

CHAPTER 5

RANGE USE AND ACTIVITY

5.1 INTRODUCTION

This chapter has two aims; to investigate the spatial and temporal use of home-range and habitat, and to examine levels and patterns of activity in wombats. Through examination of these parameters, I attempt to address three of the hypotheses given in the first chapter, which have been expressed as the questions below:

1. Are the areas used for feeding different between 'poor' and 'good' seasons?
2. Are home-ranges larger during 'good' seasons than during 'poor' seasons?
3. Are activity levels lower during 'poor' seasons than during 'good' seasons?

The first question examines the possible use of area selection as a mechanism to influence dietary quality. As food quality declines, wombats might attempt to maintain dietary quality by increasing selectivity for higher quality items (though at the expense of rate of food intake). Alternatively, wombats might attempt to maintain a similar level of energy intake to that of good seasons by increasing food intake (at the expense of dietary quality). A third option is to maintain the same level of food intake and not attempt to maintain the same level of energy intake, using stored reserves instead. Increasing selectivity for plants or plant parts from amongst the grass sward is likely to be more difficult for larger herbivores (because of their larger mouths) and a better strategy might be to select feeding areas which have a greater abundance of higher quality food items.

This would also allow larger herbivores to couple higher quality diet with higher rate of food intake than would be possible in areas with a lower proportion of good quality food items, and hence satisfy their larger absolute energy requirements (see Chapter 1). A shift in the area used for feeding between poor and good seasons would suggest that wombats are adopting a strategy of attempting to maintain dietary quality as food resource quality declines.

The second question examines whether wombats conserve energy during the poor season by altering their ranging behaviour. Lower energy expenditure during the poor season would be consistent with smaller home-ranges and/or smaller 'core' areas within the home-range. Alternatively, an expansion of the home-range during poor seasons might be the result of wombats foraging more widely for higher quality food items as these resources become relatively scarce in areas closer to burrows. An expansion in home-range area is probably associated with increased activity and hence greater energy expenditure.

The third question examines whether wombats conserve energy during the poor season by reducing their overall activity levels (which might also include more conservative ranging behaviour). I make the assumption here that movement detected by the sensor on the collar reflects activity which is positively correlated with energy expenditure. Activity levels examined in this chapter, therefore, should be closely correlated with Field Metabolic Rate, which is the subject of Chapter 7.

There have been few studies of home-range or habitat use for any of the three wombat species. McIlroy (1976) tracked radio-collared common wombats on foot in *Pinus radiata* plantations and was able to determine home-range boundaries and habitat use. Taylor (1993) established the home-range boundaries of two male common wombats in cleared agricultural land by radio-tracking. Home-range boundaries and habitat use by radio-collared northern hairy-nosed wombats at Epping Forest National Park have been examined by Johnson (1991) (with assistance from the myself), and home-range of this species is currently being examined by A. Woolnough (pers comm). To my knowledge, there have been no published studies of home-ranges of southern hairy-nosed wombats.

To address the above questions, I required information on home-ranges, habitat use and levels of activity. I examined habitat use for common wombats but not for the two other species. Habitat use by northern hairy-nosed wombats was being examined as part of another study (A. Woolnough, pers comm), and time and resource constraints prohibited examination of habitat use by southern hairy-nosed wombats. Data on activity patterns in northern hairy-nosed wombats is currently being collected by A. Woolnough. In the present study, I collected activity data for common wombats and southern hairy-nosed wombats.

5.2 METHODS

5.2.1 General

To determine whether wombats used different areas for feeding between ‘poor’ and ‘good’ seasons (Question 1, section 5.1), I examined the locations of home-ranges and ‘core’ areas (see section 5.4.2), and the proportions of each habitat type included in home-ranges and core areas, during each season for common wombats. To determine whether home-ranges were larger during the ‘good’ season than the ‘poor’ season (Question 2, section 5.1), I examined the size of home-range and core areas between seasons for common wombats. To determine whether activity levels were lower during the ‘poor’ season than the ‘good’ season (Question 3, section 5.1), I examined activity levels for common wombats and southern hairy-nosed wombats during each season and examined the size of home-ranges and core areas, and the ratio of a home-range to its core area, between seasons for common wombats. Examination of home-ranges of common wombats required attaching radio-transmitters to wombats. Measuring activity levels of common wombats and southern hairy-nosed wombats required attaching activity sensors to wombats (these methods are described in detail in sections 5.2.5 and 5.2.6).

Home-range and habitat use by wombats was determined by radio tracking. I employed two methods for radio-tracking; tracking on foot using a hand-held antenna, and triangulation of radio bearings from fixed-location tracking stations. Tracking on foot was done mostly in the daytime when wombats were in their burrows, and was used

to establish burrow occupancy by collared individuals. Triangulation was used during the night to follow the above-ground movements of wombats to determine home-range boundaries and home-range use and habitat use.

Numerous methods have been employed to determine the locations (fixes) of an animal from triangulation of radio-bearings and to describe home-ranges or habitat use. Because many of these methods have been used inappropriately (Harris *et al.* 1990), this chapter includes a brief review of the most commonly used methods and a justification of those chosen for this study. The collection and analysis of radio-tracking data can be clearly divided into two steps: firstly, the position of the animal is estimated and mapped and secondly, using these mapped positions the home-range is described.

5.2.2 Estimating Animal Locations

Bearings obtained by radio-tracking are usually subject to some degree of error and therefore location 'fixes' determined by triangulation (intersection of two or more bearings) may not be accurate (eg. Cochran and Lord 1963; Springer *et al.* 1979; Lee *et al.* 1985). Sources of error include signals reflected from topographic features or vegetation, signal quality, observer error and equipment accuracy (Garrott *et al.* 1986). For this reason, location fixes determined from radio bearings are only estimates, not exact locations.

Numerous methods have been used in an attempt to quantify the level of error in location estimates. The simplest method is to compare the distance between the estimated and true transmitter locations, but this does not account for variations in the error due to distance from the receiver and the angle of intersection of the bearings (Lenth 1981; Priddel 1983). Heezen and Tester (1967) attempted to estimate the error of fixes through 'error polygons'. By comparing bearings taken by radio-tracking with the true bearing, these workers determined 'error arcs' about each bearing (bearing \pm error). The size of the polygon resulting from the intersection of the arcs can be used to determine the precision of the tracking system and to assess the quality of the fix. For example, Tidemann *et al.* (1985) studying ghost bats *Macroderma gigas* rejected all fixes where the error polygon was greater than two km². Saltz and Alkon (1985) concluded

that the length of the longest diagonal rather than area of the polygon was a better measure of the quality of a location fix, though White and Garrott (1990) disagreed.

The orientation of the tracking stations in relation to the transmitter also affects the size of the error polygon, and hence the accuracy of the location fix (White 1985). Errors are greater when a transmitter lies on or close to a line passing through both stations. This is because the bearings are almost parallel and a small error in a bearing results in a large shift in the location of their intersection. The location of a transmitter positioned between two stations can be determined more accurately when a third station is used. The use of error polygons, however, is invalid when three stations are used because of the lack of independence of the probabilities of the true location lying within the three error arcs (Nams and Boutin 1991). Other methods that have been used include placing the location fix at the centre (geometric mean) of the triangle resulting from the three bearing intersections (Pyke and O'Connor 1990) and the variation of this by Priddel (1983). However, these methods do not give a measure of precision or probability of the triangle containing the true location.

Lenth (1981) proposed a method based on maximum likelihood estimation to estimate both location and precision of fixes when two or more stations are used. Lenth (1981) also developed two variations of this method, the Huber and Andrews estimators, which are less affected than the original maximum likelihood method by outlier bearings which often result from reflected signals, a common occurrence in wildlife radio-tracking studies (White and Garrott 1990). Garrott *et al.* (1986) concluded that the more conservative Andrews estimator was the better estimator because it was more likely to fail to estimate a location than to estimate an inaccurate one.

5.2.3 Home-range Description

Home-range has been defined as “that area traversed by the individual in its normal activities of food gathering, mating and caring for young” (Burt 1943). Implicit in this definition is that the home-range is not all the area an animal traverses in its lifetime, but rather the area where it normally moves. I have defined ‘description’ of the home-range to be the shape and location of this area, and ‘use’ of the home-range to be distribution of activity or time spent within the home-range area (often called ‘intensity

of use'). Clearly, the two measures are not independent since an animal's use of an area can be used describe the boundary of its home-range. Two criteria have been commonly used to define what activity or area is 'normal' in Burt's (1943) definition of home-range; the first is subjective evaluation by the researcher and the second is the use of a probability level. The use of a probability level is the more objective and more widely used of the two methods and involves defining an area in which the animal is found, for example, 95% of the time. Morris (1988) states that the time period over which the home-range is measured is one of the most important parameters needed to fully define home-range. Thus, home-ranges may be determined for an area the animal uses on, for example, a daily, seasonal, yearly or lifetime basis. Methods for home-range description have been reviewed by Macdonald *et al.* (1980), Jaremovic and Croft (1987), Harris *et al.* (1990) and White and Garrott (1990). The most commonly used descriptors are the Minimum Convex Polygon, Grid Cells, Bivariate Normal models, Harmonic Mean and Fourier Transform; and each has its advantages and disadvantages. Each descriptor can define the boundary of the home-range and most can provide information on home-range use.

