and LI, and higher RH. Autumn and spring were

intermediate between summer and winter, with weather in spring more similar to summer conditions, and autumn more similar to winter.

All numbat activity occurred between sunrise and sunset (e.g. Figure 1). The time of initial numbat activity differed significantly between season ($F_{2,55} = 57.0$, $p < 0.001$), with activity beginning later in autumn and winter months than in summer and spring (Figure 2; quadratic contrast, $F_{1,28} = 135.2$, $p < 0.001$). In summer, the time of the first daily activity for individual numbats ranged from 0754 h \pm 6 min to 1013 h \pm 4 min, while in winter initial activity ranged from 0834 h \pm 6 min to 1216 h \pm 17 min; there was a significant difference between individual numbats ($F_{4,28} = 61.7$, $p < 0.01$), and a significant interaction between season and numbat ($F_{7,8,55} = 15.1$, $p < 0.001$).

Once they had emerged from their nest boxes, numbats generally remained active throughout the day in all seasons (e.g. Figure 1). The time of final daily activity also differed between season (Figure 2; $F_{2,1, 59.5} = 5.8$, $p = 0.004$), with the numbats' last recorded daily activity occurring earlier in autumn and winter than in summer or spring (Figure 2; quadratic contrast, $F_{1,28} = 7.47$, $p < 0.011$). Final daily activity for individual numbats ranged from 1542 h \pm 36 min to 1731 h \pm 9 min during summer, and 1452 h \pm 14 min to 1622 h \pm 4 min in winter. Again, individual numbats differed significantly with respect to the time of their final activity ($F_{4,28} = 4.76$, $p = 0.005$), and there was a highly significant interaction between season and numbat ($F_{8,5,59.5} = 7.3$, $p < 0.001$).

The time difference between sunrise and initial activity, and final activity and sunset also showed highly significant seasonal variation ($F_{2,3,64.2} = 8.7$, $p < 0.001$; $F_{2,1, 59.5} = 5.0$, $p = 0.008$ respectively). Again there was a significant difference between individual numbats ($F_{4,28} = 56.9$, $p < 0.001$; $F_{4,28} = 8.3$, $p < 0.001$ respectively) and a significant

interaction between numbat and season ($F_{9,2,64.2} = 9.9$, $p < 0.001$; $F_{8,5,59.4} = 6$, $p < 0.001$ respectively). The shortest and longest times between initial activity and sunrise varied for different numbats, and ranged from 1.92 ± 0.117 h to 4.25 ± 0.067 h in summer and from 1.90 ± 0.083 h to 5.03 ± 0.283 h in winter. The difference between final activity and sunset ranged from 1.72 ± 0.150 h to 3.32 ± 0.617 h in summer, and from 1.42 ± 0.083 h to 2.78 ± 0.233 h in winter. Generally numbats became active sooner after sunrise in spring and summer than in autumn and winter. In summer and spring the numbats generally ceased activity earlier before sunset than they did in autumn and winter.

The number of five minute periods during which numbats were active per day varied greatly between individual numbats ($F_{4,28} = 38.1$, $p < 0.001$; Figure 3). Again there was a highly significant seasonal effect ($F_{2,3,63.9} = 77.3$, $p < 0.001$). During winter, the number of 5-min periods during which numbat activity was recorded ranged from 23 ± 5 to 71 ± 4 , and in summer from 55 ± 10 to 105 ± 6 . There was no significant effect of daily LI, T_a or RH on the frequency of numbat activity ($F_{1,121} = 1.51$, $p = 0.22$; $F_{1,121} = 1.15$, $p = 0.28$; $F_{1,121} = 0.61$, $p = 0.44$ respectively). The percentage of available daylight during which numbats were active (*i.e.* the proportion of 5-min periods between sunrise and sunset during which activity was recorded) was also significantly affected by season ($F_{3,70} = 32.8$, $p < 0.001$; Figure 3), and ranged from 17 ± 4 to 59 ± 3 % of potential available daylight (sunrise to sunset) in winter and 39 ± 3 % to 65 ± 4 % of the potential available daylight in summer. Neither mean daily LI, T_a or RH had a significant influence on the proportion of the day that the numbats were active ($F_{1,121} = 1.47$, $p = 0.23$; $F_{1,121} = 0.644$, $p = 0.42$; $F_{1,121} = 0.607$, $p = 0.44$ respectively).

