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# Home range and spatial organisation of rock-dwelling carnivorous marsupial, *Pseudantechinus macdonnellensis*

Chris R. Pavey<sup>A,D</sup>, Nicola Goodship<sup>B</sup> and Fritz Geiser<sup>C</sup>

 <sup>A</sup>Parks and Wildlife Commission, Department of Infrastructure, Planning and Environment, PO Box 2130, Alice Springs, NT 0871, Australia.
 <sup>B</sup>Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom.

<sup>C</sup>Zoology, BBMS, University of New England, Armidale, NSW 2351, Australia.

<sup>D</sup>To whom correspondence should be addressed. Email: chris.pavey@nt.gov.au

*Abstract.* We studied home-range size, range length and spatial organisation of fat-tailed false antechinus, *Pseudantechinus macdonnellensis*, at Ormiston Creek, central Australia. Animals were tracked using transmitters implanted into the body cavity. Mean home-range size was 0.76 ha based on the minimum convex polygon (MCP) method and 1.14 ha based on the fixed kernel method (95% contour). Mean size of core areas of the home range was 0.07 ha based on the 50% kernel contour. Mean maximum range length was 148.83 m. Males occupied larger home-range areas than females (MCP: 0.98 v. 0.31 ha, 95% fixed kernel: 1.50 v. 0.43 ha) and also had greater maximum range lengths (180 v. 86 m). Home-range areas showed little overlap within the sexes; however, ranges of males overlapped those of females by an average of 37.95%. By comparison with data from a previous mark–recapture study at the same site, radio-tracking produced home-range estimates (MCP) that were greater by a factor of 24.5 for males and 15.5 for females, whereas maximum range lengths were lower for females, but similar for males. The results of this study support the proposition that the rock-dwelling *P. macdonnellensis* has a more stable home range and undergoes fewer long-range movements than similar-sized arid-zone dasyurids that occupy open environments. These differences likely result from the stability in resources provided by rocky habitats, specifically year-round availability of insects, availability of plentiful shelter sites that are very effective thermal buffers in both summer and winter, and a diversity of accessible microclimates.

#### Introduction

Australia supports a rich fauna of mammals that is restricted to rocky habitats. Rock-dwelling specialists constitute over 14% of Australia's marsupial and rodent species (32 of 223 species), with most species being restricted to northern Australia (Freeland et al. 1988; Menkhorst and Knight 2001). In arid regions, rocky areas provide a more stable thermal environment than surrounding open habitats. Rock surfaces do not warm during the daytime to the same degree as sand surfaces nor do temperatures fall as dramatically at night (George 1986). The thermal stability of rocky environments appears to result in a more predictable availability of food resources than in surrounding arid environments. For example, in the rocky ranges of central Australia, Gilfillan (2001a) observed a lack of seasonality and low month-to-month variation in insect abundance. This pattern contrasts with the distinct seasonality and low winter abundance of insects in other arid environments of Australia (Morton 1978; Read 1987).

The increased stability in thermal niches and food resources has implications for the ecology and physiology of rock-dwelling mammals. For example, the rock-inhabiting carnivorous marsupial (Dasyuridae) the fat-tailed false antechinus, Pseudantechinus macdonnellensis (body mass 18-33 g), has a different pattern of population dynamics to that of sympatric arid-zone dasyurid species that occupy open habitats (Gilfillan 1995, 2001a, 2001b). Specifically, P. macdonnellensis lacks both a strong intra-annual population cycle and marked population fluctuations, and populations exhibit a low number of transients relative to residents. By comparison, carnivorous marsupials that occupy open environments, including sand plains and dunes, gibber plains and cracking clay soils, typically display marked population fluctuations seasonally or between years, and populations of many species are composed mostly of transient individuals (Read 1984; Dickman et al. 2001; Letnic 2002). Differences in resource availability between the two environments may also produce differences in spatial

ecology. For example, *P. macdonnellensis* appears to occupy a relatively stable home range (Gilfillan 2001*b*), whereas sand-inhabiting dasyurids are highly mobile, undergoing long-range movements to exploit ephemeral food sources (Dickman *et al.* 1995, 2001; Letnic 2002).

