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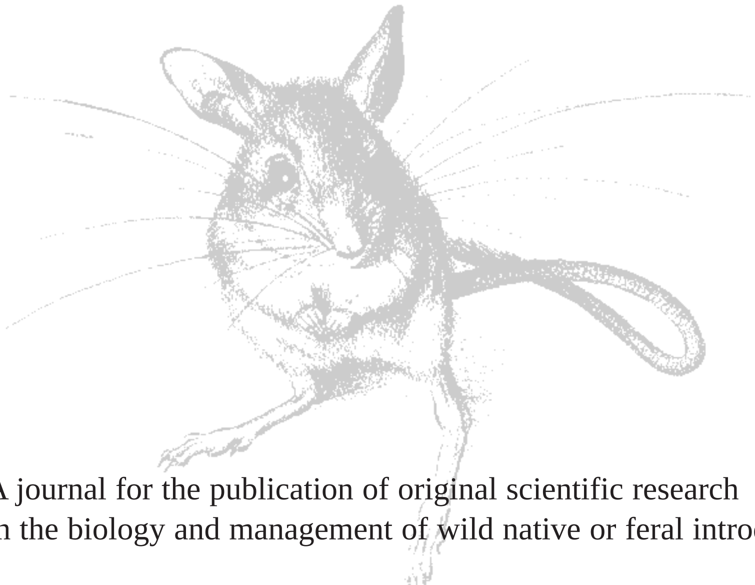

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Shelter selection and home range of echidnas, *Tachyglossus aculeatus*, in the highlands of south-east Queensland

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Abstract

We recorded physical attributes of sites used for daily shelter or as hibernacula by nine echidnas, *Tachyglossus aculeatus*, living on a sheep-grazing property in south-eastern Queensland. Home ranges were also determined. For daily shelter sites, echidnas most often used hollow logs and depressions under the roots of fallen trees. Daily shelters were found more often on north-facing slopes and usually provided >90% cover. Hibernation sites always provided 100% cover but, in contrast to daily sites, were distributed randomly in relation to the slope of the terrain. Rabbit burrows, which offer much better thermal buffering than hollow logs, were used most commonly as hibernacula. There were differences between individuals in the type of shelter they used and, moreover, echidnas did not use shelter sites in proportion to what was available, indicating that choice was being exercised. Re-use of sites occurred non-randomly, implying that echidnas can recognise previously used shelters and probably have a learned familiarity with their living area. Home ranges varied between 20.6 ha and 93.3 ha (mean = 49.8, s.d. = 25.4), overlapped with those of other echidnas and correlated positively with body weight.

Introduction

Shelter is an important resource for many animals. The use of a shelter may reduce both the energetic cost of thermoregulation (Smith *et al.* 1989) and the risk of predation (Marler and Hamilton 1966; Olsen 1973), especially when an animal is inactive during periods of rest or hibernation. The physical characteristics of a particular resting place will influence both the energy budget and predation risk of an animal (Weber 1985, cited in Weber 1989); the choice of a shelter may therefore have important implications for survival.

It has long been known that short-beaked echidnas, *Tachyglossus aculeatus* (Shaw), use shelters. Bennett (1860) and Semon (1899) reported that echidnas were nocturnal, retreating to shelters during the day. Augee *et al.* (1970, 1975) conducted detailed studies into activity patterns of echidnas and concluded that sheltering behaviour was correlated with ambient temperature rather than with light cycle. They found that in mild conditions echidnas appeared to limit their activity to an air temperature range of 18–32ºC. Abensperg-Traun and De Boer (1992), working in the Western Australian wheatbelt, determined that echidnas, although preferring temperatures of 16–20ºC, were active in the range of 9–32ºC. Thus, the use of shelters may be a component of thermoregulation. Another reason that echidnas shelter was revealed by Grigg *et al.* (1989, 1992*a*) in studies which showed that, in the Snowy Mountains of New South Wales, echidnas hibernate during winter and that shelters are used when doing so. Echidnas have also been shown to hibernate in Tasmania (Nicol and Andersen 1996) and in the Stanthorpe–Texas area of south-eastern Queensland (Grigg and Beard, unpublished data). This suggests that hibernation may be a common behaviour for echidnas living in temperate and cool-temperature Australia.

There has been only one detailed study of the shelter sites used by echidnas. Abensperg-Traun (1991) examined the home range and movements of, and shelter use by, ten adult and six juvenile echidnas in reserves in the Western Australian wheatbelt. He found that juveniles

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showed no clear preference in their choice of shelter, but that adults preferred subterranean shelters at all times, even though they occurred at low density. Abensperg-Traun (1991) did not examine the sheltering of hibernating animals, nor the extent to which shelters may be characterised by identifiable sets of physical attributes.

There have been four studies so far in which home ranges of echidnas have been determined. Augee *et al.* (1975) assessed home ranges of echidnas on Kangaroo Island, South Australia. The home ranges in this study were determined by calculating the maximum distance between two positions at which an animal had been located and taking this distance as the diameter of a circular home range. A mean home-range size of 65 ha (range = 26–102 ha, n = 5) was calculated. Griffiths *et al.* (1988) determined the home range diameters of three lactating echidnas, also on Kangaroo Island. Using the method of Augee *et al.* (1975) these were calculated to be 14, 28 and 50 ha. Abensperg-Traun (1991) found the average home ranges of adult echidnas in wheatbelt reserves in Western Australian to be 65 ha (range = 24–192 ha, n = 10), using a modified minimum-area method (Harvey and Barbour 1965). Augee *et al.* (1992) used a method of plotting all positions at which known individuals were located on a topographical map to calculate a mean home-range size of 45 ha (range = 24–76 ha, n = 11) for echidnas in the Snowy Mountains.

