HOME RANGE OF ECHIDNAS IN THE SNOWY MOUNTAINS

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³John Raison died in March 1991. His contribution to this and an amazing variety of scientific studies will long be remembered by his many colleagues.

ABSTRACT

Radio tracked echidnas in the Snowy Mountains of New South Wales had a mean home range \pm SD of 42 \pm 20 ha, n=11, determined by direct plotting of multiple data points. Using this large data base, various statistical techniques for the estimation of home range were compared. Within the home range there were no fixed nest sites and a variety of site types were used as retreats. Sites used as hibernacula provided more secure shelter and burrows were only constructed for use as maternity sites. Several animals shared overlapping home ranges. All but one echidna remained within the observed home range throughout the course of the study.

Augee, M.L., Beard, L.A., Grigg, G.C. and Raison, J.K. (1992). Home range of echidnas in the Snowy Mountains. Pp. 225-231 in 'Platypus and echidnas' (M.L. Augee, ed.). The Royal Zoological Society of NSW, Sydney.

INTRODUCTION

In the first published radio tracking study of echidnas (Augee et al. 1975), home range was reported as the greatest distance between two positions of an individual animal over the period of the study. Taking this distance as the diameter of a circle, the mean home range from that study was 65 ha (range 26-102 ha). The same calculations applied to the data of Griffiths et al. (1988), obtained by radio tracking three lactating echidnas, give home range areas of 14, 28 and 50 ha. A much larger area (113 ha) can be calculated from data reported by Abensperg-Traun (1989) for one lactating female in the wheatbelt of Western Australia. However, this seems to have been an atypical value, since the same author (Abensperg-Traun 1991) found a mean home range of 65 ha (range 24-192 ha) for ten adult echidnas in the same habitat. Therefore it appears that the home range of echidnas is very similar in different habitats, although there is a great deal of variation between individuals within each of the above studies. The present study was made in a very different habitat, above the snowline and down to 1,000 m altitude in the Snowy Mountains. In the present study we also examine carefully the techniques of home range determination, since the apparent agreement between the results of Augee et al. (1975) and Abensperg-Traun (1991) is surprising given the difference in techniques for calculating home range. The maximum diameter technique used by Augee et al. (1975) should give a much larger result

than the much more sophisticated technique (Harvey and Barbour 1965) used by Abensperg-Traun (1991).

METHODS

Study area

The study was carried out in Kosciusko National Park. Two echidnas (E10 and E12) were above the snowline in subalpine habitat on Prussian Plain (1815 m). Two (E15 and E23) were located in the vicinity of Rennix Gap (1560 m) and Island Bend (1370 m), just below the snowline, and moved between subalpine habitat and dry sclerophyll forest. The remaining six echidnas were located in dry sclerophyll forest on the shore of Lake Jindabyne (920 m) at Waste Point.

Telemetry

The above echidnas were part of a larger study into temperature regulation and hibernation (Grigg et al. 1989). Therefore calibrated temperature-sensitive radio transmitters (J. Stuart Enterprises or Austec Electronics) had been implanted in their peritoneal cavities. Details of the telemetry procedures and surgical techniques are given in Grigg et al. (1990). The range of these transmitters was typically one kilometer, increasing to as much as three kilometers with clear line of sight and decreasing to 500 m or less in heavily wooded areas. Tracking was

achieved using Telonics directional antennas and VHF receivers. The exact position of the animals was usually determined in the morning or evening when the animals were in the retreats they had used during their inactive period. Less precise information about location was obtained by the use of fixed receiving stations (Grigg et al. 1990) which monitored some animals, by recording radio signals at predetermined intervals, for long periods when we were absent from the study area. Because these stations used an omni-directional antenna they did not supply data points for home range determinations, but they did provide many days of evidence that echidnas being recorded were close by and within their home range.

Direct determination of home range

Home ranges were determined directly in three steps:

- 1. All positions determined for an individual were plotted on a topographical map.
- 2. All positions were enclosed in a smooth outline, taking into account features which appeared to be consistent boundaries.
- 3. The area of the resulting home range was determined using a plotting tablet attached to a desktop computer. We used a Gentizer GT2121B tablet attached to an IBM 386 and driven by Design CAD 2-D software, but there are other products that will do the same job.