Testing predictions of contrasting patterns of use of space by arid-zone dasyurids is hampered by difficulties with carrying out long-term radio-tracking studies. As a consequence, information on movements and home ranges of small (<50 g) dasyurids is based almost entirely on mark-recapture estimates (e.g. Dickman *et al.* 1995; Gilfillan 2001*b*). However, no research is available that compares home-range estimates between mark-recapture and radio-tracking methods for any species of dasyurid.

Here, we report the results of a radio-tracking study of *P. macdonnellensis* in the West MacDonnell National Park, central Australia, in which transmitters were surgically implanted into the body cavity of study animals. Such implant transmitters are commonly used in ecophysiological research on mammals (e.g. Körtner and Geiser 2000) and in our study were effective in obtaining information on home-range patterns and movements of *P. macdonnellensis*. Because we carried out radio-tracking at the site of a previous long-term mark–recapture study of the species (Gilfillan 1995), we were able to compare home-range and movement measures obtained by the two methods. In addition, we summarise information on the spatial organisation of *P. macdonnellensis*.

#### Methods

## Study area

The study area is near Ormiston Creek (23°37′S, 132°45′E) in the West MacDonnell National Park, Northern Territory, Australia. The site lies within the MacDonnell Ranges bioregion and elevation ranges from about 600 m to over 1000 m above sea level. Vegetation is a mixture of spinifex, *Triodia brizoides*, and acacia, *Acacia spondylophylla*, growing on rocky hills. Further details of the site are given in Gilfillan (2001*a*). Ambient temperature during the study period ranged from daily minima of 1.5–12.5°C to maxima of 19.5–23.5°C. Weather was clear except for a single cloudy day.

#### Trapping

We trapped animals in two areas: the first site (A) included several of the trapping grids (so-called *B*-lines of Gilfillan 2001*a*) used during a previous study from September 1991 to March 1993, the other (Site B) was near the ranger base. The two sites are within 400 m of each other. Site B was trapped after the start of the study when it was discovered that *P. macdonnellensis* was regularly present near buildings at the ranger base. Animals were captured in Elliott traps  $(23 \times 8 \times 9 \text{ cm})$  baited with a mixture of peanut butter and rolled oats. Site A was trapped over four nights in June 2001 (356 trap-nights), whereas Site B was trapped opportunistically (30 trap-nights).

#### Implant of transmitters

We checked traps at first light each morning. As soon as possible after capture, we implanted 2-g temperature-sensitive transmitters (Sirtrack, Havelock North, New Zealand) intraperitoneally under Oxygen– Forthane anaesthesia. Surgery was carried out in a field laboratory. After surgery, animals were placed individually in holding cages where their condition was regularly monitored. Food (dog food) and water were supplied *ad libitum*. We implanted transmitters into a maximum of two animals per day. After recovery, animals were released at their capture site in the late afternoon.

#### Radio-tracking

Animals were tracked between 14 June and 11 July 2001. This period is likely to cover the completion of the non-breeding season and the onset of the mating season in the study population (Gilfillan 2001a). Tracking commenced the day after animals were re-released into the wild. Radio-tagged animals were located with the use of manual receivers (Telonics TR4) and hand-held Yagi antennae. On most days, animals were searched for during two periods: within 3 h of sunrise (range of sunrise times during study period: 0718-0722 hours), and between early afternoon and 1 h after sunset (range of sunset times during study period: 1800-1806 hours). The morning session identified shelter sites and recorded locations of animals that basked in the sun, whereas the afternoon session provided information on foraging areas. Animals typically basked in the sun during the morning and were active from early afternoon into the first half of the night (Geiser et al. 2002). The relatively constant sampling periods that we used should be sufficient to overcome problems associated with autocorrelation of our data (Rooney et al. 1998; de Solla et al. 1999).

Initially, we searched for the signal from a tagged animal by scanning the area near its release site 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 received, 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 Garrot 1990). Once detected, each animal was monitored for at least 30 min before the observer shifted to another animal. On many occasions the position of tagged animals was established by observing them basking in the sun or foraging among rocks. These observations confirmed that fixes were very accurate, usually to within 5 m. We used flagging tape to mark the position of the tagged animal. GPS.