Although different methodologies have been used to determine them, there is a remarkable similarity between the average size of home ranges of echidnas from vastly different habitats. Studies from other habitats are required to determine the extent to which this generalisation applies.

In the present study, we aimed to describe the physical characteristics of shelter sites used by echidnas in sheep-grazing country in south-east Queensland, to determine whether there was any evidence that echidnas showed preference for certain types of shelters and to determine the home ranges of the echidnas.

Materials and Methods

Study site

The study site was located on the sheep properties of ‘Reatta’ and ‘Langlands’ (28°43´S, 151°29´E), approximately 50 km west of Stanthorpe, Queensland. The annual rainfall for the district is 767 mm, with average daily temperature ranges of 15.5–27°C in summer and 0.7–14.4°C in winter (Department of Administrative Services 1988).

Three major habitat types were represented within the study site. Most of the area was undulating, cleared sheep paddocks, with remnant stands of *Eucalyptus sideroxylon* (Mugga, Red Iron Bark) and numerous *Acacia* species. Part of the site consisted of steeply sloping gullies that had been partly cleared of their thick scrub. A third area within the site consisted of uncleared, steeply sloping gullies. The substrate throughout the study site consisted of compacted soil and rocky ground. Hollow logs and rabbit burrows were common in all habitats.

Study animals

Nine animals were studied, seven males and two females, numbered according to a larger series in an on-going study by Grigg and Beard. Seven echidnas were found prior to the commencement of the study and two were found during it. The capture weights of the animals ranged from 1.4 kg to 4.1 kg (Table 1). One individual (#68) was found to lack eyes and had lost its right hind leg. Temperature-sensitive radio-transmitters (Sirtrack N.Z. Pty Ltd), approximately 55 x 25 mm and weighing 30–35 gm, were implanted into the peritoneal cavity of each echidna under a protocol approved by the University of Queensland’s Animal Experimentation and Ethics Committee. Details of the surgical techniques have been given by Grigg *et al*. (1989, 1990).

Location and description of shelter sites used by echidnas

Animals were located by using a VHF receiver and directional antenna (Telonics TR-2E, 150/154MHz). An average reception range of 1 km was obtained, increasing to 2–3 km with a clear line of sight. Reception range decreased to less than 500 m in heavily wooded country and within gullies.

Table 1. Echidna number and capture weights

Echidna No.	Sex	Capture weight (kg)
56	M	3.9
63	M	4.1
64	M	4.0
68	F	2.7
69	F	2.9
70	M	2.1
72	M	2.5
77	M	1.4
81	M	3.4

Echidnas were located on foot once per day, at times when previous experience dictated that they were likely to be in shelter rather than out and about, i.e. by night during winter and by day during summer. Additionally, body temperature (which varies markedly on a daily cycle: Grigg *et al* 1989, 1992*a*) and variability of signal strength (Grigg *et al.* 1992*b*) were a reasonable guide to whether an individual was active or at rest. Sheltered echidnas were often well hidden, but could be located to within 0.5 m using the radio-tracking equipment and did not need to be disturbed in order to get an accurate assessment of the shelter in use and the relevant entrance.

Whenever a sheltered echidna was located, the type of shelter, the percentage of the echidna covered by the shelter, the azimuth faced by the entrance of the shelter and the azimuth of the slope on which the shelter was located were recorded. The shelter was marked with a strip of surveyor's flagging tape on which was written echidna number and the date of location. No data were recorded if there was any suspicion that the animal may have been active and had taken shelter only as the investigator approached. It was known already from casual observations in the area that echidnas sometimes used the same shelter on subsequent days. To determine whether an echidna was remaining continuously for several days or leaving and then re-entering, perhaps on a daily basis, a row of small sticks was placed across the entrance (or entrances) of the shelter. An echidna was considered to have remained in a shelter continuously if the animal was found to be in the same shelter on the following day with the sticks undisturbed. Sometimes sheltered echidnas remained partly exposed. When this occurred, the percentage of the echidna covered by the shelter was estimated by standing directly over the echidna and viewing downwards. When no part of an echidna could be seen, percentage cover was recorded as 100%. The location of each shelter site was determined to within 25 m using a Global Positioning Receiver (Magellan GPS NAV 1000, model 11000). The azimuth faced by the entrance of the shelter and the aspect of the slope on which the shelter was located were determined using a Ranger pocket compass.

Density and distribution of potential shelter sites

As the study progressed and experience grew, it became possible to identify and classify potential shelter sites. A potential shelter site was defined as any type of structure that echidnas were known to use as a shelter which could just accommodate an average-sized adult and provide at least 90% cover.

Line transects were walked within each echidna's home range to determine the density and distribution of potential shelters. The transects were aligned parallel to the long axis of the home range and were spaced at 20-m intervals across its width. Each transect was 2 m wide and was as long as the home range allowed.