Minimum Convex Polygon

The Minimum Convex Polygon (MCP) (Mohr 1947; Southwood 1966) is one of the earliest and simplest techniques to describe a home-range boundary and, according to Harris *et al.* (1990), is still the most frequently used. The method can be used to provide minimum convex polygon contours of intensity of use. Harris *et al.* (1990) state that it is the only technique that is strictly comparable between studies, and Jones (1983) found that it was one of the few methods to give comparable results between grid trapping data and radio-tracking data. However, White and Garrott (1990) consider the disadvantages of this method to be major. The MCP is strongly influenced by peripheral fixes, is sample-size biased, and has the restriction of not being able to describe a home-range with a convex shape (and so large areas can be included which the animal very seldom or never utilises). The MCP method would appear to be most useful for simple descriptions of the home-range and comparisons between studies or species where location data does

not appear to have an obvious concave pattern and level of sampling intensity of location data is similar. The MCP method is less useful for examination of intensity of use.

Grid Cells

Another simple method for home range description is to superimpose a grid over the study area and record which cells are used by the animal from the location fixes. The number of fixes falling within a grid cell can be used to define intensity of use. Kenward (1987) considers this method to be good for analysing habitat use and investigating interactions between individuals from their overlap in, and timing of, grid cell use. This method suffers from two major weaknesses (White and Garrott 1990). Firstly, if insufficient fixes are obtained to record the animal in all grid cells within its home-range, grid cells become disjunct and cells will sum to only a portion of the home-range area. Compared to other home-range descriptors, this method requires far more fixes to reach sampling saturation (Kenward 1987). Secondly, calculation of home-range areas based on grid cells can lead to over-estimates because the outermost cells project beyond the true home-range boundary. The coarser the grid, the greater the overestimate of the home-range area. Grid cells are useful for home-range description from grid-based trapping data and the method has direct application to the statistical examination of interactions between individuals. Grid based methods appear to be less useful for home-range descriptions or examination of home-range use than some other techniques.

Bivariate Normal Ellipse

Various workers (Jenrich and Turner 1969; Koeppel *et al.* 1975, 1977; Samuel and Garton 1985) have proposed the use of Bivariate Normal Ellipses to describe a home-range. The Bivariate Normal Ellipse has the advantage that it is not biased by sample size (Jenrich and Turner 1969). The most serious disadvantage would appear to be the validity of the assumption that an animal's movements within the home-range conform to bivariate normality. A bivariate normal distribution implies that the animal is moving randomly throughout its home-range except for a tendency to stay near the middle. Moreover, this method can only describe the home-range boundary as an ellipse, which is an improbable shape for an animal's true home-range. The Bivariate Normal

Ellipse would appear to have more use as an index of home-range area rather than as a method for describing the home range boundary. Ellipse methods have limited application for investigating intensity of use, home-range description or examination of 'attraction points' (nest sites etc.) within the range.

Fourier Transform

Anderson (1982) developed a non-parametric technique for describing the home-range by applying the Fourier Transform method of smoothing data to the Utilisation Distribution (UD). The UD of activity within the home-range is based on grid cells, and is best conceptualised in a three dimensional sense as a chequer board (grid) with chequers stacked on the squares according to the number of location fixes falling within them. The Fourier Transform is then used to reduce the 'steps' of this three dimensional histogram into smooth continuous 'hills'. The shape and volume of the hills now form the new UD and (when viewed from above) the contour heights equate to probability levels that describe a boundary within which an animal can be located with a given level of probability. The boundary at the base of the hill is equivalent to the 100% probability level and encompasses the total home-range area. The contours equate to the distribution of time spent (intensity of use) within the home range.

The main disadvantage of this method is that it does not describe the shape of the three dimensional surface accurately at the edge of the home-range because of lack of data (Anderson 1982). The edge of the home-range is where few fixes are located. The method is also sensitive to peripheral fixes. Another disadvantage is that the position and choice of grid cell size used to construct the UD affects the Fourier Transform in ways that are poorly understood. Thus the Fourier method is useful for examination of home-range use, but less so for home-range description.

Harmonic Mean

The Harmonic Mean (Dixon and Chapman 1980) is a non-parametric method that has been widely used for home-range description (see Harris *et al.* 1990). The method is useful for producing contour (isopleth) lines which enclose a given proportion of fixes and hence equate to the distribution of time spent (intensity of use) within the home

range. Harris *et al.* (1990) consider that the home-range boundary and intensity of use within the home-range relate well to the actual distribution of the fixes. As with other methods based on grid cells, the method suffers from the home-range estimate being dependent on the size and position of the grid which is superimposed over the fixes. The Harmonic Mean method appears to be useful for both home-range description and home-range use.

5.2.4 Justification of Methods

I estimated location fixes using the Andrews estimator. This method, like the maximum-likelihood estimator upon which it is based, appears to have the advantage over the other techniques in being able to *statistically* estimate the most probable location with a known level of accuracy, and reject spurious or inaccurate fixes. The Andrews estimator variant of the maximum-likelihood estimator has the added advantage of being able to reject inaccurate outlier fixes.

I described home-range boundaries from the innermost 95% of location fixes using the Harmonic Mean method. I used the Harmonic Mean isopleth contours to define use of the home-range enabling the identification of core and fringe areas. Although no home-range descriptor developed so far is ideal, the Harmonic Mean method was chosen because it does not make (unrealistic) assumptions about the distribution of location fixes (as does the Bivariate Normal Ellipse), has no restrictions on the shape of the home-range boundary (as do the Bivariate Normal Ellipse and MCP methods) and is likely to describe the boundary of the home-range more accurately than the Fourier Transform method.

5.2.5 Capture and handling

The method of capture, anaesthesia and collaring of wombats is given in Evans (1997), Evans and Green (1997) and Evans *et al.* (1998) (Chapter 3, appendices 1, 2 and 3). Apart from capture to fit collars containing radio transmitters or activity sensors, wombats were also captured and recaptured at various times during the study to undertake physiological measurements (Water Turnover and Field Metabolic Rate; Chapters 6 and 7).

5.2.6 Radio tracking

Wombats were fitted with a collar incorporating a double-stage radio-transmitter (Titley Electronics, Australia) and a lithium C-cell battery, giving an expected transmitter life of approximately two years. The transmitters had a range of several kilometres above ground, but signals could not be detected at the burrow entrance using a 3-element Yagi antenna when transmitters were in deeper burrows. Several test collars were also made (see Chapter 3) and these incorporated a single-stage transmitter with a Duracel AA battery. I used a three-element hand-held Yagi antenna (Titley Electronics) when tracking on foot, and four-element Yagi antennae (Biotelemetry Receiver Services, Australia) on the fixed-location tracking stations. Radio-receivers were Telonics TR-4 (Telonics, USA) operating in the 151 MHz range.

Nocturnal movements of collared individuals were tracked from three fixed-location tracking stations situated between 200 m and 400 m apart, their positions being largely determined by topography. Two stations were positioned on the elevated ends of a ridge in the middle of the study area, providing good coverage of the whole study area, particularly the cleared paddocks to the north. A third station was positioned in the extreme south of the site to help improve the accuracy of triangulated locations in the southern forested area. Prior to erecting the stations, I checked that the proposed station locations could receive adequate signals from a transmitter placed at various locations around the study area. Each tracking station consisted of two four-element Yagi antennae mounted at the ends of a 2 m steel horizontal cross-arm. This cross-arm was attached at its centre to the top of a rotatable 5 m aluminium mast, the base of which passed through a compass rose. A pointer was fixed to the mast above the compass rose enabling the direction of the antenna to be determined to within one degree. The mast passed through the roof of a 2 m x 3 m steel (garden) shed, which provided protection to the station attendants from rain, strong winds, snow and falling branches. Contact was maintained between stations by CB hand-held radios connected to 2 m whip antennae mounted on the shed roofs. This enabled bearings on the same animal to be taken simultaneously and aided in the rejection of spurious bearings. Initially, lighting was provided by portable 12V fluorescent tubes, but these gave off radio-frequencies which interfered with the tracking receivers and CB radios. Car trailer tail-lights (12V, 10W



Plate 12 Collar placed on an anaesthetised southern hairy-nosed wombat. The aluminium canister contains a miniature data-logging computer and battery. A radio transmitter and battery are housed in clear epoxy resin on the outside of the canister.



Plate 13 The author hand-tracking a collared common wombat to its daytime resting location deep in a burrow under logs and tree-ferns.



Plate 14 One of three fixed-location huts with mast and antenna used to track nocturnal ranging of radio-collared common wombats on the Great Dividing Range. Despite guy-rope anchors huts occasionally had to be abandoned during strong gales or electrical storms.



Plate 15 Inside of hut showing rotatable mast and compass rose.