Home-range calculations were carried out using the Ranges V program (Institute of Terrestrial Ecology, Wareham, England). We calculated home ranges based on the minimum convex polygon (MCP) method and the fixed kernel method. The MCP method is a non-statistical procedure for estimating total home range that is comparable between studies. A convex polygon is fitted to all data points including occasional fixes outside the main area of activity. Therefore, if the distribution is not convex, the home range estimated is inflated by inclusion of areas that are not visited. However, despite this shortcoming, the method is more robust than other home-range estimators when the number of fixes is low (Harris et al. 1990). Kernel density estimators are arguably the most effective methods currently available for estimating home-range areas and home-range utilisation distributions when the number of fixes is not low (e.g. Powell et al. 1997). We used the fixed kernel estimator with bandwidth chosen by least-squares cross-validation. This technique gives dependable estimates of home-range area with as few as 20 location estimates (Powell et al. 1997). Fixed kernel estimates were calculated using  $50 \times 50$  grids. On the basis of the kernel analysis, we calculated home range based on the 95% utilisation contour and defined the core area as that area enclosed by the 50% utilisation contour.

#### Statistical analysis

The size of the sample of tagged animals was relatively low, resulting in home-range and range-length datasets that were small, sparse and

Animal no.	Sex	Dates tracked	No. of fixes	Maximum range length (m)	MCP (ha)	95% Kernel (ha)	50% Kernel (ha)
1	Male	19.vi–11.vii	25	189	0.75	1.38	0.05
14 <sup>A</sup>	Male	19-20.vi	2	-	_	-	_
15	Male	18.vi-10.vii	23	196	1.16	1.83	0.00
22	Male	23.vi-11.vii	33	116	0.24	0.58	0.05
40	Male	15.vi–11.vii	38	220	1.77	2.20	0.06
18	Female	15.vi–11.vii	40	108	0.46	0.71	0.20
34	Female	18.vi–11.vii	31	64	0.15	0.14	0.03
Mean				$148.83\pm25.06$	$0.76\pm0.25$	$1.14\pm0.32$	$0.07\pm0.03$

 

 Table 1.
 Home-range estimates for radio-tracked Pseudantechinus macdonnellensis during winter 2001 at Ormiston Creek, West MacDonnell National Park, central Australia

<sup>A</sup>External transmitter.

Table 2. Comparison of home range (MCP) and range-length estimates for *Pseudantechinus macdonnellensis* at Ormiston Creek, West MacDonnell National Park, between radio-tracking data from this study (2001) and mark-recapture data collected from 1991 to 1993 (Gilfillan 2001b) Values in perartheses one complexies

Values in parentheses are sample sizes

Variable	Sex	Method	
		Radio-tracking	Mark-recapture
Home range (ha)	Male	0.98 ± 0.32 (4)	$0.04 \pm 0.02$ (7)
	Female	0.31 ± 0.16 (2)	$0.02 \pm 0.02$ (5)
Range length (m)	Male	$180.25 \pm 22.42$ (4)	$167.0 \pm 127.6(38)$
	Female	86.0 ± 22.0 (2)	$146.0\pm80.6\ (51)$

unbalanced. Such data cannot be tested statistically without violating the assumptions of parametric tests. We therefore used exact nonparametric inference to analyse our data to minimise possible Type I errors (Manly 1991). To examine whether there was a correlation between the number of fixes and home-range size/range length, we calculated the exact P-values for Spearman's rank-order correlation coefficient. Exact P-values are P-values based on deriving the true distribution of the test statistic, i.e. enumerating every single outcome in the reference set. To examine variation in mean overlap indices across sex combinations, we used a randomisation procedure applied to one-way ANOVA. The randomisation procedure calculated Monte Carlo P-values based on 10 000 random samples from the reference set. It also calculated 99% confidence intervals (CIs). Although it is preferable to use exact P-values for all tests, computationally this becomes very difficult once the sample size increases so Monte Carlo P-values are calculated. The analyses were carried out using StatXact ver. 4.0.1 (Cytel Software Corporation, USA). We used an  $\alpha$  value of 0.05 for all tests. P-values and CIs are presented to four decimal places. Means are presented  $\pm$  standard error.

## Results

## Radio-tracking

We captured seven adult *P. macdonnellensis* during the study period. Two males and two females were captured at Site A (capture rate of 1.12 per 100 trap-nights) and three males at Site B. Mean ( $\pm$ s.e.) body mass of the seven animals was  $31.27 \pm 1.78$  g (range 22.4–37.2 g). We implanted transmitters into six individuals (four males, two females) and fitted an external transmitter to the other male. All animals with implanted transmitters successfully recovered from surgery and each one was released at the point of capture within two days of surgery. All animals remained within the study area for at least 19 days after re-release into the wild.