The total number of PID “movements” per day recorded for the 5 numbats ranged from 854 ± 445 to 10284 ± 1958 in summer to 63 ± 6 to 534 ± 120 in winter. Once again the activity of individual numbats differed significantly ($F_{4,28} = 17.3$, $p < 0.001$). The influence of season on activity was highly significant ($F_{1,3,37.3} = 57.4$, $p < 0.001$; e.g. Figure 1), with total movements being highest in summer, decreasing through autumn to minimal movements in winter, then increasing again in spring (quadratic contrast, $F_{1,28} = 109.5$, $p < 0.001$). Again there was a highly significant interaction between individual numbats and season ($F_{5,3,37.3} = 16.5$, $p < 0.001$).

Daily LI and RH had a significant influence on total daily numbat activity ($F_{1,121} = 6.463$, $p = 0.012$ and $F_{1,121} = 5.152$, $p = 0.025$ respectively), but there was no significant effect of daily T_a ($F_1 = 0.370$, $p = 0.544$). This is illustrated by Figure 1, where winter and summer activity and weather data show the two extremes of weather and activity, although the patterns described below also occur during spring and autumn. In Figure 1, summer-day I, and in particular winter-day VI show the dramatic reduction in numbat activity associated with days of low LI and high RH during both winter and summer.

The minimum air temperature experienced by an active numbat was $3.7\text{ }^\circ\text{C}$, minimum LI was 0.0096 units, and minimum RH was 1.5 %, all of which occurred during winter. Both the minimum T_a and RH experienced by active numbats varied with season ($F_{3,144} = 14.40$, $p < 0.001$; $F_{3,144} = 6.83$, $p < 0.001$ respectively; Table 1). On average, the minimum T_a at which numbats were active was higher in summer than in the other seasons. The minimum RH that numbats experienced while active was lower in summer than in the other seasons. Minimum LI when numbats were active was not influenced by season. There was no difference between individual numbats with regard to the minimal conditions they experienced while active ($F_{3,141} = 1.86$, $p = 0.139$).

The maximum LI, T_a and RH at which numbats were active all differed significantly with season ($F_{9,343} = 22.86$, $p < 0.001$; Table 1), and between individual numbats ($F_{3,143} = 9.01$, $p < 0.001$). The maximum light levels at which numbats were active were higher in summer and spring than in autumn or winter. Maximum temperatures at which numbats were active were higher in summer than in other seasons. Summer maximum RH during numbat activity times was slightly lower than that in autumn, but other seasons were similar. The maximum temperature at which a numbat was active (across all seasons and all numbats) was 39.4 °C, the maximum LI > 47.8 units and maximum RH was 100 %.

Discussion

The majority of marsupials are predominantly nocturnal (bandicoots, gliders, possums, wombats and most dasyurids), but some are crepuscular or arrhythmic (*e.g.* brown and yellow-footed antechinuses, *Antechinus swainsonii* and *A. flavipes*; dibbler, *Parantechinus apicalis*; Russell *et al.* 1993). The numbat is the only Australian marsupial considered to be exclusively diurnal (despite being most closely related to the predominantly nocturnal dasyurids; Croft 2003), although some large macropods are active during daylight *e.g.* begin activity before sunset and cease after sunrise, and the musky rat-kangaroo *Hypsiprymnodon moschatus* is predominately diurnal (Clark *et al.* 1989; Russell *et al.* 1993; Denis and Johnson 1995). The continuous monitoring of captive numbats in this study found that they were exclusively diurnal (*e.g.* Figure 1), which confirms the results of field radio-tracking studies (Maisy and Bradbury 1983; Christensen *et al.* 1984). This is despite earlier reports that numbats were crepuscular or arrhythmic (Wood Jones 1923; Le Souef and Burrell 1926) and anecdotal reports of some Aboriginal people that numbats were nocturnal (Friend *et al.* 1982). The activity pattern of captive animals does not necessarily reflect that of free-living individuals. For

example, the regular provision of adequate food for captive numbats and absence of predation pressure may reduce some activity (although captive numbats remain wary of potential predators). However, activity patterns related to weather and season should still be evident in captivity, and perhaps be even more obvious because of the absence of predator avoidance and foraging activities.