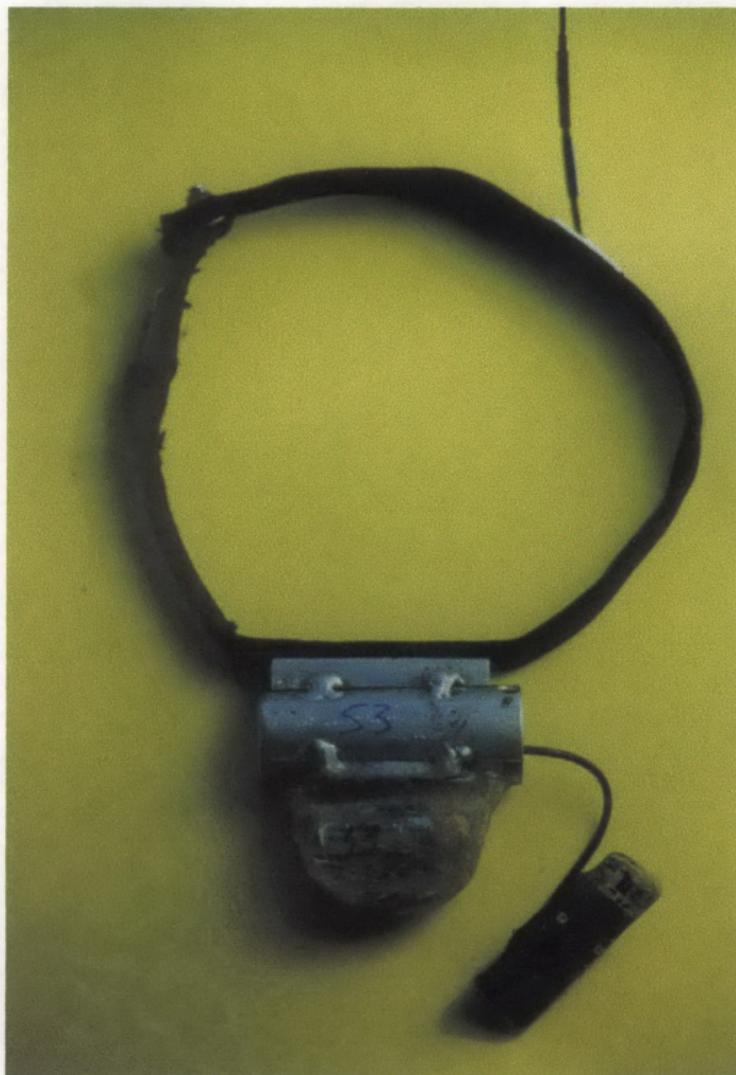


Plate 16 Detail of collar, showing miniature data-logging computer (containing activity sensor) removed from aluminium canister, and radio-transmitter and battery housed in clear epoxy resin on outside of canister.

incandescent) with the covers removed were a successful alternative.

I had previously found a Null-Peak system (Evans 1996) to be a more accurate method of obtaining bearings than no null-peak system, and so I used Null-Peak switch boxes (Biotelemetry Receiver Services, Australia) during the first wombat tracking session. It soon became apparent, however, that the sloping topography, presence of nearby ridges and large boles of trees in close proximity to tracking stations caused signal scatter and reflection that was excessive for a Null-Peak system, and the system was abandoned in favour of using just one Yagi antenna on each station. In addition, the Yagi antennae seemed to be less susceptible to receiving signal reflections when they were mounted horizontally on the cross-arm instead of the usual vertical position.

All transmitter frequencies were scanned at 30 minute intervals, and bearings determined simultaneously by two or three stations (depending on the location of the transmitter). Bearings were not recorded for scattered signals which could not be determined to within five degrees, or for signals that were suspected to be reflections. Tracking was conducted in nightly shifts that either began at dusk and went to 02.00, or began at 02.30 and went until all collared wombats had retired to their burrows (no radio signals).

Radio-tracking trips were planned to coincide with major seasonal changes in pasture biomass and quality. Thus, radio-tracking trips were conducted during summer (good season) when warm conditions promoted pasture growth, and during winter when low temperatures restricted pasture growth and many species became 'hayed off' (dry and brown) (see Chapter 4 for details of seasonal pasture conditions). Radio-tracking trips were done in conjunction with pasture sampling and the collection of wombat faecal pellets. Three radio-tracking trips were conducted, and each trip was of three weeks duration (total of nine weeks tracking). One radio-tracking trip was conducted in summer (January/February 1996) and two radio-tracking trip were conducted during winter, one each during June/July 1995, and July/August 1996 (refer to Figure 3.13 of Chapter 3). Cold nightly conditions and strong winds (causing difficulty in hearing signals and signal scatter from blowing vegetation) during the first winter trip made radio-tracking difficult (particularly between 02.00 and 06.00), and so a second trip was

made during the following winter to increase the sample size of radio-locations for each collared wombat.

5.2.7 Activity Levels

I measured activity levels in common wombats and southern hairy-nosed wombats by attaching miniature, motion-sensitive, data-logging computers to collars worn by wombats. Details of collars and methods of capture and fitting collars to wombats are given in Evans (1997) (Chapter 3 and Appendix 3). The motion sensor differed from the standard motion sensors used in wildlife studies (mercury tilt-switches) in being essentially a miniature 'ball in a cage'. The data logger counted each time the ball contacted the various sides of the cage as changes in orientation or 'shakes' moved the ball around the cage. According to the manufacturer (Zelcon Technic, Tasmania) the WB04 series archival tag loggers were capable of recording continuously (ie. without changing the small battery) for two years, and storing the data for a further 20 years. Each logger plus battery was totally enclosed in waterproof epoxy resin, and the total package measured 55 x 24 x 12 mm and weighed 25 g. Connection to a PC for programming and data downloading was via an infra-red optic link (with the infra-red light transmitting through the clear epoxy resin). The total weight of the collar including logger, transmitter and transmitter battery was approximately 200g which was less than 1% of the weight of the smallest (25 kg) wombat to wear a collar in this study.

Despite initial assurances, the manufacturers of the loggers were unable to provide a program to decipher the large volume of coded hexadecimal data from the loggers, and so I wrote custom software to perform this task. The manufacturers supplied 5 loggers, although another 5 that had been ordered and paid for at the beginning of the study have not yet been supplied.

5.2.8 Burrow-use

I intensively searched the Riamukka SF study area during the initial stages of the study in an attempt to locate all burrows. Burrows located in the dense *Lomandra* or fern ground-layer of the forest were marked by tying plastic flagging tape to the nearest tree. The locations of all known burrows were later numbered and mapped during a

topographic survey of the site undertaken by myself and engineering students of Division of Resource Engineering, University of New England. I opportunistically discovered a number of other burrows during the course of the study by radio-tracking wombats or by stumbling across them. Burrows were subjectively categorised as major, medium or minor (after McIlroy 1976). Major burrows had two or more entrances and were clearly heavily used as indicated by the large amount of freshly excavated and trampled soil and the well-trodden pathways leading to the burrow. Burrow entrances of major burrows were 'well worn' and usually large in diameter. Medium burrows had a single entrance and were clearly currently used, as indicated by recently excavated or trampled soil. Minor burrows had a single small entrance and were not clearly currently used as indicated by the presence of vegetation and debris around or in the burrow entrance and lack of recent soil excavation or footprints.

Radio signals from a transmitter in a burrow can be difficult to detect from above-ground because the signal attenuates as it passes through the soil; the deeper the transmitter (wombat), the fainter the signal received. I often detected signals from transmitters that were above-ground from two or three kilometres away. Signals from transmitters that were underground but within about one metre of the surface (such as near the entrance of the burrow or in a shallow burrow) could often be detected from up to 100 metres away. Transmitters deep in burrows sometimes could not be detected from above-ground, even at the burrow entrance. To determine burrow-use by collared wombats, I visited all known burrows in the daytime during radio-tracking sessions, and occasionally at other times. Using a hand-held Yagi antenna and receiver, I scanned for radio-signals while standing near the burrow entrance and, when a signal was detected, I noted the burrow number and the signal frequency (from which the identity of the individual could be determined). I also obtained burrow-use information by radio-tracking on foot during the night and from trapping records. Trapping records provided information on burrow use by non-collared animals.



Plate 17 Burrow of common wombat in cleared pasture in summer. Radio-tracking and trapping enabled data to be collected on burrow use.

5.3 RESULTS

5.3.1 Number of location fixes

For reasons outlined in section 5.2.2 and to account for errors associated with aberrant (outlier) location fixes, the outer 5% of fixes were excluded when estimating the home-range size and boundary. Thus, the home-range boundary was described using the Harmonic Mean method from the innermost 95% of location fixes (equivalent to the 95% harmonic mean isopleth). The number of location fixes required to adequately describe the home-range was determined by assessing the effect of sample size (number of location fixes) on home-range size, as shown in Figures 5.1, 5.2 and 5.3. For these analyses, home-ranges were calculated separately for each animal, and were calculated on subsamples of fixes randomly chosen from the animal's range dataset. The analysis was restricted to the five animals whose ranges contained greater than 100 fixes. The accuracy of the home-range area estimate was found to depend on the number of location fixes. From Figure 5.1 at least 60 location fixes are required to bring the area to within 10% of the complete home-range area, when range areas for any given sample size are described using the 95% isopleth. When range areas were calculated using the 100% isopleth (Figure 5.2), 60 location fixes bring the range area to within 80% of the complete range area. Data was collected on 18 home-ranges, of which 2 contained less than 60 locations, and so were excluded from further analyses.

5.3.2 Characteristics of the home-range

Boundaries of home-ranges were typically almost circular, and use within the home-range was relatively uniform with a tendency for higher use towards the centre of the range. Figure 5.3 shows the proportion of total area enclosed by successive 10% Harmonic Mean isopleths. These isopleths correspond to range-use contours and, when plotted on a map, show the distribution (or intensity) of activity or time spent within the home-range. The 95% isopleth encloses the area that the animal spent 95% of its time; the 50% isopleth represents the area where 50% of the time was spent, etc.