Indirect determination of home range

There are many techniques used to estimate home range from a limited number of data points. Abensperg-Traun (1991) makes an important distinction between data points that represent the position of an inactive echidna (which we have termed 'retreats') and those that represent sightings of active echidnas. Anderson (1982), whose technique is used below, stresses the importance of independent data points. Consecutive positions of a moving echidna, determined as part of behavioural observations of foraging for example, are not independent from themselves nor from the possible influence of the presence of the observer. Therefore in the statistical analyses used in this paper only data points which represent a retreat site or the position of an inactive echidna are used, and all of these positions were actually sighted. For animals that were monitored continuously during hibernation large numbers of data points could be included for the site. However, these data do not seem to meet Anderson's requirement for independence as their accumulated effect in his statistical analysis is to minimize all other points, causing gross underestimation of true home range. Therefore in the indirect analyses a retreat site is used as only one data point during a continuous period of occupation.

The circle method (or maximum diameter technique) is the easiest technique to use to estimate home range and gives the greatest overestimate. In this procedure, the two data points furthest from each other are joined by a straight line. That line is taken as the diameter of a circle whose area represents the home range. This procedure is rarely used now, but it was used in the first report of radio tracking studies of echidnas (Augee et al. 1972).

The convex polygon method is widely used. It involves connecting the outermost data points so that the edges of the resulting polygon never indent and determining the area enclosed. There are a number of computer programs available to achieve this. In this study, the convex polygon was drawn and the area calculated using a program created by John Raison based on the equations of Jennrich and Turner (1969).

The minimum polygon method attempts to reduce the influence on the calculated home range of the outermost, and presumably infrequent, data points. In this case the outermost data points are joined to form a polygon but there is no requirement that the polygon be convex. Again, this home range estimate was obtained using a computer program created by John Raison based on equations derived by Jennrich and Turner (1969). A commonly used "share-ware" program called McPAAL (Stuwe & Blohowiak 1988) is based on the same concept and gives essentially the same result although much more difficult to couple with an X/Y plotter.

The ellipse method is a covariance matrix method developed by Jennrich and Turner (1969). This statistical method assumes a normal distribution of activity around a focal point and calculates home range as the area of an ellipse which accounts for 95% of an animal's utilization of its habitat around that focal point. The equations of Jennrich and Turner (1969) are the basis of a computer program created by John Raison for this study and are also included in the McPAAL package (Stuwe & Blohowiak 1988). Both programs give the same result.

Nonparametric techniques are necessary when there is no reason to assume a normal distribution of activity around a focal point. From the direct plots described above, it was clear that echidna activity, in this study at least, is not distributed normally. Very often retreat sites would be near the edge of the home range and there were no fixed 'nest' sites except in the case of mothers with young. Analysis of echidna home range therefore requires a nonparametric technique, the most widely used being that of Anderson (1982). There have been a number of refinements to the technique subsequently, and we used a computer program written by Anderson available as 'share-ware'. This program determines a 'contour', a line enclosing the area corresponding to the selected percentage of the animal's space utilization. For mammals, 95% is usually selected, and Anderson (1982) recommends that the 50% contour area be used for comparative studies. Any of a number of commercially

available geographical plotting programs can be used to print out the contour to the appropriate scale to allow it to be superimposed on a topographical or other map.

RESULTS

Home range (direct)

The home range area of echidnas in the Snowy Mountains is 42 \pm 20 (SD) ha as obtained by direct plotting of all data points on a topographical map (Table 1, Figs. 1 & 2). Individual home ranges take into account natural boundaries, such as Lake Jindabyne and the Thredbo and Snowy Rivers. However it is obvious from individual maps based on hundreds of data points that other features were recognized as boundaries. The home range of E11 (Fig. 1B) was clearly bounded by a steep gully on the NW and by Summit Road, a busy paved highway linking Jindabyne and Perisher, on the west. E11 frequently spent its inactive period in loose soil and road rubble at the base of Summit Road on the east side, but in the four years this animal was tracked, it was found on the west side of Summit Road only once; about 5 m from a culvert that ran under the road. A culvert was the link for E13

(Fig. 1A) between two halves of his home range which were on opposite sides of Summit Road. This animal was observed to use a culvert under a high road fill and sometimes made the 'crossing' twice a day.

Home range (determined by indirect methods)

Taking the home ranges calculated by the direct method as the basis for comparison, those calculated by the circle and ellipse methods give a gross overestimate. The convex polygon method gives results much closer to the direct method but still twice as large. On the other hand the mean obtained by the minimum polygon method is less than half that determined directly.