The numbat's diurnal activity pattern in the wild is clearly related to its termitivorous diet. Activity coincides with the increased diurnal activity, close to the soil surface, of the subterranean termites on which it feeds (Friend 1986; Evans and Gleeson 2001). The exclusively termitivorous numbat lacks the powerful forelimbs and massive claws of most other specialist myrmecophagous mammals, and so it can not break into termite mounds to expose its prey. It must therefore feed when termites are most abundant and active in their subterranean soil galleries. Most other myrmecophagous mammals are nocturnal (Walker 1975). They attack ant and/or termite mounds, and so their activity is not closely linked to their prey's activity. They are presumably nocturnal to avoid predation and extreme environmental conditions. The nocturnal activity pattern of the aardwolf (*Proteles cristatus*) is determined by its prey availability; aardwolves feed mostly on *Trinervitermes* spp. that are active on the soil surface at night (Williams *et al.* 1997). Echidnas, which are sympatric over the numbat's distribution, are active by both day and night, presumably as they are not restricted to feeding while their prey is active (they have powerful digging forelimbs and claws, and break into ant and termite mounds) and they have protective spines that limit predation. Timing of activity in echidnas is primarily determined by ambient temperature rather than photoperiod (Abensperg-Traun and DeBoer 1992; Brice *et al.* 2002).

The diurnal activity of numbats reduces the thermoregulatory costs associated with activity. By being diurnally active, numbats experience relatively high ambient temperatures when active, and can also use solar radiation for thermoregulation (which is not possible for nocturnal marsupials). Related to this, the biophysical properties of the numbat's pelt are very different to those of nocturnal marsupials (Cooper *et al.* 2003). These mechanisms of energy conservation may be of particular importance in balancing the energy budget for a termitivore such as the numbat, which has a low energy density diet (Redford and Dorea 1984; McNab 1984, 2000).

On average, captive numbats were active for 21.2 % (approx 5 h) of the day, and inactive in their nest boxes for the remaining 78.8 % (19 h) of the day. This inactive period is similar to the time spent in the nest by both captive short-nosed bandicoots (*Isoodon obeselus*; 71 %; Larcombe 2003) and brush-tailed possums (*Trichosurus vulpecula*; 71 %; Herbert and Lewis 1999). However, there was consistent, significant individual variation in activity patterns between numbats. Post hoc tests consistently grouped numbat 104 alone, numbats 37, 62 and 171 together, and numbat 105 alone, with respect to their duration of activity and their times of initial and final activity. These patterns did not appear to be correlated with age or origin of the numbats in any way. Brush-tailed possums also show similar individual variation in activity patterns (Herbert and Lewis 1999).

Season has a highly significant effect on numbat activity. Like brush-tailed possums (Herbert and Lewis 1999), numbats were active for a longer period each day during spring and summer, and a shorter period during autumn and winter. This seasonal difference is not simply due to differences in the available daylight hours, as numbats become active closer to sunrise in summer than in winter, and were active for a greater

proportion of the time between sunrise and sunset in summer (39-65 %) than in winter (17-59 %; Figure 3).

Radio-tracking studies of wild numbats indicated that during winter they were more likely to be active in the middle of the day (Maisey and Bradbury 1983), generally becoming active between 0800 and 1000 h, and retiring at 1500 to 1700 h (Christensen *et al.* 1984). This was similar to the times of initial activity of captive numbats in the same season (0834–0950 h), although captive numbats tended to cease activity slightly earlier (1447–1608 h; Figure 2), presumably as captive numbats do not have to forage widely for food. Wild numbats radio-tracked in summer became active between 0700 and 0800 h. During the middle of the day (1100–1200 h) they would shelter in hollow logs or burrows, with activity recommencing at around 1400-1600 h and continuing till 1800-2000 h (Maisey and Bradbury 1983; Christensen *et al.* 1984). The captive numbats became active later in the day (0754–1013 h; Figure 2) and their final daily activity was earlier (1542–1731 h). Captive numbats did not have a period of inactivity during the middle of the day, unlike wild numbats (e.g. Figure 1). The differences in activity between captive and wild numbats, despite captive numbats also being exposed to similar natural weather conditions, suggests that seasonal changes in the timing of activity of wild numbats is a response to seasonal changes in patterns of food availability, rather than a thermoregulatory response to avoid higher T_a and extreme solar irradiation. Seasonal changes in the patterns of wild numbat activity correlate closely with the activity of termites in sub-surface soil galleries, with termites (that respond to soil temperature and humidity) being most abundant close to the soil surface in the mornings and evenings in summer, and in the middle of the day in winter (Evans and Gleeson 2001). Captive numbats, with a constant and regular food supply, gave no indication of reducing activity during the hottest part of the day in summer.

