

Basking and diurnal foraging in the dasyurid marsupial *Pseudantechinus macdonnellensis*

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Abstract. Several mammal species bask to passively rewarm during arousal from torpor, a strategy that can decrease energetic costs. Nothing is known about basking behaviour in these species or the trade-offs between energetic benefits of basking and potential costs associated with changes in activity patterns and increased predation risk. We assessed basking during winter in *Pseudantechinus macdonnellensis*, an Australian arid-zone marsupial that belongs to a family (Dasyuridae) that is typically nocturnal. Animals were implanted with temperature-sensitive transmitters to assess body temperatures and to assist in visually locating animals active during the day. Tagged animals regularly exhibited diurnal foraging. Foraging bouts occurred throughout the day; however, most bouts were observed within 3 h of sunset. By comparison, basking occurred much more frequently in the morning. Basking and a shift towards diurnal foraging in winter is associated with a decrease in richness and abundance of predators. *P. macdonnellensis* appears to compensate for the occurrence of torpor during the active phase (i.e. night) in winter by changing activity patterns such that foraging commences during what is usually the rest phase. These activity patterns are not expected to occur during the remainder of the year.

Introduction

In order to survive, animals need to balance energetic requirements with the need to avoid predation (Lima and Dill 1990; Lima and Bednekoff 1999). This trade-off may be particularly challenging for those endothermic mammals that bask to passively rewarm during arousal from torpor when their body temperature (T_b) and coordination are reduced. Nevertheless, recent studies have documented this previously unknown behaviour in several small (body mass <100 g) marsupial and placental mammals (Geiser *et al.* 2002, 2008; Mzilikazi *et al.* 2002). A specific challenge faced by nocturnal endothermic mammals that passively rewarm by basking is that these species undergo torpor during the latter half of the night, during what is normally their active phase, and subsequently rewarm by basking in sun-exposed microhabitats in the morning, during their normal rest phase. Passive rewarming by basking is an energetically advantageous strategy and has been estimated to reduce the cost of rewarming by up to 85% in marsupial mammals and can increase rewarming rates (Geiser *et al.* 2004, 2008).

Nocturnal torpor and early morning basking by nocturnal endotherms involves a trade-off between the energy savings of passive rewarming and potential costs of increased predation risk during diurnal exposure and reduced foraging time from disruption to nocturnal activity rhythms. However, passive rewarming by basking also provides the opportunity for animals to shift activity periods across seasons. Specifically, during the torpor season the cost of reduced nocturnal foraging activity can

be overcome if animals can forage during the day. Diurnal foraging during winter may be energetically advantageous, especially for insectivores, because of greater prey availability during the day. Foraging during the later period of the day and for several hours after sunset, before the period after midnight when ambient temperatures (T_a s) are the lowest of the 24-h daily cycle, is likely to be an energetically advantageous strategy during the torpor season. However, diurnal foraging could also involve an increased predation risk.

The fat-tailed false antechinus, *Pseudantechinus macdonnellensis*, a small marsupial (18–33 g body mass) is an example of a species that undergoes nocturnal torpor and passively rewarms by basking after sunrise. Therefore, it is a species that may potentially shift activity patterns during the torpor season. The species is restricted to rocky outcrops and ranges in arid and semiarid Australia where it feeds on a diversity of insects and spiders, and occasionally captures other invertebrates and rodents (Gilfillan 2001a; Burwell *et al.* 2005). During winter *P. macdonnellensis* is active for several hours during the first half of the night, typically enters torpor after midnight and undergoes passive rewarming by basking on sun-exposed rocks soon after sunrise in the morning (Geiser *et al.* 2002; Geiser and Pavey 2007). Annual variation in activity pattern and torpor use of *P. macdonnellensis* has not been assessed; however, the results of mark–recapture studies indicate that the study population is nocturnal during the remainder of

the year (Gilfillan 1995, 2001*b*; C. Pavey, unpubl. data). Therefore, we expect that the activity pattern described above occurs only in winter (May–August) when nocturnal T_{as} fall close to 0°C and diurnal T_{as} are mild (Geiser and Pavey 2007).