Results of analyses by use of a computer program based on the nonparametric technique of Anderson (1982) are also given in Table 1. The results are given for the area inside the 95% contour (which encloses the calculated area in which 95% of the animal's activity occurs) and the 50% contour. Anderson (1982) suggested that the 50% contour area would give the best estimation for most cases, but this is clearly not the case with echidnas. As shown in Table 1, the area of the 50% contour is much smaller than that determined by the direct method. The

Table 1. Home ranges (ha) of echidnas in the Snowy Mountains determined by different techniques. *n refers to the number of data points used in the indirect analyses in columns 6-11. Weights given are the maximum and minimum measured during the study.

Animal	Sex	Wts (kg)	Direct	n*	Anderson analysis		Convex	Minimum	Circle	Ellipse
					95%	50%	polygon	polygon		
E10	F	2.95-3.55	40	23	53	19	63	3.7	171	138
E11	M	4.20-5.65	68	91	61	19	72	7.2	126	104
E12	F	3.35-3.55	36	30	45	17	37	11	115	90
E13	M	3.80-4.70	29	27	110	39	79	5.7	317	167
E15a	M	2.90-3.65	32	11	47	19	111	100	574	519
E15b			74	22	100	32	150	59	288	269
E21	M	2.75-5.15	24	48	26	8	26	4.6	59	39
E23	M	3.90-4.95	76	17	95	36	223	4.9	671	418
E25	F	3.90-5.90	24	49	20	6	46	15	60	61
E31	M	3.90-5.70	33	27	57	18	116	6.8	263	264
E32	F	4.80-6.95	28	40	23	8	27	3.9	47	47
Mean			42		58	20	86	20	245	192
SD			20		31	11	60	31	210	158

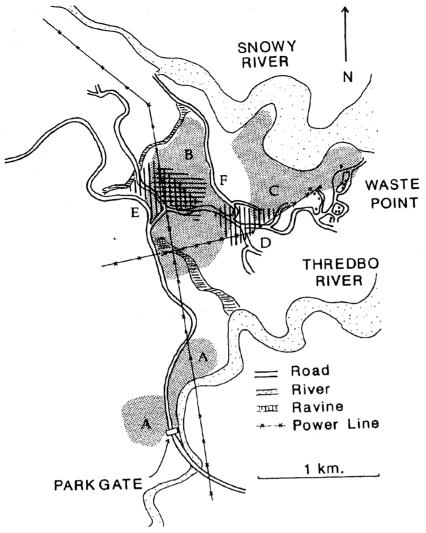


Figure 1. Home ranges of six echidnas determined by direct plotting. Dotted areas are E13 (A), E11 (B) and E31 (C). Vertical lines are E25 (D) and E21 (E). The horizontal lines are E32 (F).

PERISHER

PRUSSIAN
PLAIN
PLAIN

Figure 2. Home ranges of E10 (dots) and E12 (vertical lines)

area based on the 95% contour gives a mean area (58 ha) 38% greater than the area determined by the direct method. Interestingly, the individual home ranges (E13, E15a, E31) that are greater when calculated by the Anderson technique (95% contour) than the direct method by more than 38% are noticeably irregular due to the presence of boundaries. E13 (whose home range is actually dumbbell shaped due to the Summit Road and bounded on one side by the Thredbo River) is given an area by the computer method more than double that obtained by the direct method. However, when the Anderson 95% contour maps are produced to the same scale and placed over the actual topographical map, it is possible to delete the overlapping areas that are clearly out-of-bounds for the individual. If the remaining area is determined, the result is in much better agreement with the direct method. The 'adjusted' 95% contour areas for E13, E15a and E31 are 36, 39 and 42 ha respectively, bringing the mean of the 95 % contour areas to 49 ± 27 (SD) ha which is close to the mean determined by the direct method (42 ha).

Home range correlates

There were no significant differences (p>0.1) between the home ranges of males and females and there was no correlation between home range size and body weight. There was no correlation between home range size and season (summer and winter) or altitude (above vs. below the snowline). The hypothesis that males, after arousal from hibernation, would have a larger home range area due to a search for a mate was tested by comparing home range values for data points one and two months after arousal from the last torpor bout with home range values for data points collected during the rest of the year, but there were no significant (p>0.1) differences.