The significant influence of season on total numbat activity is dramatic (e.g. Figure 1), with numbats moving around much more while active in summer than in winter. Differing weather conditions in summer and winter do not entirely account for this pattern, as LI, RH and T_a were used as co-variates in the analysis. For wild numbats, increased foraging times during the summer when termites are least abundant and more dispersed (Abensperg-Traun and DeBoer 1990; Evans and Gleeson 2001) may account for this increased activity. However, in this study of captive numbats there was no seasonal variation in the availability of food, and so presumably this pattern of increased movement during the numbats' activity period is a response to the summer breeding season. As this study is restricted to male numbats, it is possible that this increase in activity during the breeding season is not as dramatic for females.

On a daily basis, there is a significant effect of both LI and RH on numbat activity (e.g. Figure 1). Reduced activity on days with a lower LI is presumably a thermoregulatory response, as the numbats' solar heat gain (SHG) would decrease with decreasing incident solar radiation, meaning that numbats would have a greater metabolic cost of thermoregulation. High RH is associated with rain in winter, that numbats avoid (Maisey and Bradbury 1983), and during summer may reduce the effectiveness of evaporative cooling. Weather also influences the activity of other marsupials, including brush-tailed possums (Herbert and Lewis 1999), southern hairy-nosed wombats (*Lasiorhinus latifrons*; Wells 1978) and sugar gliders (*Petaurus breviceps*; Kortner and Geiser 2000). As for wild numbats (Maisey and Bradbury 1983), rain was associated with a reduction in possum activity (although there was no correlation between T_a or wind and possum activity; Herbert and Lewis 1999), while sugar gliders were less active on cold and wet nights (Kortner and Geiser 2000). Unlike numbats (for which T_a

appears to have little influence on activity), T_a appeared to be an important factor influencing the activity of wombats, as they timed their activity to avoid extreme T_a , thus reducing the demand for physiological thermoregulation (Wells 1978).

There was an energetic cost of thermoregulation for active numbats, as almost all numbat activity occurred at T_{as} below thermoneutrality ($30\text{ }^\circ\text{C}$; Cooper and Withers 2002); minimum, mean and maximum T_{as} with activity were all $< 30^\circ\text{C}$, except summer maximum T_a with activity, which was within the thermoneutral zone. The increase in metabolic rate (MR) with decreasing T_a can be calculated from the equation $\text{MR} = -0.053 T_a + 1.991$, ($R^2 = 0.98$; data from Cooper and Withers 2002). Calculated mean energetic costs of thermoregulation during active periods (MR – BMR) ranged from $0.274\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ in summer to $0.586\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ in winter (this assumes no substitution of locomotor/digestive energy for thermoregulation). Energetic savings from SHG compound this seasonal difference in energy expenditure, as during summer mean LI during activity is higher than in winter. Therefore SHG, which can be a significant source of heat, (potentially providing between 50 and 220% of resting metabolic rate at T_{as} of $15\text{-}25\text{ }^\circ\text{C}$; Cooper *et al.* 2003) will be greater in summer than in winter (Walsberg *et al.* 1997). Environmental conditions under which numbats are active in winter result in greater physiological demands than in summer. However, for wild numbats, winter is associated with increased food availability (Abensperg-Traun and DeBoer 1990; Evans and Gleeson 2001) and reduced activity compared to summer, which may balance these increased thermoregulatory costs.

Acknowledgements

We thank the Perth Zoo for permission to work with the numbats and for providing laboratory space. Animal ethics committees of both the University of Western Australia

and Perth Zoo approved all experimental work. Financial support was provided by the Zoology Department at UWA, an APA Scholarship to C. Cooper, and by the Australian Government's Cooperative Research Centres program through funds from the CRC for conservation and management of marsupials.