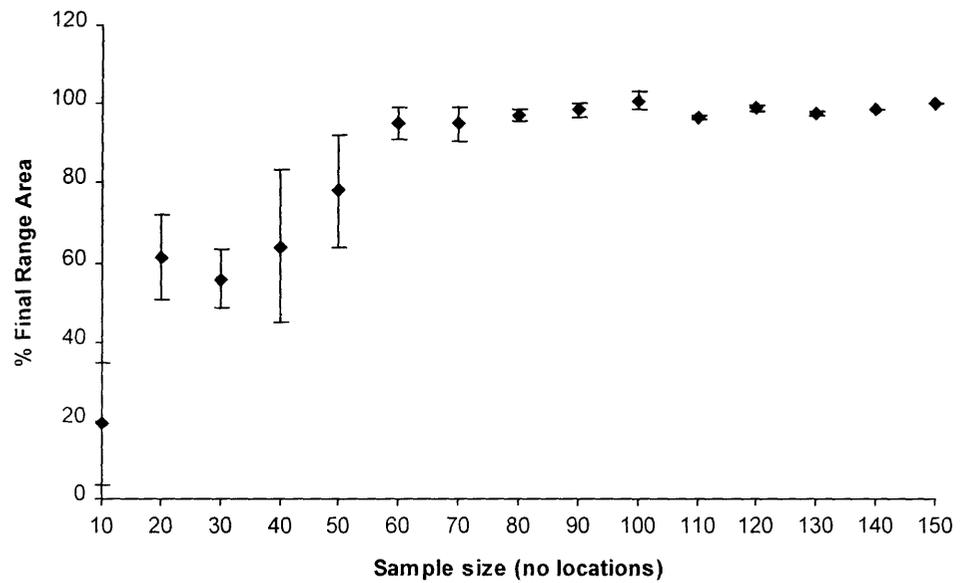


Figure 5.1 Effect of sample size (number of locations) on estimates of home-range size. Home-range size (shown with one standard deviation) was determined using the **95% isopleth** and is expressed as a percentage of the final home-range size.

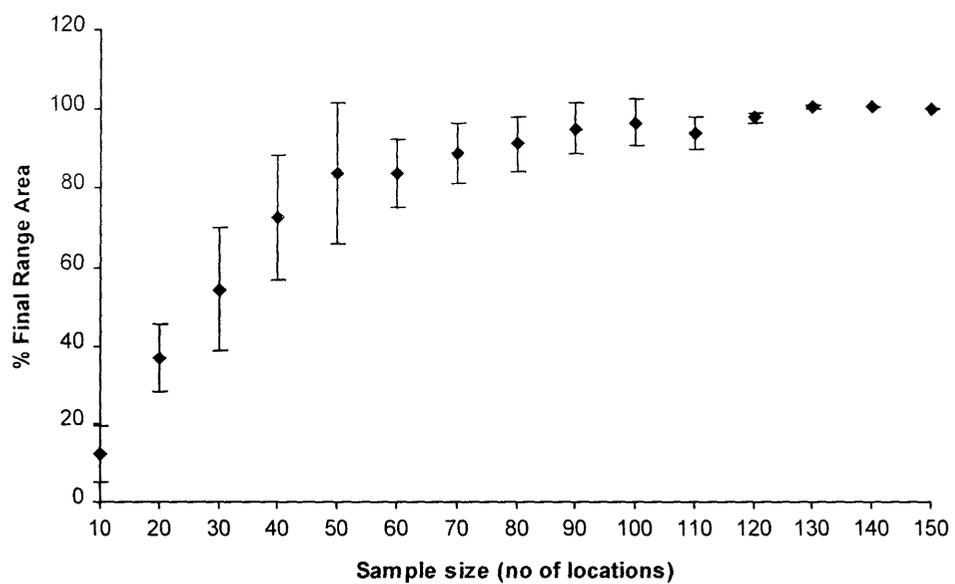


Figure 5.2 Effect of sample size (number of locations) on estimates of home-range size. Home-range size (shown with one standard deviation) was determined using the **100% isopleth** and is expressed as a percentage of the final home-range size.

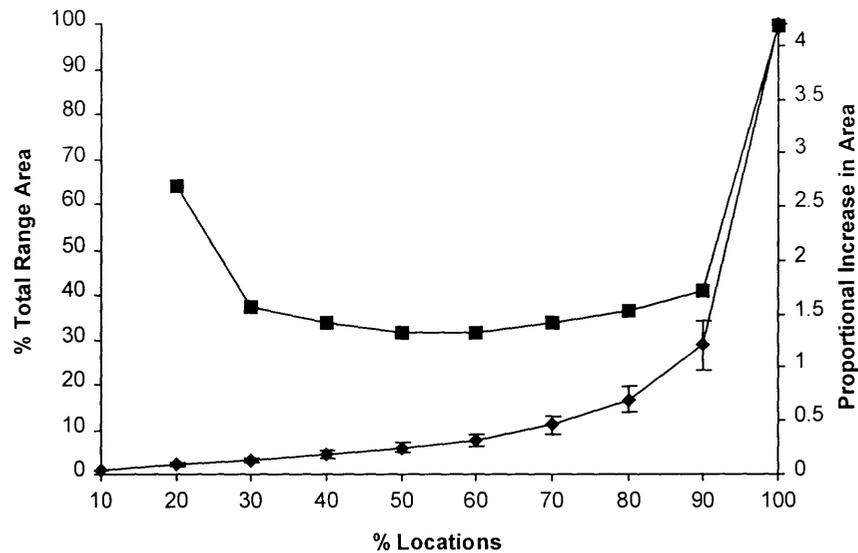


Figure 5.3 Distribution of activity within the home-range (95% isopleth). Diamonds represent percentage increase in total area (shown with SE) as successive 10% increments of location fixes are added from the centre of the home-range outwards (ie. area contained within 10% activity isopleths). Squares represent the proportional change in area between successive increments of fixes.

Additions of location fixes from the centre of the range outwards produced progressively smaller increases in range area until about 60% of fixes had been used, beyond which successive increases became larger (Figure 5.3). The proportional change in area between successive 10% contour intervals is relatively uniform until the 90% contour, beyond which the area markedly increased. On average, the 95% isopleth represented only 56% of the area enclosed by the 100% isopleth. In other words, the outermost 5% of fixes (which may contain outliers) account for almost half of the area enclosing all fixes. Conventionally (and arbitrarily but reasonably), the range core area is defined as the area containing the innermost 50% of locations, though other definitions have been used (eg. Johnson 1991a; Evans 1996). From Figure 5.3, there is no point at which the 10% incremental contours markedly changed the rate of increase in area until the 90% contour, so I have chosen the 50% isopleth to represent the core area for convenience of comparison with other studies. On average, the core area represented only 6% the area containing *all* location fixes (100% isopleth) (Figure 5.3), and only 16% of the home-range area (95% isopleth).

Home-ranges of five individuals were determined during both summer and winter, and home-ranges of another six individuals were determined for one season only due to transmitter and collar problems. Home-ranges of common wombats pooled from each season averaged 17.7 ha (SE = 1.5, n = 16), and core areas pooled from each season averaged 2.9 ha (SE = 0.3, n = 16). Home-range size varied from 7.8 ha to 32.0 ha. Mean home-range area estimated during winter (16.8 ha, SE = 1.9, n = 10) was not significantly different ($t_{14} = 0.79$, $P = 0.44$) from mean home-range area estimated during summer (19.3 ha, SE = 2.7, n = 6). Seasonal ranges were not significantly different for the five individuals whose home-ranges were measured during both seasons (paired $t_4 = 1.42$, $P = 0.23$). Mean core area estimated during winter (3.2 ha, SE = 0.4, n = 10) was not significantly different ($t_{14} = 1.33$, $P = 0.21$) from mean core area estimated during summer (2.4 ha, SE = 0.4, n = 6). The mean ratio of core area to home-range area did not differ significantly between seasons (winter mean = 0.18, SE = 0.02, n = 10; summer mean = 0.15, SE = 0.02, n = 6; $t_{14} = 1.09$, $P = 0.29$).

Mean home-range area for males (15.8 ha, SE = 1.9, n = 8) and females (19.7 ha, SE = 2.3, n = 8) did not differ significantly ($t_{14} = 1.32$, $P = 0.21$). Mean core area for

males (2.5 ha, SE = 0.5, n = 8) and females (2.9 ha, SE = 0.3, n = 8) also did not differ significantly ($t_{14} = 0.08$, $P = 0.93$).

5.3.3 Ranges and vegetation types

Typical seasonal home-ranges for common wombats at Riamukka SF are shown in Figure 5.4, 5.5 and 5.6, and core areas of all ranges are shown in 5.7. Almost all (15/16) home-ranges encompassed more than one of the three habitat types at the study site. All home-ranges included Forest habitat, and almost all (94%) included Cleared pasture. Around half (56%) of the 16 seasonal home-ranges included Woodland habitat, and these home-ranges also included both of the other habitat types. Only one home-range included only a single habitat type, which was forest. Most core areas included either Forest (81% of areas) or Cleared pasture (18% of areas) with 63% of core areas including both habitat types. Few (25%) core areas included Woodland and even fewer (13%) included all three habitat types. I did not track all members of the local wombat population, though the results show that ranges are not exclusive; home-ranges and core areas overlapped within and between sexes. Wombats defecated and scratched soil in prominent locations and placed dung on prominent objects such as rocks and logs on trails (pers obs), suggesting that although ranges are not actively defended, individuals do mark their ranges.