Home range overlap

Home ranges of echidnas can have extensive overlap with each other as shown in Figures 1 and 2. However these figures do not show the full extent of overlapping home ranges. There

Table 2. Sites used by echidnas in the Snowy Mountains of NSW 1987-1990

RETREAT SITES

(numbers in brackets = percent of total retreat sites recorded)

INSIDE HOLLOW LOGS (30%)

IN HOLLOW AT BASE OF TREE (18%)

IN RABBIT BURROW (7%)

UNDER ROCK (7%)

BESIDE LOG (7%)

IN CENTER OF DECAYING TREE STUMP (6%)

UNDER CLUMP OF LIVING BRUSH (4%)

UNDER PILE OF BARK AND TREE LITTER (4%)

IN WOMBAT BURROW (3%)

AMONGST ROCKS (3%)

UNDER LOG PILE (3%)

HIBERNACULA

(28 hibernacula were identified. Numbers in brackets = the number of times that type was used. No animal used the same site twice.)

CAVITY IN BASE OF TREE STUMP (6)

HOLLOW LOG (4)

WOMBAT WARREN (4)

NATURAL UNDERGROUND CAVITIES (2)

CAVITY FORMED BY LIVING TREE ROOTS (2)

CAVITY IN MAN-MADE PILE OF ROCK AND EARTH (2)

RABBIT WARREN (1)

UNDERNEATH ROCKS (1)

SOFT CENTER OF PARTLY DEAD TREE (1)

SOFT CENTER OF PARTLY DEAD STUMP (1)

SOFT EARTH UNDER FALLEN TREE (1)

PILE OF DEAD TREES (1)

DEBRIS AT BASE OF TREE (1)

BASE OF TERMITE MOUND (1)

NURSERY BURROWS

AROUND BASE OF TREE IN ROCKY SOIL

IN MOUND OF SOFT EARTH (ROADWORKS STOCKPILE)

IN TANGLED BASE OF LOW HEATH VEGETATION

were for example three other echidnas, besides those shown in Figure 1, sighted in the home range of E11, and we were still finding echidnas in the area shown on the

map in Figure 1 right up to the end of the study. There is simply no way to determine the number of echidnas living in any particular area and hence the question of how many individuals might have overlapping ranges remains open.

Inactive sites

Echidnas can be inactive for long periods, most noticeably during hibernation. On Kangaroo Island, South Australia, Augee et al. (1975) found echidnas to be nocturnal, diurnal or, most commonly, crepuscular depending on the weather, but in this study we found them to be mostly diurnal. They have no fixed site such as a nest, except for mothers with nursing young who dig a specific burrow which is used for several months (Beard et al. this volume). Certain situations are preferred for retreats during periods of inactivity, and those observed to be used in this study are listed in Table 2. Retreat sites always provide protection in that the animal is difficult to see, but they do not always provide shelter; sometimes there is only scanty cover over the animals back and on occasion the animal is amongst grass or litter but not fully covered. Hibernacula on the other hand were always sites that provided secure shelter. Like retreat sites, hibernacula never appeared to be burrows dug entirely by the echidna but were pre-existing cavities. Nursery sites on the other hand seemed to be true burrows constructed entirely by the mother. The importance of fallen logs, stumps and decaying trees in this habitat is clearly shown in Table 2.

DISCUSSION

Echidnas have a home range in the Snowy Mountains of about 42 ha with considerable individual variation (range 24-76 ha). Echidnas have been known to remain in the same home range for as long as 16 years in forested mountain habitat in the A.C.T. and 10 years on Kangaroo Island (Griffiths 1989), and at least 4.5 years in the Snowy Mountains in this study (E11). Adult echidnas probably spend their entire life within the same home range. Within that area there is no fixed nesting site, although appropriate sites may be re-used, especially as hibernacula (Table 2) and nursery burrows. The home ranges have boundaries, some of which, such as roads, rivers, lakes and gullies, are easily recognized by humans. In the Snowy Mountains some individuals made regular use of culverts under roads and in the case of roads with heavy traffic survival of such individuals is probably

dependent on culverts.