References

- Abensperg-Traun, M. A. and DeBoer, E. S. (1990). Species abundance and habitat differences in biomass of subterranean termites (Isoptera) in the wheatbelt of Western Australia. *Australian Journal of Ecology* **15**, 219-226.
- Abensperg-Traun, M. A. and DeBoer, E. S. (1992). The foraging ecology of a termite- and ant-eating specialist, the echidna *Tachyglossus aculeatus* (Monotremata: Tachyglossidae). *Journal of Zoology, London* **226**, 243-257.
- Archer, M. (1984). The Australian marsupial radiation. In: Vertebrate Zoogeography and Evolution in Australasia (Animals in Space and Time). (Eds. M. Archer and G. Clayton) pp. 633-808. (Hesperian Press, Carlisle.)
- Archer, M. and Kirsch, J. A. W. (1977). The case for the Thylacomyidae and Myrmecobiidae, Gill, 1972, or why are marsupial families so extended? *Proceedings of the Linnean Society of New South Wales* **102**, 18-25.
- Baverstock, P. R., Krig, M. and Birrell, J. (1990). Evolutionary relationships of Australian marsupials as assessed by albumin immunology. *Australian Journal of Zoology* **37**, 273-288.
- Brice, P. H., Grigg, G. C., Beard, L. A. and Donovan, J. A. (2002). Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. *Australian Journal of Zoology* **50**, 461-476.

- Calaby, J. H. (1960a). Observations on the banded anteater *Myrmecobius f. fasciatus* Waterhouse (Marsupialia), with particular reference to its food habits. *Proceedings of the Zoological Society of London* **135**, 183-207.
- Calaby, J. H. (1960b). The numbat of south-western Australia. *Australian Museum Magazine* **13**, 143-146.
- Christensen, P., Maisey, K. and Perry, D. H. (1984). Radio-tracking the numbat, *Myrmecobius fasciatus*, in the Perup Forest of Western Australia. *Australian Wildlife Research* **11**, 275-288.
- Clark, J. L., Jones, M. E. and Jarman, P. J. (1989). A day in the life of a kangaroo: Activities and movements of Eastern Grey Kangaroos *Macropus giganteus* at Wallaby Creek. In "Kangaroos, Wallabies and Rat-Kangaroos". (Eds G. Grigg, P. Jarman and I. Hume) pp. 611-618. (Surrey Beatty and Sons: Chipping Norton NSW.)
- Cooper, C. E., Walsberg, G. E. and Withers P. C. (2003). Biophysical properties of the pelt of a diurnal marsupial, the numbat (*Myrmecobius fasciatus*), and its role in thermoregulation. *Journal of Experimental Biology* **206**, 2771-2777.
- Cooper, C. E. and Withers, P. C. (2002). Metabolic physiology of the numbat (*Myrmecobius fasciatus*). *Journal of Comparative Physiology B* **172**, 669-675.
- Croft, D. B. (2003). Behaviour of carnivorous marsupials In "Predators with Pouches" (Eds M. Jones, C. Dickman and M. Archer) pp. 332-346. (CSIRO Publishing: Collingwood, Victoria.)
- Denis, A. J. and Johnson, P. M. (1995). Musky rat-kangaroo. In "The Mammals of Australia" (Ed. R. Strahan) pp. 282-284. (Reed Books: Chatswood.)
- Evans, T. A. and Gleeson, P. V. (2001). Seasonal and daily activity pattern of subterranean, wood-eating termite foragers. *Australian Journal of Zoology* **49**, 311-321.

- Fleay, D. (1949). The yellow-footed marsupial mouse. *Victorian Naturalist* **65**, 273
- Friend, J. A. (1982). The numbat – an endangered specialist. *Australian Natural History* **20**, 339-342.277.
- Friend, J. A. (1986). Diel and seasonal patterns of activity in the numbat (*Myrmecobius fasciatus*). *Australian Mammal Society Bulletin* **9**, 47.
- Hall, S. (1980). Diel activity of three small mammals co-existing in forest in southern Victoria. *Australian Mammalogy* **3**, 67-79.
- Herbert, P. A. and Lewis, R. D. (1999). The chronobiology of the brushtail possum, *Trichosurus vulpecula* (Marsupialia: Phalangeridae): tests of internal and external control of timing. *Australian Journal of Zoology* **47**, 579-591.
- Kirsch, J. A.W. (1968). Prodrum of the comparative serology of Marsupialia. *Nature* **217**, 418-420.
- Kortner, G. and Geiser, F. (2000). Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* **123**, 350-357.
- Larcombe, A. N. (2003). Activity rhythms of southern brown bandicoots *Isodon obesulus* (Marsupialia: Peramelidae) in captivity. *Australian Mammalogy* **25**, 81-86.
- Le Souef, A. S. and Burrell, H. (1926). 'The Wild Animals of Australia.' (G. G. Harrap and Co.: London.)
- Maisey, K. and Bradbury, H. (1983). New light on the numbat. *Forest Focus* **2**, 14-24.
- Martin, G. G. (1973). Time patterns of *Peromyscus* activity and their correlations with weather. *Journal of Mammalogy* **54**, 169-188.
- McDonough, C. M. and Loughry, W. J. (1997). Influences on activity patterns in a population of nine-banded armadillos. *Journal of Mammalogy* **78**, 932-941.
- McNab, B. K. (1984). Physiological convergence amongst ant-eating and termite-eating mammals. *Journal of Zoology London* **203**, 485-510.