The proportions of either Forest, Cleared pasture or Woodland in home-ranges did not differ significantly between winter and summer (Mann-Whitney U test: Forest, $P = 0.95$, $n = 16$; Cleared, $P = 0.74$, $n = 16$; Woodland, $P = 0.41$, $n = 16$). The proportions of either of the three habitat types in core areas also did not differ significantly between seasons (Mann-Whitney U test: Forest, $P = 0.87$, $n = 16$; Cleared, $P = 0.52$, $n = 16$; Woodland, $P = 0.38$, $n = 16$).

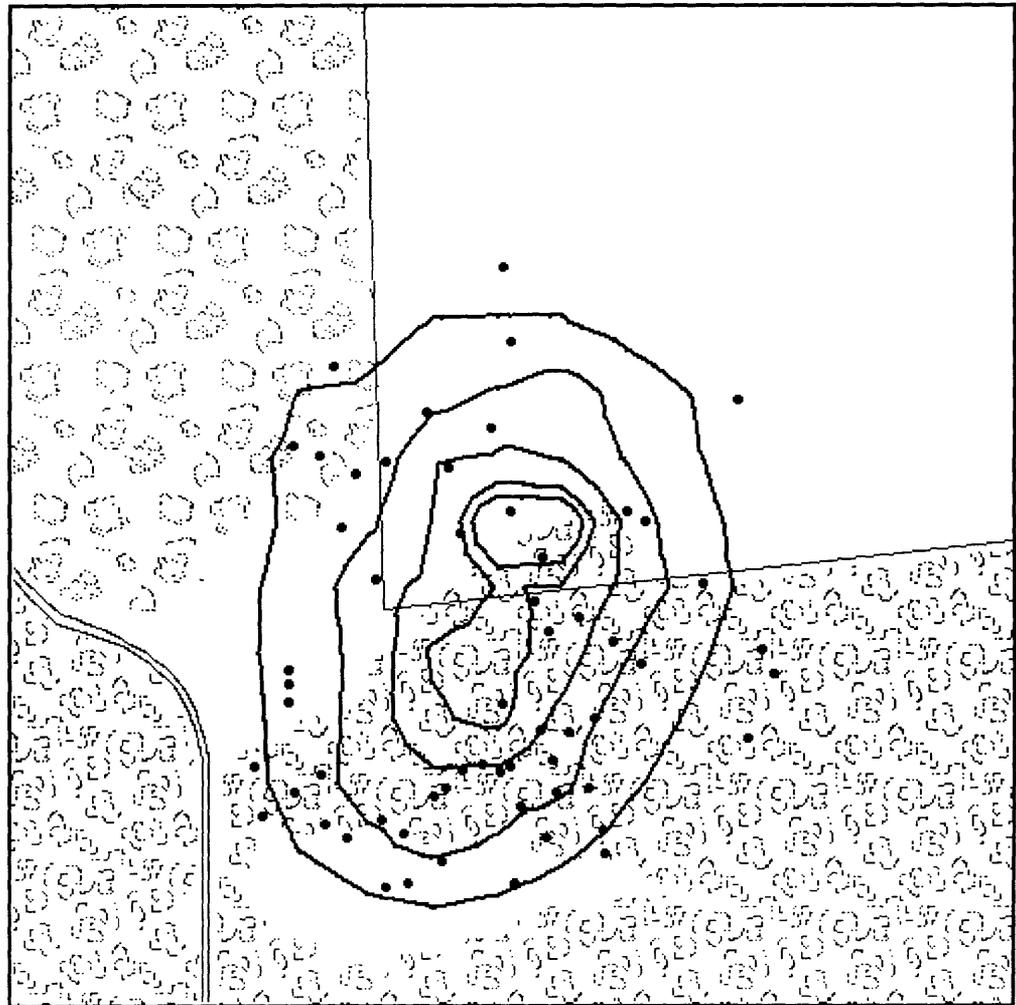


Figure 5.4 Typical home-range of a common wombat at the Riamukka Forest site. Home-range and intensity-of-use contours were calculated using the harmonic mean method. Contours are the 20%, 40%, 60%, 80% and 95% isopleths. Three vegetation types are shown; Forest (dense pattering), Woodland (sparse pattering) and Cleared Pasture (no pattering). Also shown are wombat burrows (dots), dirt road (parallel lines) and fence (single line).

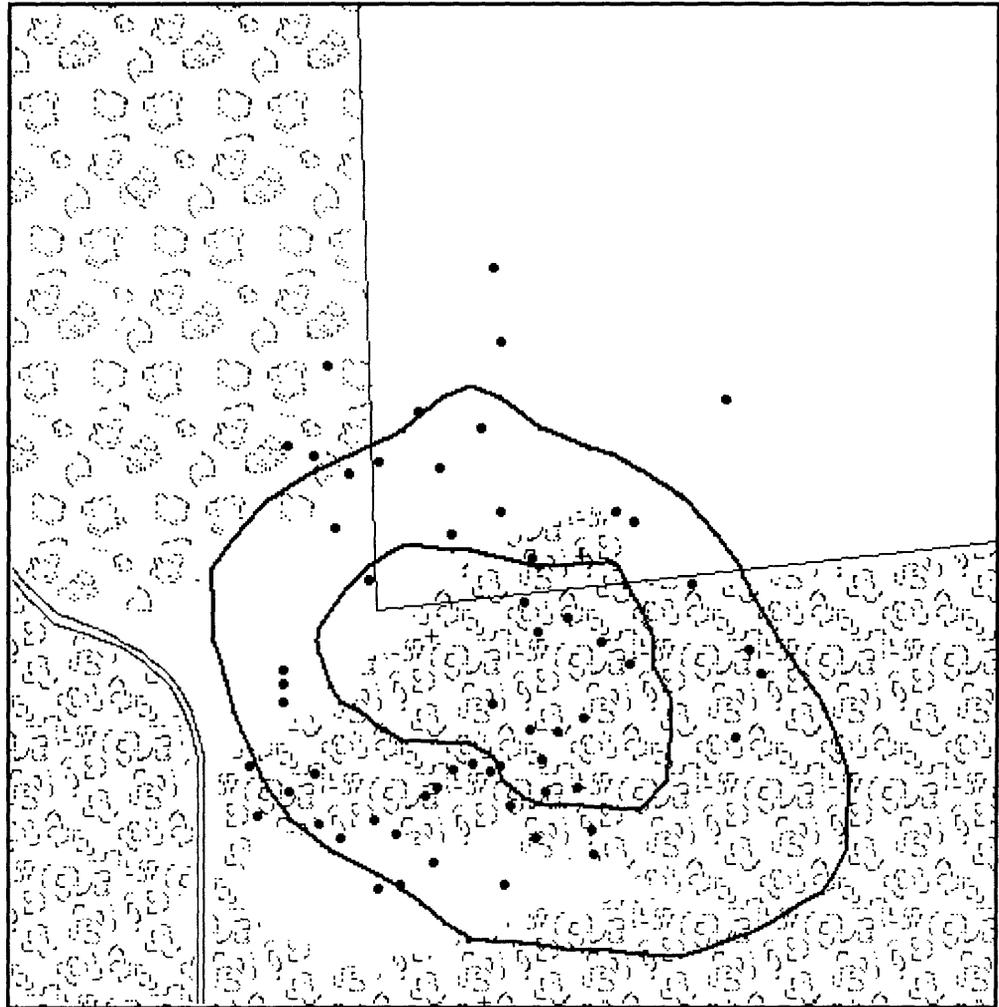


Figure 5.5 Typical home-range of a common wombat at the Riamukka Forest site, full range area (95% isopleth) and the core area (50% isopleth). Three vegetation types are shown; Forest (dense patterning), Woodland (sparse patterning) and Cleared Pasture (no patterning). Also shown are wombat burrows (dots), dirt road (parallel lines) and fence (single line).