Comparison of the thermal buffering properties of hollow logs and rabbit burrows

The probable use of shelters to avoid high daytime temperatures during summer and, perhaps, low temperatures in winter dictated the need to determine the thermal buffering properties of the most common shelter types, hollow logs and rabbit burrows. A site was chosen at which a log shelter and a burrow shelter, each known to have been used by an echidna, were in close proximity. Calibrated temperature probes connected to a data-taker were placed 2 m inside the burrow, 2 m inside the log and in a position where shaded ambient temperature could be recorded. Measurements of temperature at these positions were recorded for a few weeks during February. Separate data-loggers were placed in similar situations in July (winter) and again temperature data was recorded for a few weeks.

Re-use of shelters

Casual observations had suggested that echidnas may commonly re-use the same shelter, either on sequential nights or with breaks in between. An echidna was defined to be re-using a shelter when it was found within a shelter it had used on a previous, independent occasion, either as a daily shelter site or a hibernaculum. Remaining within a shelter for consecutive days was not considered re-use.

The percentage re-use of shelters was calculated for each echidna by expressing the total number of times an echidna re-used shelters as a percentage of the total number of independent observations of sheltering.

Home range

All independent locations of echidnas were used to determine home ranges. Independent locations were defined as:

(1) all locations of echidnas not in shelters, and

(2) all locations of echidnas in a shelter, except that occupation of the same shelter for more than one consecutive day was counted only once.

The minimum number of observations required to determine home range was set at 15 (Augee *et al.* 1992). By this criterion, sufficient data were available for the calculation of home ranges and their boundaries for seven individuals. Sizes of home ranges and overlaps between them were calculated using the SEAS computer software package. The minimum convex polygon method (Mohr 1947) was used to determine the sizes of home ranges, as scatter plots of the echidnas' positions showed that locations were distributed evenly throughout the home ranges. Home-range boundaries were plotted onto a line map of the study site using the McPAAL computer software package.

Statistical analysis

A one-way ANOVA was used to determine whether the mean values of the percentage cover of the daily shelter sites differed between echidnas. The angular mean and angular variance for the shelter aspect for each echidna were calculated using circular statistics (Batschelet 1981). Mean values of percentage cover of all daily shelter sites were compared with the mean values of the percentage cover of all hibernacula using an unbalanced Student's t-test. Data describing the type of shelter could be pooled into one of the following categories: 'Hollow log', 'Under ground under log', 'Rabbit burrow' and 'Other'. Comparisons between relative use of each of these categories of shelter type by each echidna were made using Fisher's exact test. The possibility that the number of shelters found to be re-used may be correlated with either the total number of observations or the size of the home range was examined by calculating Spearman's rank correlation coefficients for each. Chi-squared tests were used to determine whether the number of shelters located within each transect differed from the number of shelters that would be expected if the shelters were distributed evenly throughout the entire study site, and whether the distribution of shelter types actually used by each echidna differed from the distribution of shelters available. For this last comparison, insufficient data were available for echidnas #56, #64 and #81. The possibility that the size of home range might correlate with body size was examined by calculating Spearman's rank correlation coefficient.

Results

In total, 69 days were spent in the field and 221 daily shelter sites and 13 hibernacula were examined.

Shelters used by echidnas

Echidnas were found to use a variety of structures as daily shelter sites and/or hibernacula. Overall, hollow logs were used most frequently (37.18%), followed by rabbit burrows (23.08%) and depressions in the ground under fallen trees (20.94%). Echidnas were also found to shelter buried in leaf litter (7.69%), within thick patches of undergrowth (2.56%), in hollow tree stumps (2.56%), under large grass tussocks (2.14%), in cavities amongst the roots of a live tree (1.71%) and in rock crevices (1.71%). Suitable shelters of these types were found to be evenly distributed throughout the study site (Chi-squared, $P > 0.05$) (Table 2)

Table 2. Percentage occurrence of each type of shelter and the density of shelters within each echidna's home range

Log, hollow log; RB, rabbit burrow; DUFT, depression under fallen tree; LL, leaf litter; UG, undergrowth; TS, tree stump; GT, grass tussock; TR, tree root; RC, rock crevice

Echidna No.	Log	RB	DUFT	LL	UG	TS	GT	TR	RC	No. ha^{-1}
56	34	2	55	0	4	4	0	1	0	45
63	23	6	54	0	11	0	0	6	0	29
64	48	12	24	0	16	0	0	0	0	41
68	55	10	30	0	0	0	0	0	0	45
69	34	2	55	0	4	0	0	1	0	45
70	27	3	55	0	6	2	0	2	0	39
72	34	2	55	0	4	0	0	1	0	45
77	36	0	55	0	5	0	0	5	0	77
81	55	10	30	0	0	0	0	0	0	45

The distribution of shelter types used by the six echidnas for which sufficient data were available was found to be independent of the distribution of available shelters (Chi squared, $P < 0.02$). This means that individual echidnas show a pattern of shelter use which is not simply in proportion to what is available, indicating an active choice of shelter.

The frequencies of use of the various structures as both daily shelter sites and as hibernacula by each echidna are shown in Table 3. There are significant differences between individuals (Fisher's exact test, $P < 0.02$) in categories used for daily shelter. This implies that the echidnas are exhibiting individual preferences for daily shelter sites.

More than 60% of hibernacula observed were subterranean, which is far higher than the proportion of availability of this type of shelter. This suggests that echidnas are exhibiting a general preference for underground shelters during winter inactivity.