- McNab, B. K. (2000). Energy constraints on carnivore diet. *Nature* **407**, 584.
- Redford, K. H. and 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.
- Roxburgh, L. and Perrin, M. R. (1994). Temperature regulation and activity pattern of the round-eared elephant shrew *Macroscelides proboscideus*. *Journal of Thermal Biology* **19**, 13-20.
- Russell, E. M., Lee, A. K. and Wilson, G. R. (1993). Natural history of the Metatheria. In "Fauna of Australia Mammalia Vol 1B" (Eds G. J. Glasby, G. J. B. Ross and P. L. Beesley) pp. 510-525. (Australian Government Publishing Service: Canberra.)
- Vickery, W. L. and Bider, J. R. (1978). The effect of weather on *Sorex cinereus* activity. *Canadian Journal of Zoology* **56**, 291-297.
- Vickery, W. L. and Bider, J. R. (1981). The influence of weather on rodent activity. *Journal of Mammalogy* **62**, 140-145.
- Walker, E. P. (1975). 'Mammals of the World.' (John Hopkins University Press: London.)
- Walsberg, G. E., Tracey, R. L. and Hoffman, T. C. (1997). Do metabolic responses to solar radiation scale directly with intensity of irradiance? *Journal of Experimental Biology* **200**, 2115-2121.
- Wells, R. T. (1978). Thermoregulation and activity rhythms in the hairy-nosed wombat, *Lasiorhinus latifrons* (Owen) (Vombatidae). *Australian Journal of Zoology* **26**, 639-651.
- Williams, J. B., Anderson, M. D. and Richardson, P. R. K. (1997). Seasonal differences in field metabolism, water requirements and foraging behaviour of free-living aardwolves. *Ecology* **78**, 2588-2602.

- Woolley, P. A., Raftopoulos, S. A., Coleman, G. J. and Armstrong, S. M. (1991). A comparative study of circadian activity patterns of two New Guinean dasyurid marsupials. *Australian Journal of Zoology* **39**, 661-671.
- Wood Jones, F. (1923). 'The Mammals of South Australia. Part 1.' (Government Printer: Adelaide.)
- Wroe, S., Ebach, M., Ahyong, S., De Muizon, C. and Muirhead, J. (2000). Cladistic analysis of dasyuromorphian (Marsupialia) phylogeny using cranial and dental characters. *Journal of Mammalogy* **81**, 1008-1024.

Table 1: Light intensity, ambient temperature and relative humidity measured during the study period.

	Summer	Autumn	Winter	Spring
Light Intensity (relative units)				
Mean daily	7.78 ± 0.322	4.39 ± 0.502	3.85 ± 0.280	8.44 ± 0.563
Mean daytime	14.4 ± 0.5	9.6 ± 0.80	8.4 ± 0.63	13.8 ± 0.88
Mean with activity	11.64 ± 1.096	20.04 ± 1.029	13.49 ± 1.291	22.30 ± 1.189
Minimum with activity	1.28 ± 0.362	0.67 ± 0.165	1.79 ± 0.488	1.42 ± 0.292
Maximum with activity	43.00 ± 0.868	23.08 ± 1.525	24.51 ± 2.625	43.94 ± 1.078
Ambient Temperature (°C)				
Mean daily	20.8 ± 0.59	15.4 ± 0.27	13.8 ± 0.37	17.7 ± 1.50
Mean daytime	24.6 ± 0.64	25.8 ± 2.99	18.2 ± 0.78	19.5 ± 0.79
Mean with activity	19.6 ± 0.54	25.1 ± 0.63	19.2 ± 0.67	20.9 ± 0.57
Minimum with activity	17.0 ± 0.69	12.6 ± 0.34	12.2 ± 0.63	13.5 ± 0.55
Maximum with activity	31.08 ± 0.84	24.6 ± 0.57	23.6 ± 0.48	25.1 ± 0.70
Relative Humidity (%)				
Mean daily	58.2 ± 1.75	72.8 ± 3.28	81.4 ± 3.41	70.9 ± 1.81
Mean daytime	45.4 ± 1.66	59.6 ± 2.52	65.4 ± 2.62	56.8 ± 2.49
Mean with activity	42.7 ± 1.87	54.0 ± 3.14	58.9 ± 4.5	54.2 ± 1.97
Minimum with activity	25.8 ± 1.68	35.9 ± 2.63	34.8 ± 3.91	42.7 ± 2.16
Maximum with activity	88.9 ± 2.50	77.8 ± 2.80	87.2 ± 4.07	82.8 ± 2.00