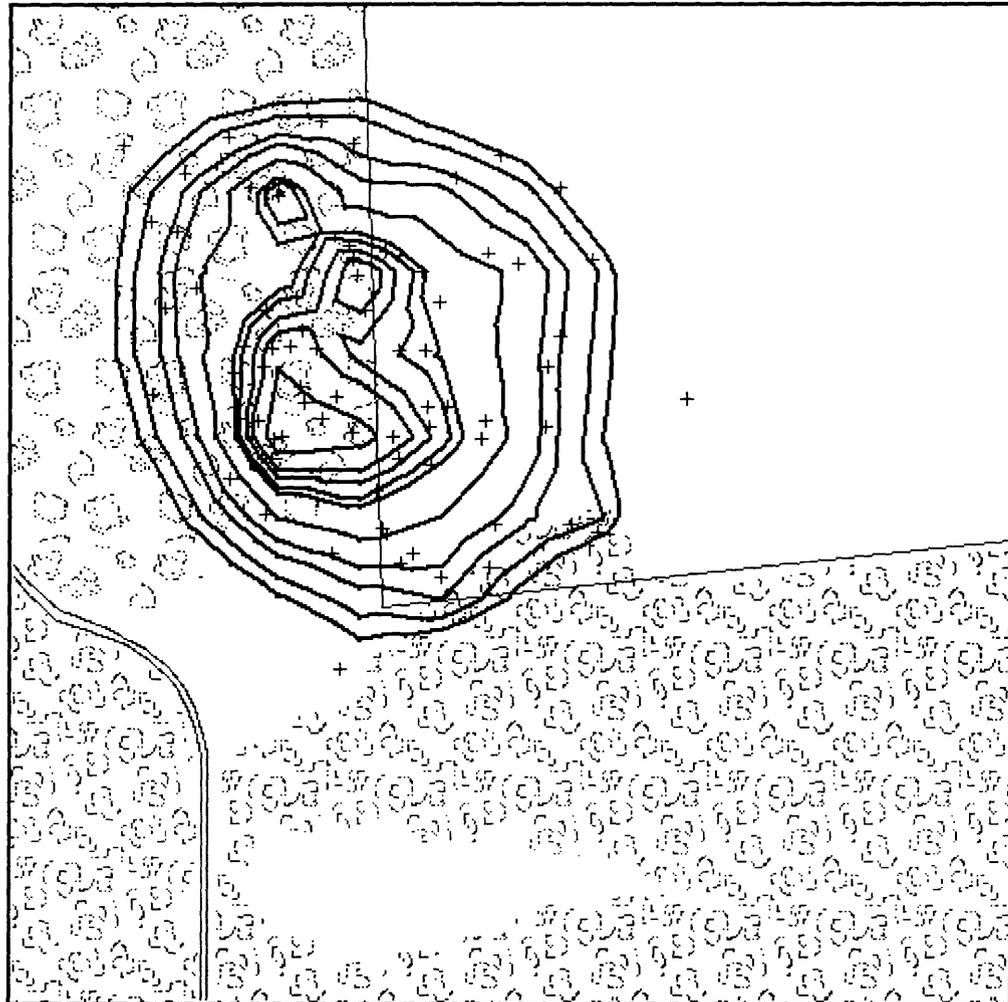


Figure 5.6 Typical home-range of a common wombat at the Riamukka Forest site showing 10% range-use contours (isopleths) from the centre to the full range area (95% isopleth). Three vegetation types are shown; Forest (dense patterning), Woodland (sparse patterning) and Cleared Pasture (no patterning). Also shown are location fixes (crosses) used to estimate the home-range, dirt road (parallel lines) and fence (single line).

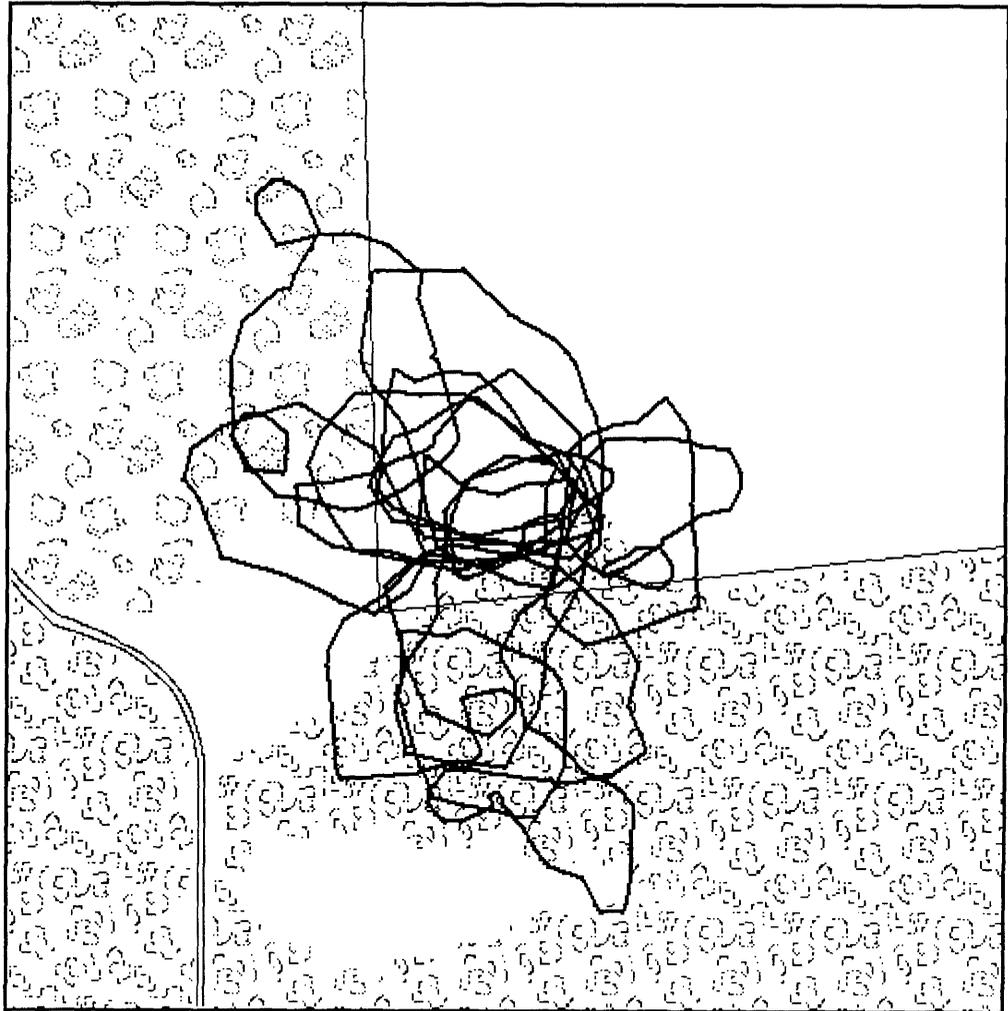


Figure 5.7 Core areas (50% isopleths) of all 16 common wombat home-ranges estimated at the Riamukka Forest site. Three vegetation types are shown; Forest (dense pattering), Woodland (sparse pattering) and Cleared Pasture (no pattering). Also shown is a dirt road (parallel lines) and fence (single line).

5.3.4 Periods for Activity Measurement

Periods for which activity sensors (data loggers) were worn by individual wombats are shown in Figures 5.8 and 5.9. Common wombats wore loggers between August '95 and October '96 and southern hairy-nosed wombats wore loggers between August '96 and February '97. Also shown in Figures 5.8 and 5.9 are the substantial proportions of these periods for which loggers were worn but no activity data are available for various individuals due to logger malfunctions, and to a lesser extent transmitter malfunctions.

Each of the five loggers worn by common wombats malfunctioned at some stage. In some cases the logger was taken off an individual, repaired by the manufacturer, and then placed on another individual if the original individual could not be recaptured. Of the five loggers placed on southern hairy-nosed wombats, four had been borrowed from Andrew Woolnough who had used them for a study of northern hairy-nosed wombats. These four loggers were an updated, more reliable version and did not malfunction. The fifth logger was one of mine that had been recently repaired, but malfunctioned for the whole time it was on southern hairy-nosed wombat #04. Three common wombats and four southern hairy-nosed wombats wore functioning activity sensors for periods spanning several months, and this should enable comparison of seasonal data for these individuals. Data are available from other individuals for shorter periods.

5.3.5 Effect of Capture and Collaring on Activity

Daily activity levels during times of capture, handling and collaring are shown in Figures 5.10 and 5.11. Activity levels recorded by collars of some individuals were apparently different during times of capture and handling. For example, following the first capture in Figure 5.10a, common wombat #03 showed relatively high levels of daily activity (more than twice that of subsequent relatively 'normal' days) for the 10 days until the second capture. Activity also remained relatively high for 5 to 6 days following this second capture. Relatively high activity levels following capture were also observed in common wombats #05, #10 and #16, southern hairy-nosed wombat #05 (Figure 5.11c) and possibly in southern hairy-nosed wombats #03 (Figure 5.11b) and #02 (Figures

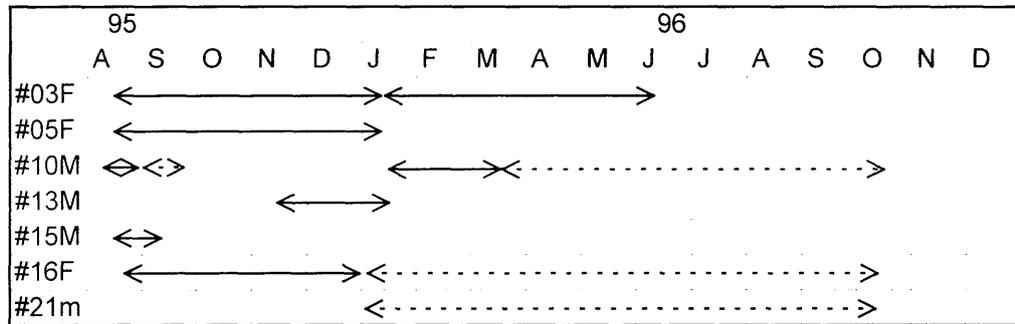


Figure 5.8 Periods for which individual common wombats wore collars with activity loggers at Riamukka SF. Solid line = periods when logger functioned, dashed line = periods when logger malfunctioned (ie. no data were able to be collected).

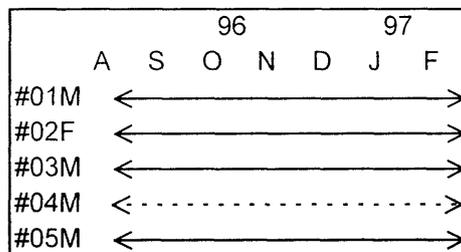


Figure 5.9 Periods for which individual southern hairy-nosed wombats wore collars with activity loggers at Brookfield CP. Solid line = periods when logger functioned, dashed line = periods when logger malfunctioned (ie. no data were able to be collected).