Re-use of shelters

Re-use of shelters was quite variable between individuals, from 0 to 28%, with six of the nine animals showing more than 10% re-use (Table 4). Re-use did not correlate with the number of observations for any echidna ($P = 0.47$) or the size of the home range ($P = 0.53$).

Physical parameters of shelters

The ability to provide almost complete cover appears to be an important attribute of a site chosen as a shelter, either for daily rest or for hibernation. Daily shelters afforded a mean percentage of cover greater than 90% and there were no significant differences between individuals ($P = 0.113$). No significant difference was found between the mean percentage cover afforded by daily shelter sites and the mean percentage cover afforded by hibernacula ($P = 0.431$).

The azimuth faced by the entrance of daily shelter sites appears to be random (Fig. 1*a*), whereas the analysis of aspect (Fig. 2*a*) showed that daily shelter sites occur more frequently on northerly facing slopes (angular mean $\phi = 359°$; angular variance $s = 60°$).

The azimuth faced by the entrance of shelter sites used as hibernacula also appears to be random (Fig. 1*b*), as does the distribution of the aspect of all shelter sites used as hibernacula (Fig. 2*b*).

Table 3. Percentage of the total number of observations that an echidna was found in a type of shelter for both daily shelter sites and hibernacula

Log, hollow log; RB, rabbit burrow; DUFT, depression under fallen tree; LL, leaf litter; UG, undergrowth; TS, tree stump; GT, grass tussock; TR, tree root; RC, rock crevice; n/a, not available

Echidna	Log		RB		DUFT		LL		UG		TS		GT		TR		RC		No. Obs	
No.	Daily	Hib	Daily	Hib	Daily	Hib	Daily	Hib	Daily	Hib	Daily	Hib	Daily	Hib	Daily	Hib	Daily	Hib	Daily	Hib
56	16.7	n/a	50	n/a	16.7	n/a	0	n/a	0	n/a	16.7	n/a	0	n/a	0	n/a	0	n/a	6	0
63	47.5	n/a	5	n/a	25	n/a	15	n/a	0	n/a	2.5	n/a	5	n/a	0	n/a	0	n/a	40	0
64	28.6	n/a	28.6	n/a	28.6	n/a	14.3	n/a	0	n/a	0	n/a	0	n/a	0	n/a	0	n/a	7	0
68	9.1	0	48.5	66.7	15.2	0	0	0	15.2	0	0	33.3	0	0	3	0	9.1	0	33	3
69	59.4	0	25	100	12.5	0	0	0	0	0	3.1	0	0	0	0	0	0	0	32	4
70	30	0	7.5	0	35	100	15	0	5	0	2.5	0	0	0	5	0	0	0	40	2
72	44.4	n/a	0	n/a	25.9	n/a	14.8	n/a	0	n/a	3.7	n/a	11.1	n/a	0	n/a	0	n/a	27	0
77	52.6	33.3	36.8	33.3	5.3	33.3	5.3	0	0	0	0	0	0	0	0	0	0	0	19	3
81	47.1	0	35.3	0	11.8	0	0	0	0	0	0	0	0	0	5.9	0	0	100	17	1

Table 4. Percentage of the total number of observations that an echidna re-used shelter sites.

Echidna No.	56	63	64	68	69	70	72	77	81
Percentage re-use	0	2.5	14.3	18.2	28.1	2.5	11.1	21.11	11.8