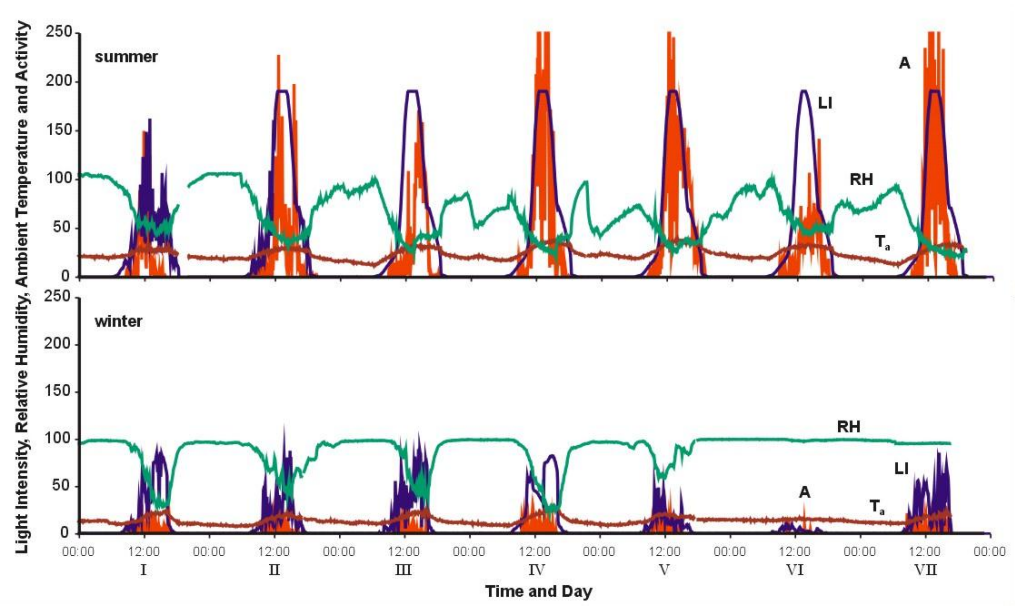


Figure 1: Five minute means of light intensity (LI; relative units), relative humidity (RH; %), ambient temperature (Ta; °C) and numbat activity (A; numbers of movements) for a typical numbat (number 62) on seven consecutive days in summer and winter.