Here we address the use of diurnal activity in *P. macdonnellensis* by examining the behaviour and activity rhythms of a population for which we have already characterised the thermal environment, and assessed torpor use, spatial ecology and diet (Geiser *et al.* 2002; Pavey *et al.* 2003; Burwell *et al.* 2005; Geiser and Pavey 2007). The behavioural and activity data described here were collected at the same time as the study of thermal biology. We first determined the extent of diurnal foraging in the study population and assessed whether early morning basking was associated with diurnal activity, i.e. whether animals that passively rewarm in the morning subsequently foraged during the day. Next, we examined whether passive rewarming by basking and diurnal foraging in the study population is correlated with a decrease in the risk of predation during winter. We did this by assessing the predator species present in the study area and determining the seasonal and daily activity patterns of each species. This enabled us to correlate predator activity with the presence of basking *P. macdonnellensis* at the site. We also assessed mechanisms by which basking animals may reduce predator pressure and maximise passive rewarming. Specifically, we examined behaviour of basking animals and the characteristics of basking sites, including location relative to torpor sites.

Methods

Study area and animals

Behavioural observations were carried out over the austral winter (between 14 June and 11 July 2001) at Ormiston Gorge (23°37'S, 132°45'E), West MacDonnell National Park, Northern Territory. This period is likely to be during the mating season for the study population (Gilfillan 2001*a*). Weather during the study period was conducive to observing basking, being sunny with the exception of a single day that was overcast early in the morning and then intermittently for much of the day.

The study population of *P. macdonnellensis* occurs in an area of hummock grassland (dominated by *Triodia brizoides*) with a sparse overstorey of acacia (*Acacia spondylophylla*) growing on rocky hills. The area is characterised by low, unpredictable rainfall and extreme T_a that ranges from –6 to 41°C on an annual basis. During the study T_a (measured to the nearest 0.5°C using data loggers: Thermochron, iButton, Dallas Semiconductor; placed 1 m above the ground in the shade) ranged between a minimum of 2.0°C and a maximum of 24.0°C with a mean of $12.6 \pm 5.8^\circ\text{C}$ (Geiser and Pavey 2007). Data loggers were wrapped in a sheet of white paper to minimise uptake of radiant heat.

We captured our study animals in aluminium box traps (Elliot type A, Elliott Scientific Ltd, Upwey, Melbourne, Vic.) baited with a mixture of peanut butter and rolled oats and containing a layer of polyester fibre for insulation. Traps were set along sandstone gullies and cliffs usually beneath rock ledges that provided protection from inclement weather and predators. Traps were set in the evening and checked at sunrise in the morning. Animals were placed in cloth bags and transferred to the field laboratory situated ~500 m from the trap site. Six animals were implanted intraperitoneally with calibrated temperature-sensitive

transmitters (FM single-stage, mass 2 g, Sirtrack Ltd, Havelock North, New Zealand) under oxygen/isoflurane anaesthesia in a field laboratory (see Geiser and Pavey 2007 for further details of the methodology). Transmitter mass was, on average, 6.5% of an animal's body mass. Our observations of apparently normal behaviour including successful foraging by the tagged animals, and use of large home ranges that were greater in size than in a previous study indicate that transmitter mass did not impair movement (Pavey *et al.* 2003).

Animals were given >24 h to recover from surgery, during which time they were placed individually in holding cages with food (commercial dog food) and water supplied *ad libitum*. We monitored the recovery from surgery regularly. Animals were released at the capture site in the late afternoon within two days of surgery. All animals recovered from surgery and remained in the study area for at least 19 days after release. Post-surgery behaviour appeared normal. Capture and care procedures were carried out under permit from the Animal Ethics Committee of the University of New England, Armidale, Australia (authority no. AEC01/029).

Assessment of predators

We assessed the predator species present within the area occupied by the study population of *P. macdonnellensis* using both field surveys (carried out between 2001 and 2006) and expert knowledge. Field survey methods included: (1) daytime walking transects for active or resting reptiles, mammals and birds of prey; (2) active searches for reptiles under rocks, logs and leaf litter; (3) spotlight transects for nocturnal reptiles, birds and mammals; (4) vehicle-based road transects (day and night) for reptiles, birds and mammals; (5) use of box traps (Elliot type A) to capture reptiles; and (6) identification of road-killed specimens.