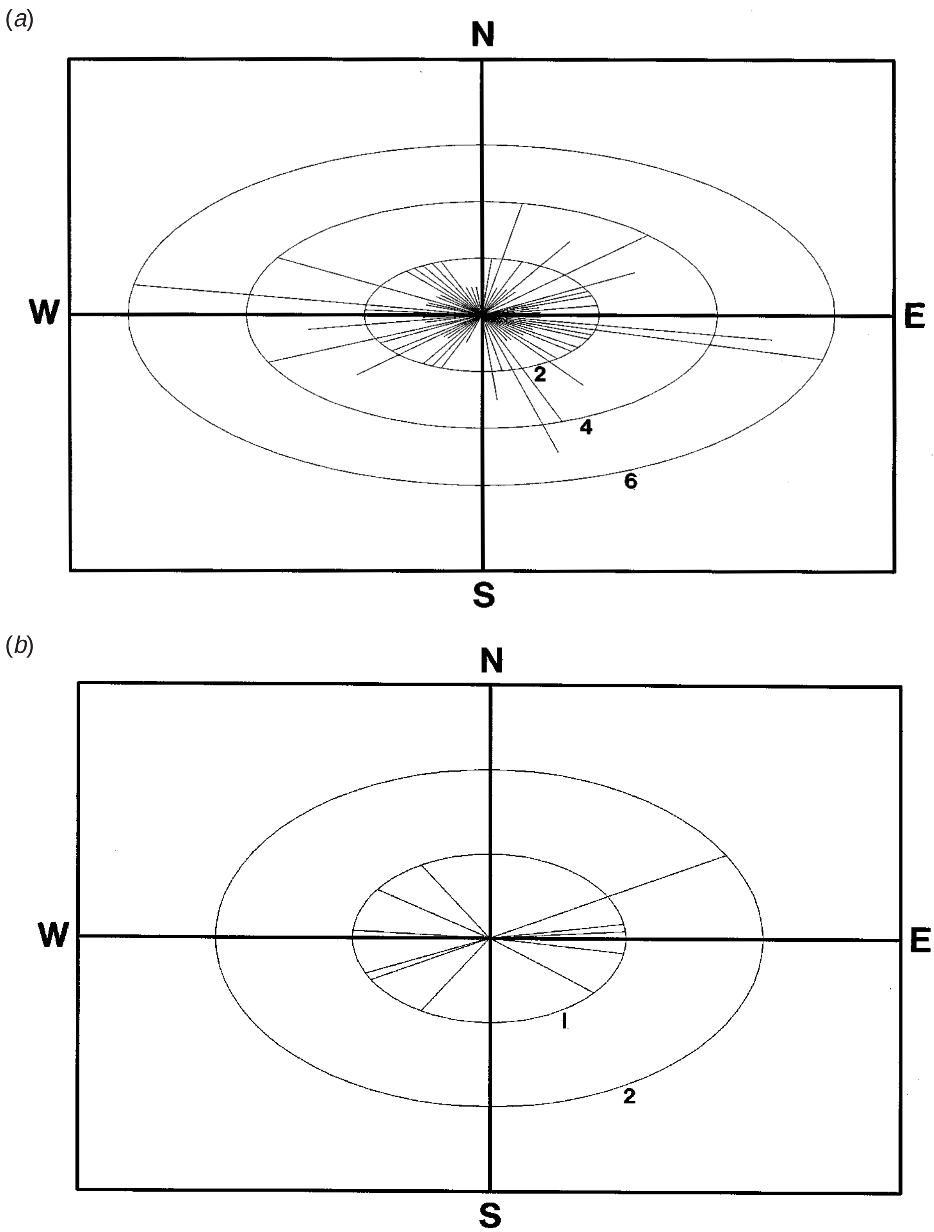

Fig. 1. Distribution of the azimuth faced by (a) the entrances to daily shelter sites, and (b) the entrances to hibernation sites.

Hollow logs and rabbit burrows as thermal shelters

Log temperature closely followed that of ambient, but was 1–2ºC cooler during the hottest part of the day and slightly warmer during the night in summer. In winter the thermal buffering of the log was slightly more marked, especially at night. In comparison, the temperatures inside the rabbit burrow remained reasonably constant within a season and were always less than daily maxima and greater than daily minima during the warmer months. In winter the rabbit burrow

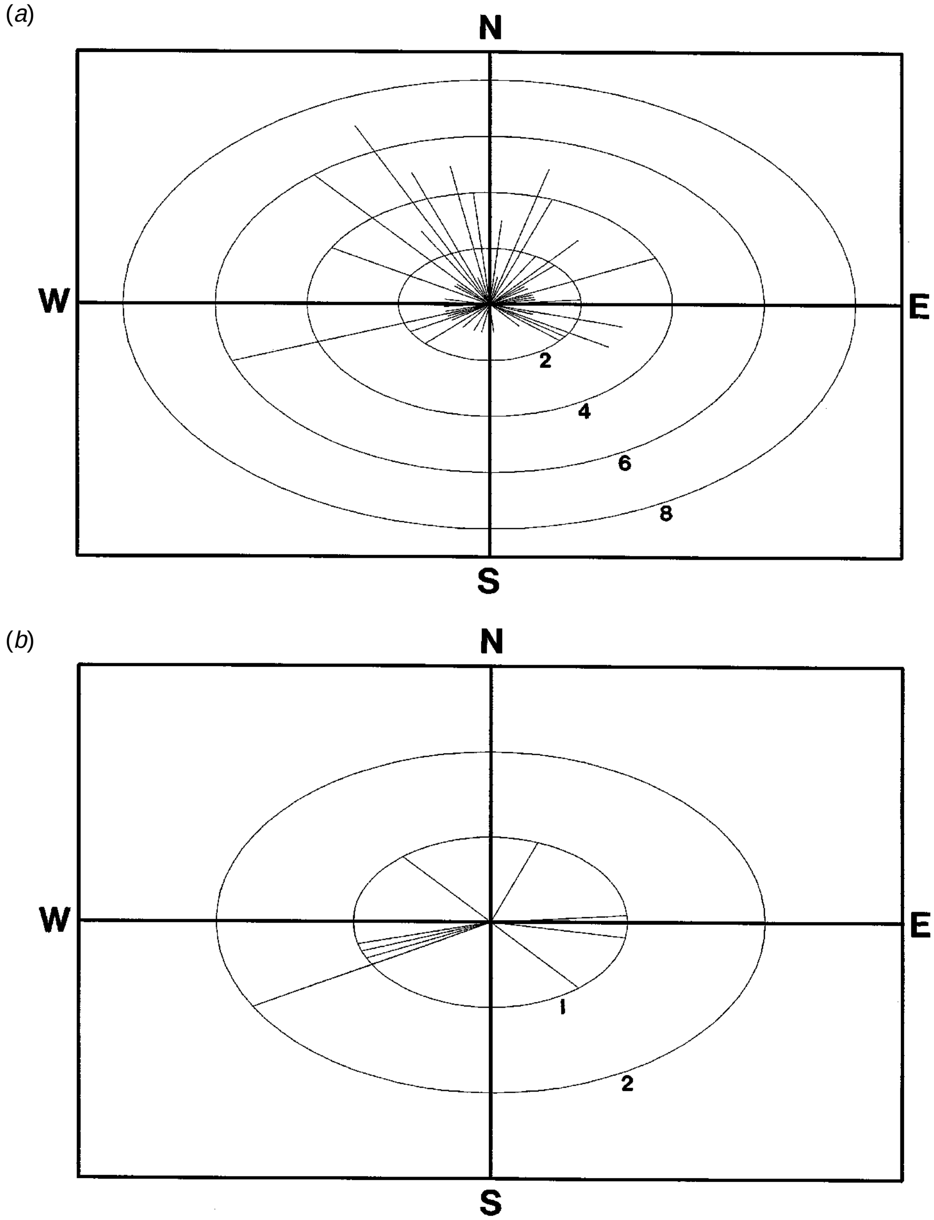

Fig. 2. Distribution of the aspect of slopes on which (a) the daily shelter sites and (b) the hibernation sites occurred.