5.11e and 5.11f). Digging traps into the entrance of burrows before trapping also appears to have been associated with higher activity levels for some individuals. This was observed in individuals that had been trapped while wearing a logger. Relatively higher levels of activity prior to capture were apparent in common wombat #03 (Figure 5.10b) and southern hairy-nosed wombat #05 (Figure 5.11d). Some individuals (eg. common wombat #13, southern hairy-nosed wombat #01) showed no overt signs of changes to 'normal' activity either before or after trapping, and yet other individuals showed apparently changed activity patterns on one trapping occasion but not on other trapping occasions (eg. southern hairy-nosed wombat #02).

5.3.6 Activity Patterns

Figure 5.12 shows a typical example of the hourly activity levels of a common wombat (#03) for a week (during September). The pattern shows a strong diel cycle, with high nocturnal activity and low diurnal activity. The pattern of nocturnal activity suggests an early-night burst of activity, a middle-night drop in activity (but still more movement than during the day), then often another rise in activity late in the night. The pattern of hourly activity for common wombat #03 over a month (September) is shown in Figure 5.13. The pattern exhibits the strong diel cycle, with activity levels varying to some extent between nights. Mean hourly activity levels for common wombats and southern hairy-nosed wombats for two different seasons are shown in Figure 5.14. To avoid any possible effect of trapping on activity, I have used activity levels during September (ie. 2 or more weeks since capture in winter) and December (summer) to investigate seasonal differences in activity for common wombats. September is the end of the 'poor' (cold) season whereas December is in the 'good' (warm/wet) season. The mean hourly activity clearly shows higher activity during the night than during the day, with the highest levels often occurring on or shortly after dusk and shortly before dawn. The 'nocturnal' activity phase of the diel cycle (ie. higher level of activity) for most individuals began, on average, earlier in poor season (winter/spring) than in the good season (summer), though timing of return to the burrow was similar in these seasons. In most cases, the mean period of nocturnal activity was shorter during summer than during winter.

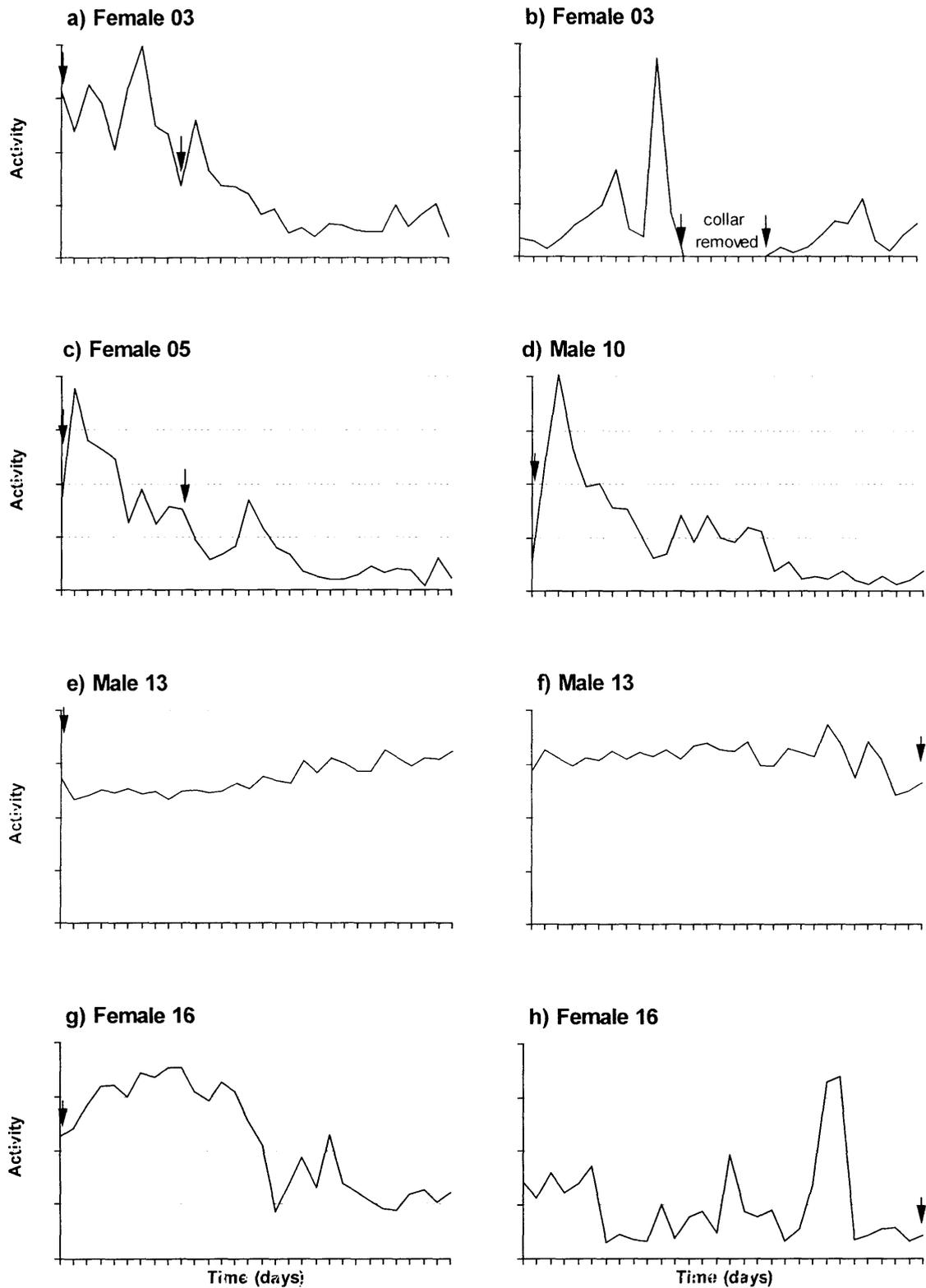


Figure 5.10 Daily activity levels of common wombats during trapping periods. Arrows indicate dates of capture. The y scale differs between graphs.

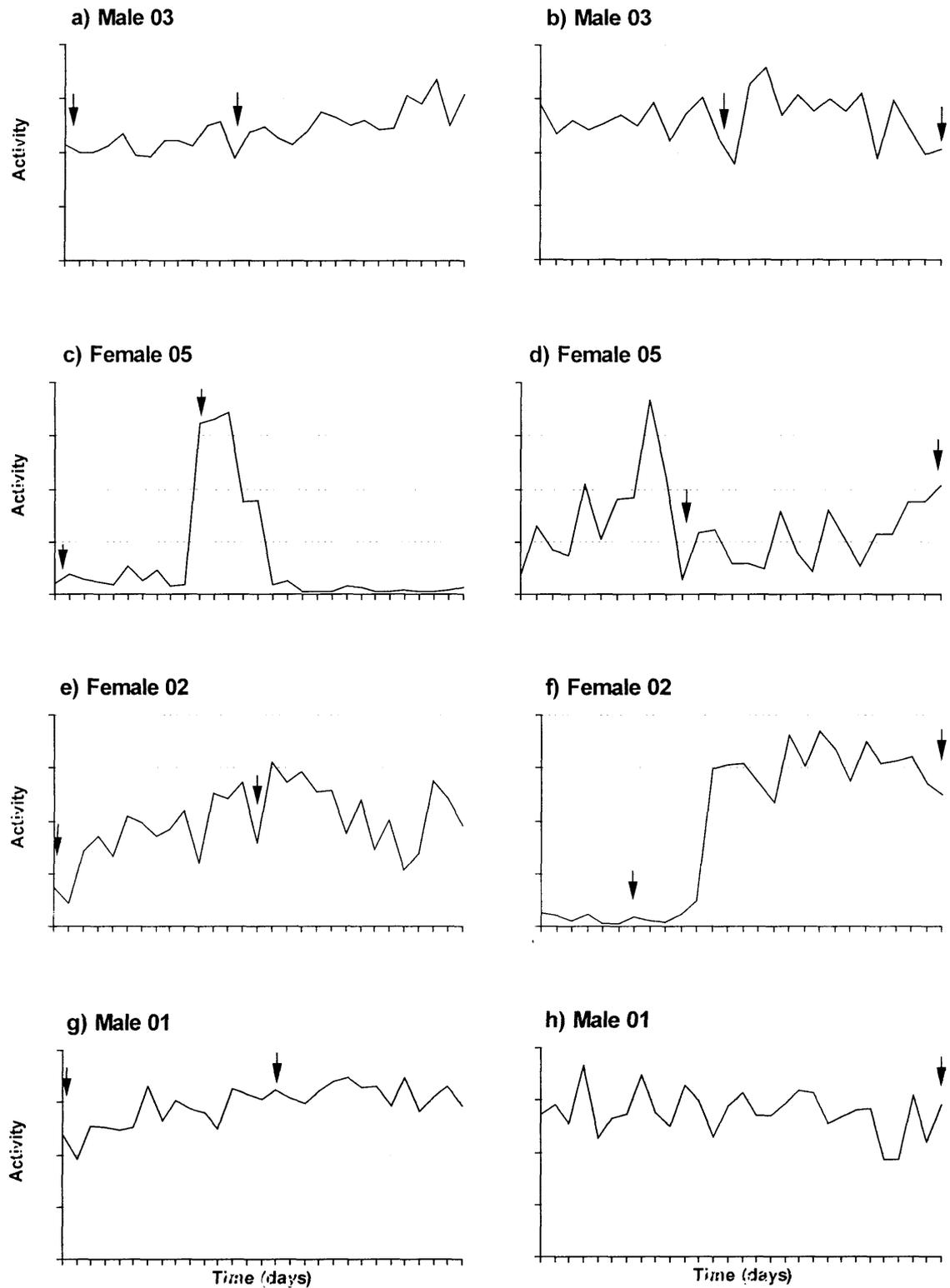


Figure 5.11 Daily activity levels of southern hairy-nosed wombats during trapping periods. Arrows indicate dates of capture. The y scale differs between graphs.