Collectively, these methods allowed us to generate a comprehensive list of predatory species. We defined a species as a 'potential predator' of *P. macdonnellensis* if it was known to capture terrestrial small mammals of similar size and foraged within the sandstone slopes and plateaus to which *P. macdonnellensis* is restricted. We used previous research on home-range size from a range of sources as an indication of the relative number of individuals of each predator species likely to reside within our study area of 625 ha (Table 1). To do this we made the assumption that suitable habitat was uniformly available across the site for each species and, therefore, that home-range size was a useful surrogate of abundance. To determine seasonality of activity we divided the year into 'winter' (May–August) and the 'rest of the year' on the basis of T_a and assessed when each species was active and whether it was nocturnal or diurnal or both. These assessments were based on seasonality in the study area. A species was considered to be inactive in winter if most individuals in the population were inactive for most of the winter (not necessarily 100% of the population).

Behavioural observations

Tracking the animals with manual receivers allowed us to obtain behavioural data during basking. On most days, search effort was intensified during two periods: within 3 h of sunrise (range of sunrise times during the study period was 0718–0722 hours), and between early afternoon and 1 h after sunset (range of sunset times

during the study period was 1800–1806 hours). We searched for signals from tagged animals by scanning the area near the last recorded location for each individual from an elevated vantage point. The rocky nature of the study area meant that such elevated positions were plentiful. If we did not receive a signal we walked across the study area and scanned for a signal every 50–100 m. Once a signal was detected, we located the position of the animal by circling the general area from which the signal was received on foot (the ‘homing-in’ method of White and Garrott 1990). During the monitoring period we attempted to visually locate the animal. Manual readings of the pulse repetition rate of the transmitter signal provided a measure of the T_b of the animal and, therefore, its likely activity as follows: T_b of 19–29°C, torpor or commencing rewarming, including potential basking; $T_b \geq 30^\circ\text{C}$, normothermic resting or active. This method was used to rapidly ascertain T_b in the field so that basking animals could be located. Accurate T_b measurements involved the methodology detailed in Geiser and Pavey (2007). If an animal was potentially basking, the observer slowly approached the general location of the signal taking care not to disturb the target animal. We scanned the area using binoculars to find the animal.

Observers monitored and recorded the behaviour of target animals for as long as possible and recorded behaviour, proportion of the animal in the sun, orientation and activity. We classified the behaviour of animals into the categories described below.

Basking. This behaviour occurred when an individual was resting, usually on a rock surface, with some or all of its body exposed to direct sunlight (Fig. 1). During basking the animal was either: (1) stretched flat with its ventral surface resting on a rock surface; (2) standing on its hind limbs with the tail under the body and the head and anterior half of the body resting on a rock; or

(3) lying on its side with the head positioned under one of the forelimbs or curled up in a ball.

Foraging. The animal was actively searching for food among vegetation or in leaf litter. Prey capture and consumption are also included in this category.

Resting in the shade. Similar to basking except that no part of the animal was in contact with direct sunlight.

Refuge use. This behaviour was assumed to have occurred when animals moved from view into cracks and crevices among rocks.

Communing. Direct and rapid movement from one location to another, for example, from a basking site to a refuge site.

Relationship between passive rewarming and basking

We were able to use radio-telemetry to both assess T_b and to assist in visually locating active animals during the day so that we could observe basking and foraging behaviour. Thermal data were collected only when an animal was close enough to a receiver/logger for its signal to be detected (see Geiser and Pavey 2007), so we cannot establish a link between basking and passive rewarming for all observations of basking. However, our thermal data, published separately (Geiser and Pavey 2007) demonstrate the frequent use of passive rewarming in the study population such that we assume that most instances of basking in the morning involved passive rewarming.

Statistical analysis

We used a Chi-square test of independence to compare the occurrence of basking and foraging in relation to time since sunrise. Our study design, which involved basking and foraging observations on six individuals, might have violated the

Table 1. Potential predators of *P. macdonnellensis* at Ormiston Gorge, Australia

Details of home-range size (as an indication of abundance) and activity patterns are provided. Activity: d, predominantly diurnal; n, predominantly crepuscular and/or nocturnal; sn, typically diurnal but some nocturnal activity during summer