was again more thermally stable than the log (Fig. 3) and actually remained warmer on cold days. It is noteworthy that daily temperatures in both logs and burrows were markedly different between seasons.

Home range

Home ranges varied between 20.6 and 93.3 ha (mean = 49.9 ha, n = 7) (Table 5), increasing with body weight (Fig. 4). The correlation coefficient of 0.714 was close to being statistically

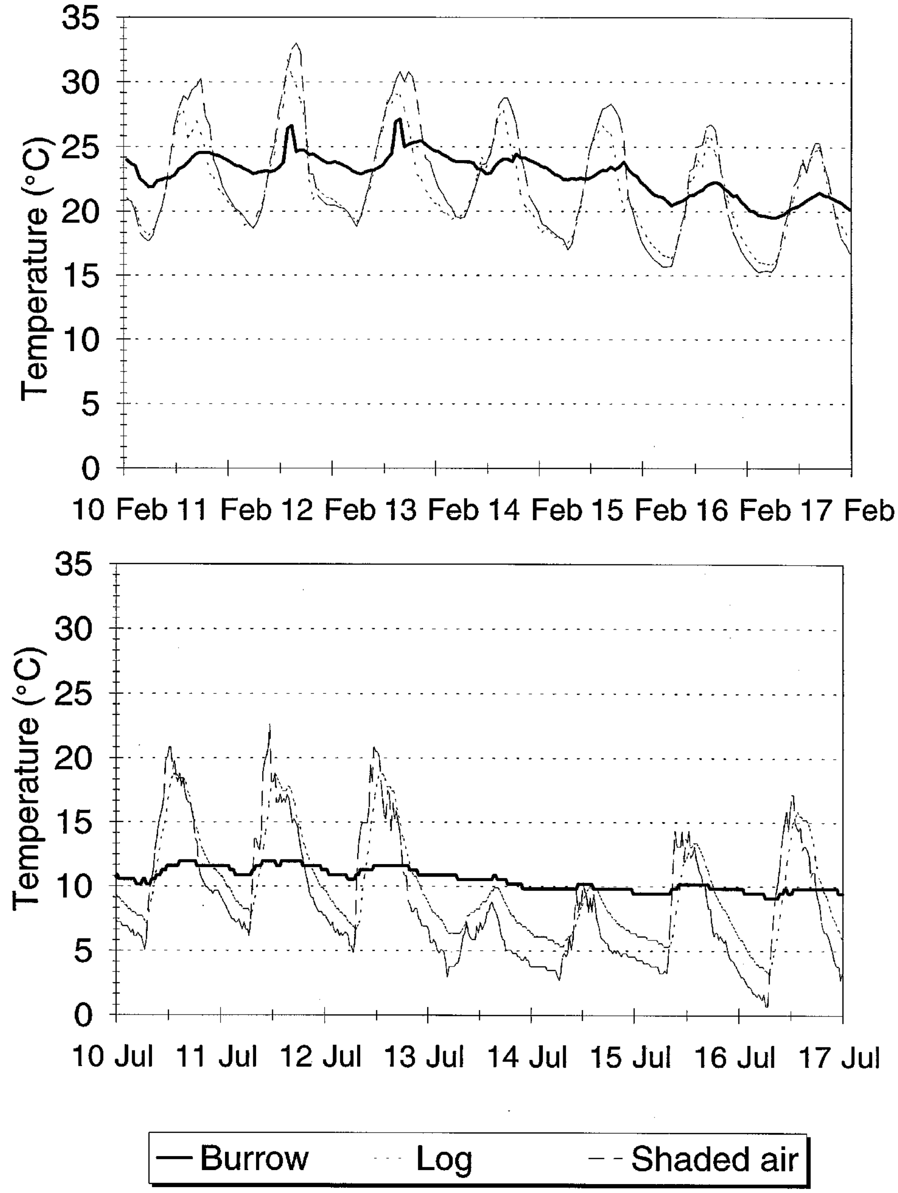

Fig. 3. Temperature profiles for burrow, log and shaded air over a typical seven-day period in summer and winter at the study site.

significant (P = 0.0545) when all echidnas were included in the calculations, and clearly significant (P = 0.033) when #68 was excluded (coefficient 0.866). Excluding #68 seems reasonable because a blind, three-legged echidna may have a reduced home range relative to others.

The percentage overlap between home ranges was found to vary between zero and 84.2% (mean = 24.04%, s.d. = 27%) (Table 6). The size and boundary of each echidna's home range is presented in Fig. 5.