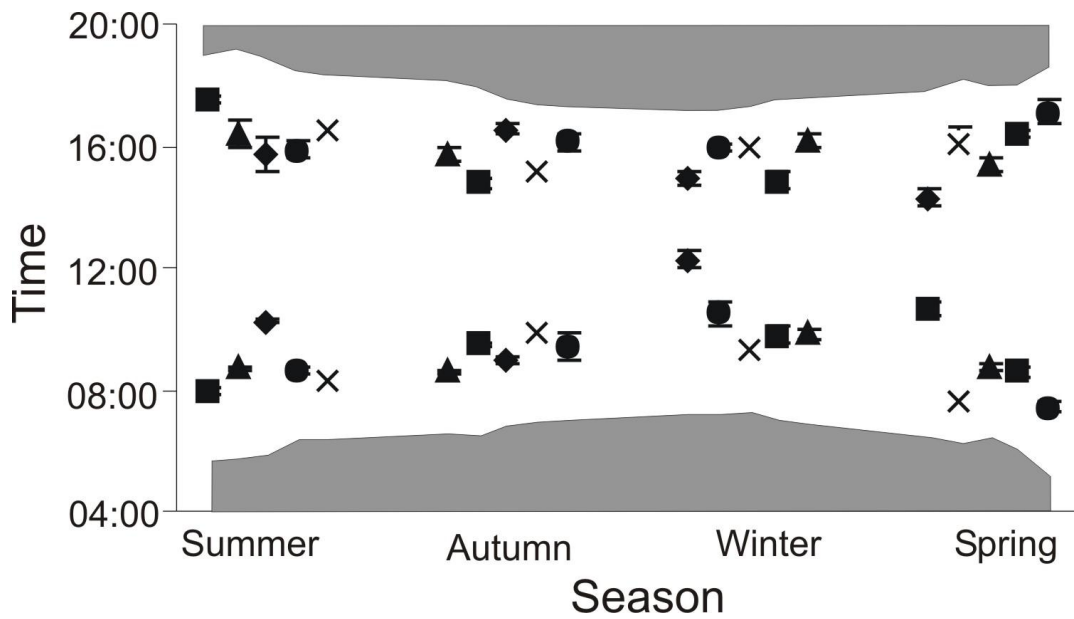


Figure 2: Time of initial and final activity for 5 numbats over four seasons (numbat 37 \square ; 62 Δ ; 104 \diamond ; 171 \circ ; 105 \times). Values are mean \pm S.E., $n = 5$ for numbat 37 in spring, $n = 8$ for numbats 37 and 171 in summer and numbat 105 in autumn and spring; $n = 9$ for numbat 104 in autumn and spring; $n = 10$ for numbats 37 in winter and 171 in spring; $n = 12$ for numbat 62 in spring; and $n = 7$ for all others. Grey areas indicate hours of darkness.

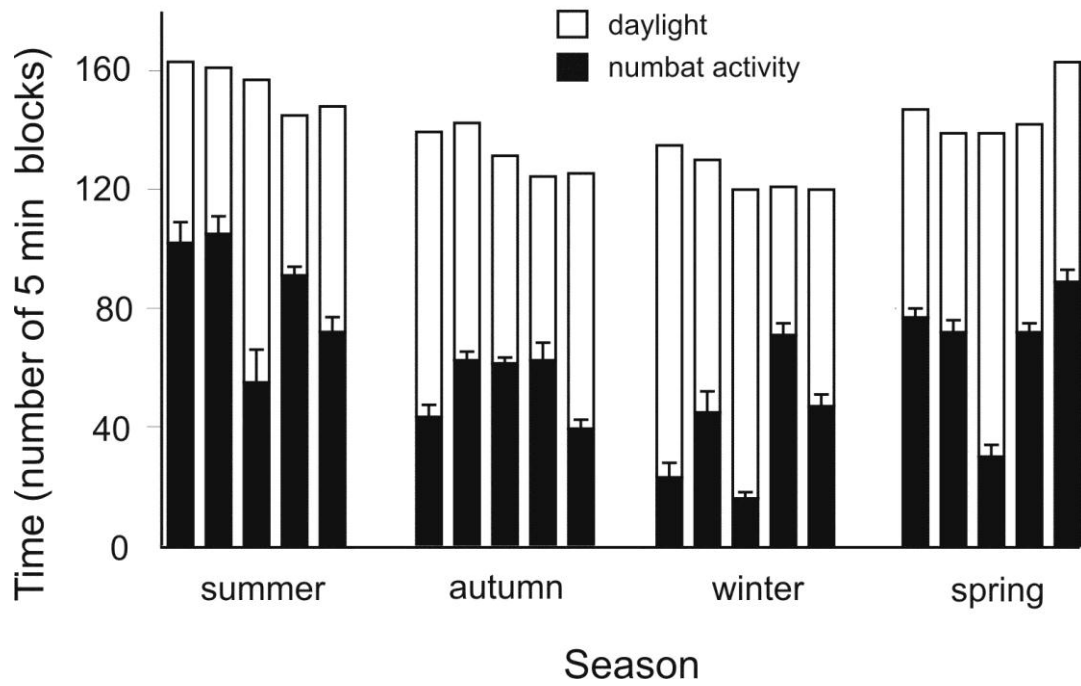


Figure 3: The number of 5-min periods of daylight (open columns) and mean (\pm S.E.; n as for Figure 1) number of 5-min periods during which numbat activity was recorded (dark columns) for numbats 37, 62, 104, 105 and 171 (left to right) over 4 seasons.