| Class/Order | Family | Species | Activity rhythm | Home range (ha) | Source |
|------------------|--------------|--------------------------------|-----------------|-------------------------|--|
| Reptilia | | | | | |
| Lacertilia | Varanidae | <i>Varanus giganteus</i> | d | 12.3 | King <i>et al.</i> (1989) |
| | | <i>Varanus acanthurus</i> | d | no data | |
| | | <i>Varanus tristis</i> | d | Male: 40.4; female: 3.7 | Thompson <i>et al.</i> (1999) |
| Serpentes | Boidae | <i>Antaresia stimsoni</i> | n | no data | |
| | | <i>Morethia spilota bredli</i> | n | 22.5 ^B | Shine and Fitzgerald (1996) ^A |
| | Elapidae | <i>Acanthopsis pyrrhus</i> | n | no data | |
| | | <i>Pseudechis australis</i> | d, sn | no data | |
| | | <i>Pseudonaja nuchalis</i> | d, sn | no data | |
| | | <i>Pseudonaja textilis</i> | d | 5.8 | Whitaker and Shine (2003) |
| Aves | | | | | |
| Falconiformes | Accipitridae | <i>Haliastur sphenurus</i> | d | Pair: 1900 | Marchant and Higgins (1993) |
| | | <i>Accipiter fasciatus</i> | d | Male: 266; female: 274 | Burton and Olsen (2000) ^A |
| | | <i>Falco berigora</i> | d | Pair: 1000 | Marchant and Higgins (1993) |
| | | <i>Falco cenchroides</i> | d | Pair: 540 | Marchant and Higgins (1993) |
| Caprimulgiformes | Podargidae | <i>Podargus strigoides</i> | n | Pair: 40–80 | Higgins (1999) ^A |
| Strigiformes | Strigidae | <i>Ninox novaeseelandiae</i> | n | Male: 37–100 | Higgins (1999) ^A |
| | | <i>Tyto alba</i> | n | Pair: 500 | Higgins (1999) |
| Mammalia | | | | | |
| Carnivora | Canidae | <i>Canis lupus dingo</i> | d and n | 18210 | Eldridge <i>et al.</i> (2002) |
| | Felidae | <i>Felis catus</i> | d and n | Male: 2210.5 | Edwards <i>et al.</i> (2001) |

^AStudy area outside arid/semi-arid zone. ^BData from another subspecies.

assumption of independence that needs to be met for Chi-square tests (Kramer and Schmidhammer 1992). However, the length of time over which data were collected (28 days) and the number of animals involved suggests that each bout we observed was likely to be independent of previous bouts. We consider the Chi-square test to be appropriate under these circumstances.

To assess the correlation between duration of basking bouts and time since sunrise we performed a Spearman rank correlation. Data were pooled across individuals to increase sample size. A one-sample *t*-test was used to compare mean minimum T_b among animals with different proportions of torpor use. Means are presented \pm standard deviation (s.d.). The α value was 0.05. *N* denotes the number of observations, whereas *n* denotes the number of individuals/species.

Results

Diurnal foraging

Radio-tagged animals regularly foraged during the day. We observed 24 foraging bouts by four tagged animals (two male, two female) on 17 observation-days (1 observation-day = an animal observed foraging on one day) (Fig. 2). Foraging bouts occurred throughout the day; however, most bouts were observed within 3 h of sunset. All foraging bouts within 2 h of sunrise were those of one animal, Male 15 (Fig. 2). This male spent only 8.1% of the recorded time in torpor, in contrast to the 19.8–38.5% observed in the other individuals. Moreover, the mean minimum T_b of this individual (27.7°C) was higher than for the other individuals ($24.2 \pm 3.2^\circ\text{C}$, $P < 0.05$, one-sample *t*-test). The other three individuals did not begin foraging until 260 min after sunrise. By comparison, the occurrence of basking, based on 44 bouts by five tagged (three male, two female) and an unmarked animal on 25 observation-days, was much greater in the morning: between 1 h after sunrise and midday (Fig. 2). Basking times ranged from 107 to 516 min after sunrise, with the latest bout within 125 min of sunset.

To assess variation in the timing of diurnal basking and foraging, daylight hours were divided into three categories, each of 3 h duration: 2–5, >5–8, and >8–11 h after sunrise. All basking



Fig. 1. *Pseudantechinus macdonnellensis* basking during passive rewarming on an exposed rock surface.

and foraging observations took place between 1 and 10.5 h after sunrise. Male 15 was excluded from the analysis. Occurrence of the two activities varied significantly in relation to time since sunrise ($\chi^2 = 24.72$, d.f. = 2, $P < 0.001$).