The six adults with implanted transmitters were tracked for periods of 18–26 days, whereas the external transmitter was dislodged from Male 14 within 24 h of attachment (Table 1). We were able to locate all individuals on 10 and 11 July, when we ceased tracking; however, we were unable to locate any of them during a visit on 13 August. Battery failure appears the most likely explanation for our inability to locate the animals because battery life was expected to be about 4 weeks.

Home ranges (MCP) ranged from 0.15 to 1.77 ha with a mean of 0.76 ha (Table 1). The three largest home ranges were those of males and mean home-range size (0.98 ha) of males was over three times that of females (0.31 ha) (Table 2). Home-range size (MCP) was not correlated with the number of fixes obtained (Exact test of Spearman's correlation coefficient,  $r_s = -0.0857$ , P = 0.9194, n = 6).

Home ranges based on 95% kernel estimates were larger than MCP estimates for all animals, except Female 34 (Table 1). Mean home-range size was 1.14 ha with a maximum of 2.20 ha (Male 40). Mean home-range size of males was greater than that of females by a factor of 3.5 (males:  $1.50 \pm 0.35$  ha; females:  $0.43 \pm 0.29$  ha). Core areas (50% kernel) averaged only 0.07 ha, with the largest being that of Female 18 (0.20 ha). The large core area of Female 18 resulted in females having a larger mean core area than males (females:  $0.12 \pm 0.09$  ha; males:  $0.04 \pm 0.01$  ha).

Maximum range length of all animals except Female 34 was >100 m, with a mean of 148.83 m (Table 1). The mean maximum range length of males (180.25 ± 22.42 m) was over twice that of females (86.0 ± 22.0 m) (Table 2). Maximum range length was not correlated with the number of fixes obtained (Exact test of Spearman's correlation coefficient,  $r_s = -0.2000$ , P = 0.7139, n = 6).

# Comparison with mark-recapture data

Gilfillan (2001b) calculated range lengths for all animals captured at least twice and home-range estimates (MCP) for animals captured >10 times over an 18-month mark-recapture study. Home-range estimates (MCP) differed greatly between the two methods. Radio-tracking data estimated mean home ranges that were larger by a factor of 24.5 for males and 15.5 for females (Table 2). Home-range estimates obtained from mark-recapture data were most similar to the core areas of radio-tagged animals, defined as the 50% fixed kernel contours (Tables 1, 2). The mean maximum range length based on mark-recapture data was slightly lower for males but much higher for females than that obtained from tracking data (Table 2). Both methods indicated that both home-range size and maximum range length were larger for males than females.

#### Spatial organisation

We observed spatial overlap in home ranges for all six implanted animals. Because unmarked conspecifics were occasionally observed within the ranges of implanted animals, the degree of overlap was underestimated. However, the density of the study population calculated by Gilfillan (2001*b*) was low (males: 0.05-0.3 ha<sup>-1</sup>; females: 0.05-0.2 ha<sup>-1</sup>) so we expect that relatively few unmarked individuals were present.

Of the implanted animals, we recorded little overlap in home ranges within the sexes. Mean overlap in home ranges of males was 8.13% (n = 4 pairs) and that of females was 12.75% (n = 2 pairs) (Fig. 1). In contrast, home ranges of males overlapped those of females by an average of 37.95% (n = 4 pairs). Home ranges of females overlapped those of males by 8.78% (n = 4 pairs). Despite the differences in percentage overlap between the four sex combinations, the variation was not statistically significant (Monte Carlo randomisation test of 1-way ANOVA, F = 6.304, d.f. = 10, P = 0.0653, 99% CI = 0.0589–0.0717).

Our field observations indicated that not only did home ranges overlap, but also that pairs of animals often shared shelter and basking sites. Male 40 was recorded basking close to Female 18 on two mornings (24 and 25 June) and the pair also shared a shelter site on the afternoon of 4 July. The same male was recorded sharing a shelter site with Female 34 on the afternoon of 29 June. In addition, an untagged male was observed basking near Female 34 on two days (27 June, 6 July). On other occasions animals used the same shelter/basking locations but without temporal overlap.