Table 5. Home range size of echidnas

Echidna No.	63	68	69	70	72	77	81
Home range size (ha)	71.3	20.6	63.8	46.9	26.9	25.9	93.3

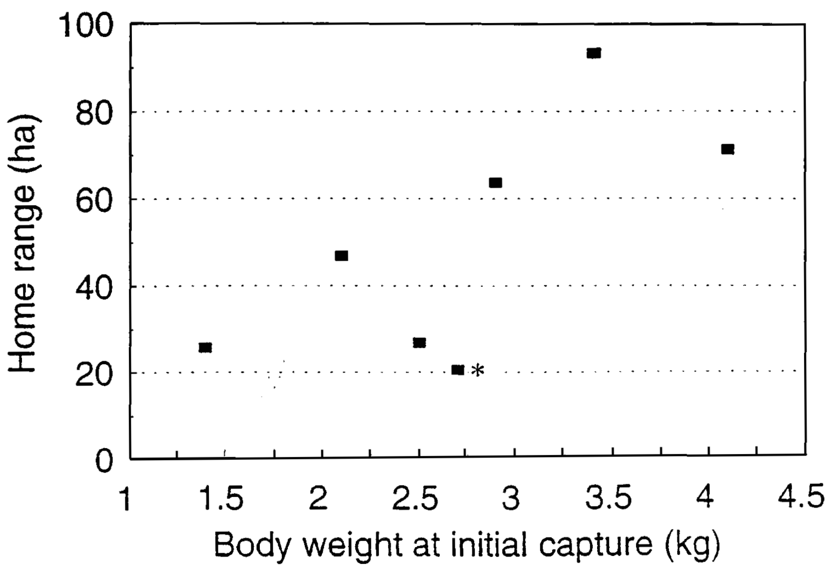

Fig. 4. Relationship between initial capture weights of study animals and the size of their home range. Echidna #68 identified with an asterisk.

Table 6. Percentage overlap of echidna home ranges

Echidna No.	Echidna No.						
	63	68	89	70	72	77	81
63	—	0	33.3	48.8	77.4	42.6	0
68	0	—	0	0	0	0	6.3
69	29.9	0	—	84.2	70.1	68.2	0
70	32.1	0	61.9	—	65.9	47.7	0
72	29.2	0	29.6	37.8	—	62.9	0
77	15.4	0	27.5	26.2	60.3	—	0
81	0	28.5	0	0	0	0	—

Discussion

The echidnas observed in this study did not utilise shelter at random. This indicates that the echidnas must have actively selected shelter sites. Active selection of a shelter site may require an echidna to travel further than random utilisation, thereby using more energy, so a benefit from selecting a site with particular characteristics is implied.