Three of the radio-tagged *P. macdonnellensis* were observed basking in the morning and foraging in the afternoon of the same day ($N = 8$ observation-days). On two occasions animals finished basking and began foraging soon after within a short distance of the basking site. However, this switching behaviour was observed only around midday or later. For example, on 6 July a female that was basking between 1015 and 1138 hours on an exposed rock surface, with a T_b of 24.1°C when first seen, briefly retreated into an adjacent rock crevice and then re-emerged and began foraging in leaf litter within 0.5 m of the crevice. The animal captured prey, a beetle larva (Coleoptera), within 5 min and returned to the crevice to consume the prey. A male behaved in a similar manner on 15 June and moved at a T_b of 31.9°C . It completed a bout of basking at 1306 hours, moved into an adjacent refuge site and returned within 60 s to pursue a large fly (Diptera, Muscidae) within 0.5 m of the basking site.

Predation risk

Pseudantechinus macdonnellensis is within the prey size range of 18 species of vertebrates that are resident in the study area and are known to capture terrestrial mammals (Table 1). Potential predators include snakes ($n = 6$), varanid lizards ($n = 3$), aerial-foraging birds ($n = 7$), and introduced carnivores ($n = 2$). Only one species, *Varanus tristis*, has been observed attempting to capture *P. macdonnellensis* (G. Fyfe, pers. comm.); no other species is known to be a definite predator.

The number of predator species active in winter (May–August) compared with the rest of the year was reduced by 50% for diurnal species and 55% for nocturnal species (Fig. 3). The reason for the decline was the lack of activity of all species of snakes and lizards in winter (Fig. 3). The home-range estimates

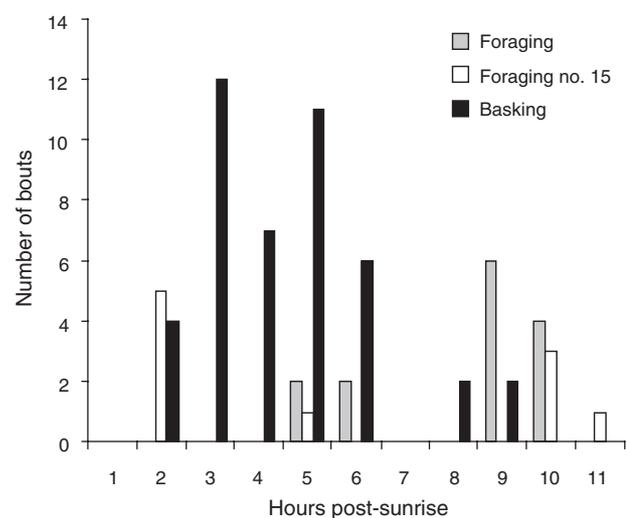


Fig. 2. Diurnal occurrence of basking and foraging observations of *P. macdonnellensis*. Foraging bouts of one individual (Male 15) are separated from those of the other animals. Sunset occurred between 10 h 40 min and 10 h 47 min after sunrise during the study period.

(Table 1) show that snakes and lizards have a smaller home range than birds of prey and carnivores and, therefore, that reptiles will be the predatory group with the highest density on the study site.

Characteristics of basking sites

Twenty discrete basking sites were located during the study. Basking sites all occurred on sandstone, either along cliffs, exposed rock surfaces on hill slopes or beside gullies. Basking sites were mostly on exposed and bare rock surfaces adjacent to vertical rock walls ($n = 12$). Other basking sites were on bare rock surfaces beneath rocky overhangs ($n = 2$), bare rock surfaces in crevices and cracks below the ground surface ($n = 3$) and rock surfaces beneath grasses (either *Eriachne* or *Triodia*) and fallen vegetation ($n = 3$). Most sites were sun-exposed in the morning and we observed animals basking at each site. Basking sites were usually within 10 m and often within 1 m of torpor sites used the same morning. Several animals alternated between basking on exposed rock surfaces and spending time within adjacent refuge sites during the course of a morning.

Basking behaviour

Animals typically basked with the back oriented towards the sun (mean proportion basking time \pm s.d. = 0.79 ± 0.14) whereas the flanks faced the sun during 0.20 ± 0.14 of basking time ($n = 5$, 261 min of observation). The percentage of the body of a basking animal in direct sunlight (mean proportion basking time \pm s.d.) was as follows: 100%, 0.60 ± 0.40 ; >90%, 0.03 ± 0.07 ; 50–90%, 0.33 ± 0.43 ; and <50%, 0.03 ± 0.05 ($n = 5$, 187 min observation). The duration of completed basking bouts varied with time since sunrise. Bout length was longest soon after sunrise and decreased with increasing time since sunrise (Fig. 4). There was a significant negative correlation between duration of basking bouts and time since sunrise ($r_s = -0.44$, $P < 0.05$, $n = 21$).