# Discussion

Our study is one of the few radio-tracking projects attempted for an arid-zone dasyurid marsupial. We successfully used a methodology that involved implanting transmitters into an animal's body cavity during surgery in the field. Although the range of implant transmitters is lower than external transmitters (Körtner et al. 2001), the relatively small home ranges of P. macdonnellensis allowed us to effectively track animals for long periods. This methodology has considerable potential for obtaining data on home ranges and spatial organisation of other small mammals and it has already been used to track rodents (e.g. Gaulin and Fitzgerald 1988). However, it is an invasive method, the effectiveness of which depends on successful surgery to implant transmitters in a field laboratory. Although all our study animals were active within the study area for over 19 days after re-release into the wild, implant transmitters have resulted in inhibition of movement and increased mortality of subjects in some studies (e.g. Daly et al. 1992). Of particular concern is that these changes in behaviour and mortality can be sex specific (Daly et al. 1992). As a consequence of these potential difficulties, use of implant transmitters should be considered only in situations where standard methods are ineffective.

Home-range estimates for P. macdonnellensis from this study are greater than those from the mark-recapture data of Gilfillan (2001b) by a factor of 24.5 for males and 15.5 for females. However, these differences may not only be a consequence of the different methodologies used. The spacing of the studies eight years apart may have contributed to the variation in home-range estimates. The mark-recapture study ran from 1991 to 1993, whereas radio-tracking was carried out in 2001. Biotic and abiotic changes at the site over this period may have resulted in changes in spatial ecology of the P. macdonnellensis population. Alternatively, the combination of a shorter study duration (6 weeks) and regular location of animals that resulted from radio-tracking is highly likely to give a more accurate interpretation of home range than a long-term (18 month) mark-recapture study where individuals are relocated only periodically.

Notwithstanding the possibility that other factors contributed to the differences between studies in home-range estimates for *P. macdonnellensis*, our results add to a growing body of research that indicates that mark–recapture data provide an underestimation of home-range size, particularly when compared with estimates based on radio-tracking data. This research covers a range of rodent



**Fig. 1.** Home ranges (MCP) of radio-tagged *Pseudantechinus macdonnellensis* at Site A (upper figure) and Site B (lower figure). Dashed lines indicate ephemeral streams.

and marsupial species across a diversity of environments (e.g. Trevor-Deutsch and Hackett 1979; Ward 1984; Brandle and Moseby 1999; Runcie 1999; Ribble *et al.* 2002). In contrast, only a few studies have indicated that mark–recapture estimates of home-range size are similar to those obtained from radio-telemetry (e.g. Wolff 1985). Despite the strength of this evidence, mark–recapture data continue to be used to estimate home ranges of small mammals (Ribble *et al.* 2002).

In contrast to home-range estimates, the two methods produced similar maximum range lengths for males, whereas range lengths of females based on radio-tracking were much lower than those based on mark–recapture data. The difference between studies in range length of females is likely related to the greater duration and larger sample of the mark–recapture study, which maximised the chances of occasional longer-distance movements being detected.

Our estimates of home-range size for *P. macdonnellensis* are lower than those for the closely related and similar-sized *Antechinus stuartii* in eucalypt forest in eastern Australia. Mean home ranges of males (body mass 35 g) were  $\sim 1.75-5.25$  ha and those of females (body mass 20 g) were  $\sim 1.25-2.25$  ha over a 5-year study period (Lazenby-Cohen and Cockburn 1991, fig. 4). However, these are estimates for so-called 'social' ranges that included communal nests used by both males and females, whereas foraging ranges averaged 0.94 ha for males and 0.38 ha for females (Lazenby-Cohen and Cockburn 1991). Our home-range

estimates for *P. macdonnellensis* are equivalent to the social range of *A. stuartii* because ranges included both foraging areas and shelter and basking sites. The only other dasyurids for which home-range estimates from radio-tracking data are available are much larger species with significantly larger home ranges. For example, mean home-range size (MCP) of *Phascogale tapoatafa* (body mass 106–311 g) in dry eucalypt forest in Victoria is 106 ha for males and 41 ha for females (Soderquist 1995).

Information on range lengths is available for a number of species of small (<50 g) arid-zone dasyurids (summarised by Gilfillan 2001b and Letnic 2002). Range lengths are highly variable across species but most are significantly larger than those recorded for *P*. macdonnellensis in the West MacDonnell National Park (Table 2). For example, Dickman et al. (1995) recorded mean long-range movements during or after rain of 4.2 km for Sminthopsis dolichura (body mass 12 g), 7.25 km for S. youngsoni (body mass 10 g), and 1.32 km for S. hirtipes (body mass 15 g). Maximum range lengths of 1.3 km and 5.0 km are reported for *Planigale gilesi* (body mass 5-16 g) and P. teniurostris (body mass 4-9 g), respectively (Read 1984). Each of these species occupies open habitat in arid and semi-arid Australia.