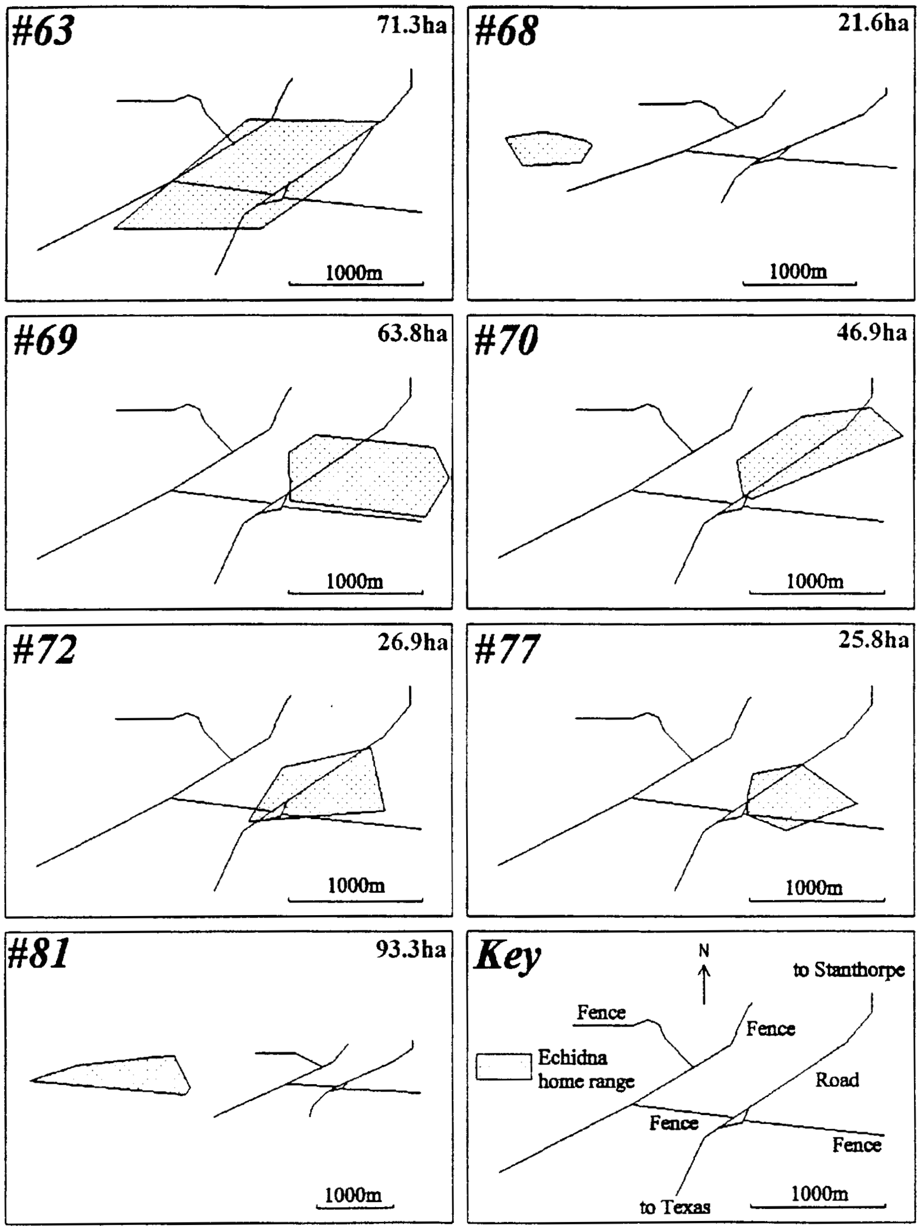

Fig. 5. Schematic showing relative sizes, shapes and positions of the home ranges of echidnas in this study.

Avoidance of predation is often quoted as a reason for animals sheltering (Marler and Hamilton 1966; Olsen 1973) and could explain the overall preference shown for shelters with a high percentage cover. Dingos are thought to be the only animal able to actively prey upon adult echidnas (Griffiths 1989) and are considered rare on the sheep-grazing properties where this study was conducted. If avoidance of predation is a criterion for shelter selection, it may be a behaviour that evolved when predation pressure was higher than that experienced by the echidnas in this study.

Sheltering is likely to be an important means of thermoregulation for echidnas. Echidnas are said to be not good thermoregulators at high ambient temperatures. They do not sweat or pant (Augee 1976) and what little evaporative cooling they have is insufficient to prevent lethal apoplexy (Griffiths 1989). They must therefore avoid high ambient temperatures by retreating to shelters (Griffiths 1989). In cold conditions, echidnas are able to stay active if shelter is available to reduce thermoregulatory costs (Smith *et al.* 1989) or they may hibernate (Grigg *et al.* 1989, 1992). Smith *et al.* (1989) suggested that hibernating animals may rely on shelters to regulate their body temperatures above a minimum level. The choice of a thermally appropriate shelter site would appear to offer a significant benefit for echidnas in both hot and cold climates.

The need for thermally appropriate shelters could explain the overall preference shown for shelters with a high percentage cover as such shelters would provide greater insulation. It may also explain the apparent preference for daily shelter sites on north-facing slopes because these slopes in the southern hemisphere are warmer in winter and cooler in summer.

A comparison of the internal temperatures of different shelter types shows that the thermal characteristics of a shelter are determined largely by the type of structure of the shelter. Subterranean shelter sites, such as rabbit burrows, offer a much more stable thermal environment than shelters above ground, such as hollow logs. Subterranean shelter sites probably confer an energetic advantage as they buffer against temperature extremes (Reichman and Smith 1990; Fig. 3.)

The echidnas in this study, unlike those in the Western Australian study by Abensperg-Traun, showed no preference for subterranean shelters during the warmer months. This is perhaps surprising given the minimal thermal buffering we measured in hollow logs (the type of shelter most commonly used as a daily retreat) and the echidna's reputed poor ability to cope with high temperatures. The answer may involve conductive heat transfer from the relatively hairless underbelly of the echidna to a substrate within the log (often earth or decomposed, friable material) which is cooler than the air temperature in the log, as measured by our suspended probe. Alternatively, echidnas may not be such poor thermoregulators in the heat as currently believed. Further study is required. Echidnas in this study did show a preference for subterranean shelters when hibernating. Subterranean shelters occur in the study site at a much lower density than other types of shelter. Presumably, more energy would be required to seek out a subterranean shelter, and during their active season echidnas balance the benefits gained from using a subterranean shelter against the energy expended in travelling to one. However, when hibernating, the balance may be more in favour of a subterranean shelter presumably because of its thermal buffering properties but also, perhaps, because of the security afforded by the rocky, compacted soil, because of predation considerations when the animal is at its most vulnerable. Augee *et al.* (1992) noted that hibernacula always 'provided secure shelter' while this was not always true of daily retreats.

One way to minimise the energy expended in seeking appropriate shelter sites would be to re-use shelters that have previously been found to be appropriate (Weber 1989; Cowan 1989). As the number of incidences of shelter re-use did not correlate with either the number of observations or the size of an animal's home range, it was concluded that it was not random. This implies that echidnas are able to recognise previously used shelters and probably have a learned familiarity with their home range.

An interesting conclusion that can be drawn serendipitously, because echidna #68 was blind and exhibited sheltering behaviour similar to that of the other echidnas studied, is that sheltering behaviour in echidnas is not heavily dependent on visual information.

Also worth noting is the fact that no animals in this study created their own shelter even though they are well equipped for digging. Again, presumably, the benefits gained would not justify the energy expenditure. With the exception of nursery burrows this was also observed by Augee *et al.* (1992)

Home Range

The echidnas observed in this study were found to have overlapping home ranges of similar sizes to those reported for the echidnas studied by Abensperg-Traun (1991) and Augee *et al.* (1992) in vastly different habitats. This suggests that echidnas do not exhibit any territorial behaviour and are not limited by resources.

The size of the home range increased with increasing body weight. This has not been noted previously in echidnas, although a positive correlation might be expected in any species because body weight determines energy requirements which, in turn, determine the food requirement (McNab 1963; Harestad and Bunnell 1979).

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