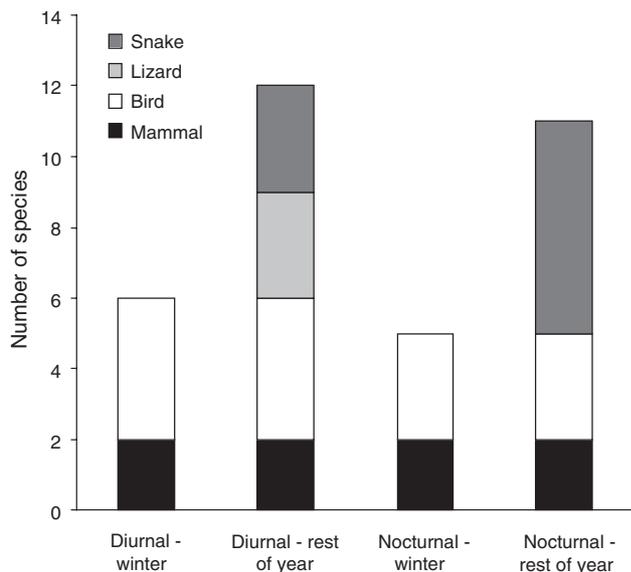


Fig. 3. The number of diurnal and nocturnal vertebrate species that are potential predators of small mammals active in the study area during winter (May–August) and the rest of the year.

Basking animals did not remain stationary for long periods and regularly changed body position or posture. These changes included altering orientation towards the sun by as much as 180° , and small movements of the body to increase or decrease the amount of sun-exposure. We also observed short-duration (<5 s) activities such as ear scratching and grooming the fur in several basking animals. Basking animals adjusted their body posture or position, on average, every 4.99 min ($n = 5$, $N = 43$ changes).

Discussion

Our findings show that the study population of *P. macdonnellensis* modified activity patterns in winter by entering torpor during the active phase, and basking and foraging during what is normally the rest phase. Radio-tagged animals actively foraged from midday onwards during daylight (Fig. 2) and continued to forage during the early part of the night, with torpor commencing around or soon after midnight (Geiser and Pavey 2007). Although entry into torpor during the active phase occurs in several placental mammals that passively rewarm during arousal (Schmid 2000; Mzilikazi and Lovegrove 2005) and seasonal shifts in activity periods within the active phase occur in other mammals (Kenagy *et al.* 2002), seasonal switching of the active phase as shown by *P. macdonnellensis* appears to be rare among mammals. The strategy employed by *P. macdonnellensis* should maximise energetic savings because animals are inactive during the period of lowest T_a .

Our observations of diurnal activity in winter by *P. macdonnellensis* coincide with a decrease in the diversity of predators active within the habitat of the study population compared with the rest of the year (Fig. 3). Significantly, the predators that are inactive in winter – terrestrial lizards (Varanidae) and snakes – are the predator group against which basking *P. macdonnellensis* have no obvious defences. Basking *P. macdonnellensis* selected sites that were protected overhead and located close to refuge sites. All 20 basking sites afforded a high level of protection, with eight sites either protected by a rocky overhang or located in cracks and crevices below the surface or beneath vegetation, and the remainder positioned

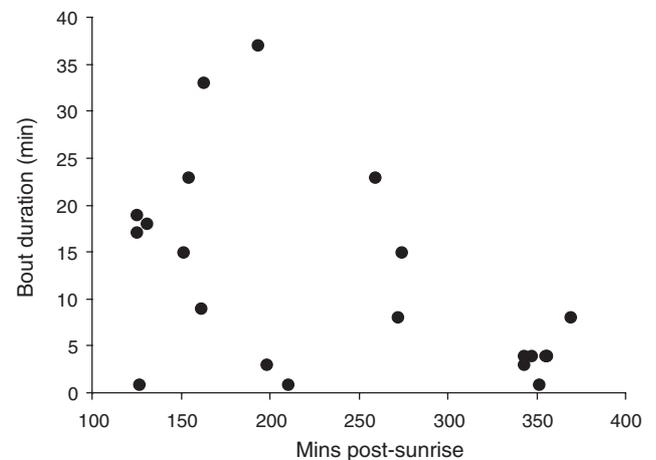


Fig. 4. Variation in duration of basking bouts of *P. macdonnellensis* with time after sunrise.