Despite the short-term nature of our study, the data we obtained on the spatial ecology of P. macdonnellensis provide support for the assertion of Gilfillan (2001b) that P. macdonnellensis occupies a relatively stable home range and that it does not exhibit the high mobility and long-range movements recorded for dasyurid species that occupy open habitats in the arid zone. The increased predictability in food resources and stability of environments provided by rocky habitats in arid Australia are likely explanations for this difference. In particular, the abundant supply of caves, rock overhangs and crevices in areas occupied by P. macdonnellensis provides shelter and rest sites that are both stable over long periods, and provide protection from aerial and terrestrial predators. Further, these sites act as thermal buffers both in summer and winter. For example, temperature within a cave that was a shelter site of Female 34 during our study ranged from 16 to 30.5°C (measured every 4 h over the 12 months from July 2001 to June 2002: F. Geiser, unpublished data). By comparison, temperatures at above-ground locations in the MacDonnell Ranges bioregion over this period ranged from -6 to 40.8°C and -3.9 to 42°C at Alice Springs and Watarrka National Park, respectively (Bureau of Meteorology, unpublished data). Such stability in thermal conditions occurs rarely in other arid environments.

Rock habitats throughout the seasonally dry tropics of northern Australia provide a greater amount and more predictable supply of food resources and more stable thermal niches than surrounding areas (Freeland *et al.* 1988). Given this pattern, it is likely that the trend for increased stability in home ranges and decreased long-range movements may apply to other mammal groups that include saxicoline and non-saxicoline taxa. Available information on home ranges of the two species of rock-dwelling possums in northern Australia demonstrates that both Petropseudes dahli (mean for family groups, 0.9 ha) and Wyulda squamicaudata (mean for males, 0.5; mean for females, 1.3 ha) occupy relatively small, stable home ranges (Runcie 1999, 2000). Range size is much lower than that recorded for most populations of Trichosurus vulpecula (Kerle 1984). Further, the allied rock wallaby, Petrogale assimilis, a north Queensland endemic, occupies a much smaller home range (mean 11.9 ha) than similar-sized plains-dwelling macropods such as Macropus dorsalis (mean 91.0 ha) and Onychogalea fraenata (mean for males, 56.0; mean for females, 24.5 ha) (Horsup 1994; Fisher and Owens 2000). However, research on a wider range of species is needed before this topic can be addressed in more detail.

The spatial organisation of P. macdonnellensis included extensive overlap of home ranges of males into those of females, but little overlap within sexes or of female home ranges into those of males. This system differs from those of other carnivorous marsupials. Specifically, in two much larger species, P. tapoatafa and Dasyurus geoffroii (body mass: males 1300 g, females 900 g), home ranges of males overlap extensively with those of females and other males, whereas those of females are smaller, with core areas that are largely exclusive of unrelated females (Serena and Soderquist 1989; Soderquist 1995). In contrast, home ranges of A. stuartii overlap extensively both within and between the sexes. As noted previously, this species is highly gregarious and communal roosts can hold up to 15 individuals simultaneously, and over 40 animals during one winter (Lazenby-Cohen and Cockburn 1988, 1991).

Our study was carried out from 14 June to 11 July, a period that overlaps with the mating period of early July to mid August estimated for this population by Gilfillan (2001*a*). As a consequence, our observations of males and females basking near each other and sharing shelter sites are likely to be of mating pairs. Therefore, the pattern of spatial organisation we describe here may not be representative of the remainder of the year.

The need to have access to suitable basking sites appears to be an important factor in the spatial organisation of the species. Solitary animals or pairs occupied crevices and small caves in rocky gullies and slopes and used nearby rocks for basking as the sun re-warmed the landscape in the early to mid morning. During bouts of basking, an animal frequently moved its position in response to changes in the position of the sun on rocks (Geiser *et al.* 2002). Whether such basking behaviour and spatial organisation is typical of other rock-dwelling dasyurids and rodents presents itself as a worthwhile focus for future research.

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