Dispersal of the population probably depends on wide

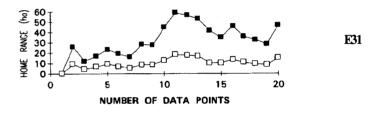
ranging movements of young animals, but in this study we observed only one possible dispersal movement. A male echidna (E30) was captured at Waste Point on 5 April 1988, weighing 2.7 kg. A transmitter was implanted and the animal was released at its capture point on 8 April. When two of the authors returned on 23 April, the transmitter signal was monitored and seemed to be coming from the general area of release. However no signal could be detected on 24 April. On 27 May the signal was detected coming from the other side of the Snowy River and on 16 June the animal was located 5 km from the point of release and on the other side of the Snowy River. We were unable to obtain sufficient data points with which to determine a home range for this animal. For those animals whose home ranges were determined above, there was no correlation between body weight and home range area, but none of the animals used in the home range analyses weighed less than 2.75 kg at the start of radio tracking. There was no correlation between sex and home range size; both the

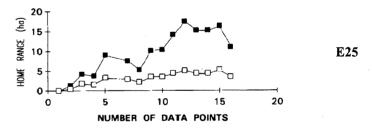
largest and the smallest home ranges in Table 1 are males. Analysis of tracking records at various times of year did not show any significant differences. We had hypothesized that immediately after arousing from torpor males would have a larger 'home range' than at other times of year as they searched for a mate, but this hypothesis was not supported by the analysis. The size of echidna home ranges is such that an animal can move from one edge to the extreme opposite in one activity period, and indeed individuals were observed to do so on a number of occasions.

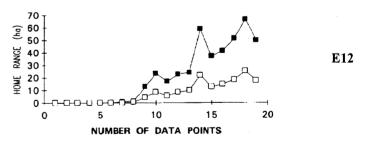
There is a wide range in home range size and shape, the most atypical being a male (E15) which spent a winter, including hibernation, in an area 4 km away from the area in which he had been captured the previous autumn and to which he returned the following summer. If each of these areas is treated as a separate home range (as they are in Table 1), they are 32 and 74 ha respectively and well within the range of home ranges calculated in this study. Unfortunately the signal was lost for this animal prior to the second winter so we do not know if this was a regular pattern. No other echidna in this study, except for the equivocal case of E30 discussed in the preceding paragraph, moved from one area to another, and the individual that was followed the longest (E11) remained within his 68 ha area for 4.5 years.

In this study we had thousands of data points collected over 50 field trips to the Snowy Mountains and collected by automated recording systems left in the field at other times. Most field studies would only be able to produce a relatively limited number of data points and therefore require some statistical technique to predict home range. There

is a vast literature on the various techniques available (see Harris et al., 1990, for a recent evaluation of techniques specifically related to radio tracking studies of mammals), and the universal conclusion is that it is necessary to understand the field biology of the species involved in order to choose and interpret an appropriate technique for determining home range. In this study we have shown that a nonparametric technique, in particular that of Anderson (1982), works well if adjustment is made for obvious boundaries that exclude echidnas. A minimum of 15 data points is necessary (Fig. 3) and they must be truly independent. It is logical to assume that the greater the time interval between data points the better but impossible to give a specific recommendation. The data points shown in Figure 3 were all collected within the first year of study of each echidna, and the asymptotes reached are consistent with values obtained near the end of the tracking of each animal (shown in Table 1). For comparative purposes the 50% contour area asymptote would be more appropriate (Fig. 3) being more 'robust',







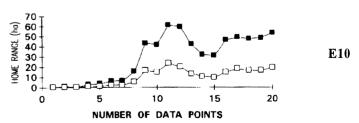


Figure 3. Home range of four echidnas in the Snowy Mountains determined by the technique of Anderson (1982) showing the area within the 95% contour (closed squares) and the 50% contour (open squares)

i.e. less influenced by variations in peripheral data points (Anderson 1982). However, this level clearly underestimates the true home range for echidnas (Table 1).

Home range areas determined by widely different techniques may lead to false comparisons. For example, the data are no longer available to reanalyse the 1975 study by Augee et al. The circle method used in that study gives, when used on the Snowy Mountains data (Table 1), a five fold overestimate of the area determined directly. Therefore the 65 ha home range for echidnas on Kangaroo Island suggested by the study of Augee et al. (1975) is not comparable with latter work using statistical analysis and indicates a much smaller actual home range than in the Western Australian wheatfields (Abensperg-Traun 1991) and in this study. The latter studies are comparable and indicate a home range of 50-65 ha for echidnas in two very different habitats.

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