adjacent to a vertical rock surface such as a cliff face or rock slab. Such basking locations reduce the likelihood of animals being located and captured by aerial-foraging diurnal birds or cursorial mammals, the two predator groups that are active in winter. However, reptilian predators can pursue *P. macdonnellensis* into refuge sites and are likely to represent a greater threat. The threat posed by varanid lizards and diurnal elapid snakes is likely to be high because these predators actively seek prey in contrast to 'sit and wait' foragers such as pythons and *Acanthopsis pyrrhus* (Bedford and Christian 1998).

In terms of relative numbers, the home-range estimates (Table 1) indicate clearly that reptiles have smaller home ranges than other diurnal predators and, therefore, will be the most abundant predators in the study area. As a consequence, the absence of reptiles in winter should represent a significant reduction in the predation risk of diurnal activity. However, the energetic differences between endothermic (mammals and birds) and ectothermic (reptiles) predators is great, with placental mammals and birds having field metabolic rates ~17 times higher than those of similar-sized reptiles (Nagy 1987). As a consequence, endothermic predators active in winter will still represent a major threat to basking *P. macdonnellensis*.

The continued predation threat faced by *P. macdonnellensis* in winter is a likely explanation for the use of basking sites located close to refuge sites. Similar behaviour has been observed in other saxicoline, basking mammals (Mzilikazi *et al.* 2002; Brown and Downs 2005). Close proximity of refuge and basking sites reduces commuting time when animals are potentially exposed to predators while their locomotor abilities are impaired at low T_b (Rodríguez-Gironés 2002), and, as with ectothermic reptiles, ensures a greater probability of escape in the event of attempted predation (Cooper 2000). A further advantage is that shuttling between sun-exposed and protected areas can readily occur (Hainsworth 1995), a strategy used by *P. macdonnellensis* in our study. The physical requirements of refuge and basking sites of *P. macdonnellensis* differ; specifically, refuge sites should provide a buffer against temperature extremes, water loss and predators, whereas basking sites should maximise exposure to early morning or afternoon sun. Therefore, the availability of torpor and basking sites in close juxtaposition must be an important characteristic of home ranges of this species.

We found that basking bouts were longest soon after sunrise and decreased with time since sunrise. This pattern may have resulted from the higher T_a in the afternoon, thus making thermoregulation cheaper. Alternatively, it may be a response to the potential presence of predatory reptiles, which are sometimes active on warm afternoons in winter after rewarming in the morning.

Several aspects of the basking behaviour of *P. macdonnellensis* indicate that animals employ a strategy that aims to maximise warming efficiency. First, basking animals typically flattened their bodies against rock surfaces thereby maximising heat gain through conduction from the sun-exposed rock. Second, animals maximised sun-exposure of the dorsal surface. Regardless of the body posture, animals typically orientated the posterior of the body towards the sun while basking. Last, basking animals frequently switched position while basking. This movement included changing the orientation of the body towards the sun and moving more of the body into or out of

the sun as required. These and other behaviours of *P. macdonnellensis* have much in common with those used by desert-dwelling ectotherms, including the frequency of basking on sun-exposed rock early in the morning, use of adjacent rock crevices for refuge, adjusting body posture in relation to solar radiation, and increased duration of basking bouts early in the day (Mayhew 1968; Nagy 1973; Carrascal *et al.* 1992). Further, most *P. macdonnellensis* commenced diurnal foraging after passive rewarming by basking, as do desert ectotherms (Huey and Pianka 1977; Cooper 2000). Given these behavioural similarities and the behavioural control of thermoregulation in many reptiles, further understanding of the degree of behavioural regulation of temperature by endotherms during basking needs further investigation.

Our study is an example of the use of new technology to provide insights into animal behaviour. In contrast to other basking mammals (e.g. Brown and Downs 2005), the small size of this species meant that we could not have located basking or foraging animals without using radio-telemetry. However, external transmitters remain attached to the study species for very short periods (Gilfillan 2001b; Pavey *et al.* 2003); therefore, implanted transmitters were needed. Although implant transmitters were developed specifically to collect thermal data they worked very well for our purposes. Therefore, wider use of this method should be considered, especially for studies in which long-term data are required.

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