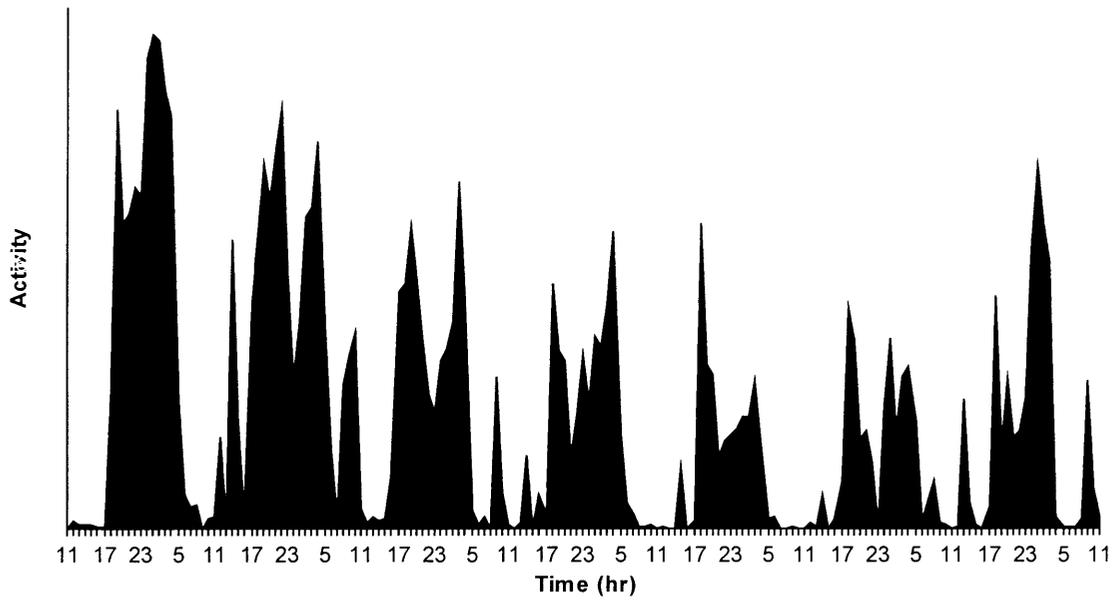


Figure 5.12 Hourly activity levels for common wombat #03 for one week. Activity levels were recorded by data logging computers attached to collars.

Daily activity levels of the individual common wombats and southern hairy-nosed wombats for which data are available for an extended period (several months) are shown in Figures 5.15 and 5.16. Trends and long-term patterns in daily activity were highly variable between individuals. Long-term daily activity for some individuals showed relatively small and consistent fluctuations compared to other individuals whose long term activity was punctuated by occasional 'spikes' or peaks of markedly higher activity lasting several days. The long-term trend in activity level for two common wombats (a and b in Figure 5.15) was relatively invariable compared to the other two common wombats whose activity decreased markedly during the first two months of wearing the logger and then remained relatively stable for the next 3 to 10 months (c and d in Figure 5.15). This marked decrease in activity during the early stages of measurement may have been due to malfunctioning of the loggers rather than a change in behaviour, as a rapid (over a few days or a week) decline in activity to zero was characteristic behaviour of loggers before they failed completely. For two southern hairy-nosed individuals (a and d in Figure 5.16), activity during winter was approximately twice that during summer. Activity for one southern hairy-nosed wombat (Figure 5.16c) was markedly higher during spring and February (though the latter was probably due to trapping disturbance).

5.3.7 Burrow-use and behaviour

Intensive searching and opportunistic observations revealed 72 burrows in the 5 km² Riamukka study area, giving a density of 14.4 burrows per km². These burrows included two major burrows, 47 medium burrows and 23 minor burrows. Most of the burrow-use data for common wombats came from radio-tracking collared individuals. Burrow-use information was obtained opportunistically and generally, more information was obtained from individuals that wore collars for longer periods. Wombats that wore collars for a number of months were found to use several burrows, with the maximum of 12 recorded for one female. Generally, burrows used by an individual were widely dispersed across the study site, rather than concentrated in one area.

Burrows were used by more than one wombat, though usually not at the same time. Wombats that have been observed to share burrows at the same time include a male with a female, or a female with a sub-adult (presumably her offspring). Of the 72

burrows in the study area 38 were observed to be used by wombats from radio-tracking of collared individuals and trapping data (though a total of 49 burrows were classed as 'actively-used' from appearance). The majority (22) of these 38 burrows were observed to be used by one individual only. The remaining sixteen burrows were each observed to be used by more than one individual during the study. Of these 16 burrows, the two major burrows were used by the largest number of individuals (nine for one burrow, seven for the other). The maximum number of individuals recorded using a medium burrow was six, though this was unusual as medium burrows were most often used by one to three individuals. On average, 2.2 wombats used each of the 38 'known-use' burrows at the site.

The limited data available for burrow-use over consecutive days suggests that wombats shifted burrows regularly, typically spending one to 4 nights in the same burrow and then moving to another. From opportunistic observations, wombats visited up to 4 burrows during a night. These 'inspection' visits sometimes involved a cursory 'sniff' and listen at the burrow entrance before urinating or defecating near the entrance and moving on. At other times wombats entered burrows for several minutes before emerging, often urinating/defecating and moving on. Following rain, inspections often involved soil excavation. When quietly approaching the entrance of a burrow, I have occasionally heard a wombat down the burrow make a loud 'shuddering' vibration through the ground, which was distinct from the sound of a wombat running along a burrow. This behaviour might serve to communicate the occupancy of the burrow to wombats near the entrance of the burrow.

Burrows of common wombats at the Riamukka site and in other places (pers obs) are mostly single entrance burrows, and these are widely scattered throughout suitable habitat. Congregations of burrows can occur in areas that appear to be favoured, such as the steep banks of small, narrow, treefern-lined creeks. Even in areas with high burrow concentrations, burrows of common wombats are not interconnected to form warrens, though exceptionally large burrows may have up to three entrances. The community structure of burrows of southern hairy-nosed wombats at Brookfield CP was different to that of common wombats. Brookfield CP is mostly covered with a calcrete (limestone conglomerate) substrate which may be two or more metres deep. Although wombats are

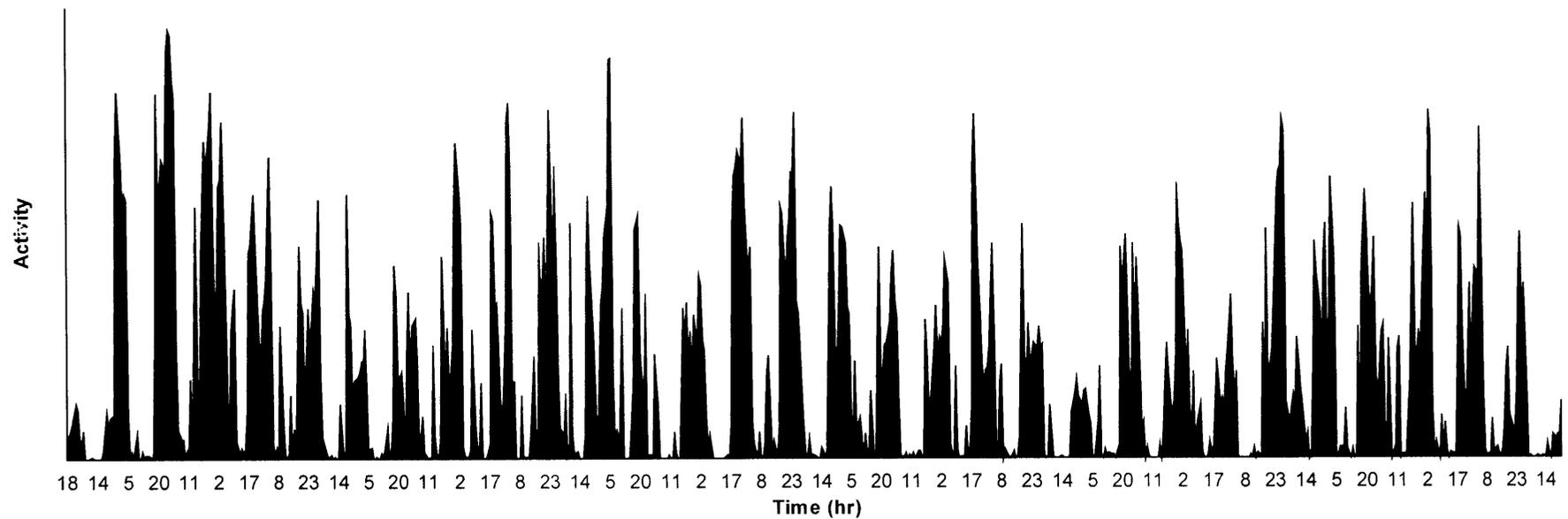


Figure 5.13 The typical diel cycle of nocturnal ranging and daytime resting in the burrow is clearly reflected in the pattern of hourly activity over a month for common wombat 03. Activity is from the period enclosed in the rectangle (September) in Figure 5.15d.

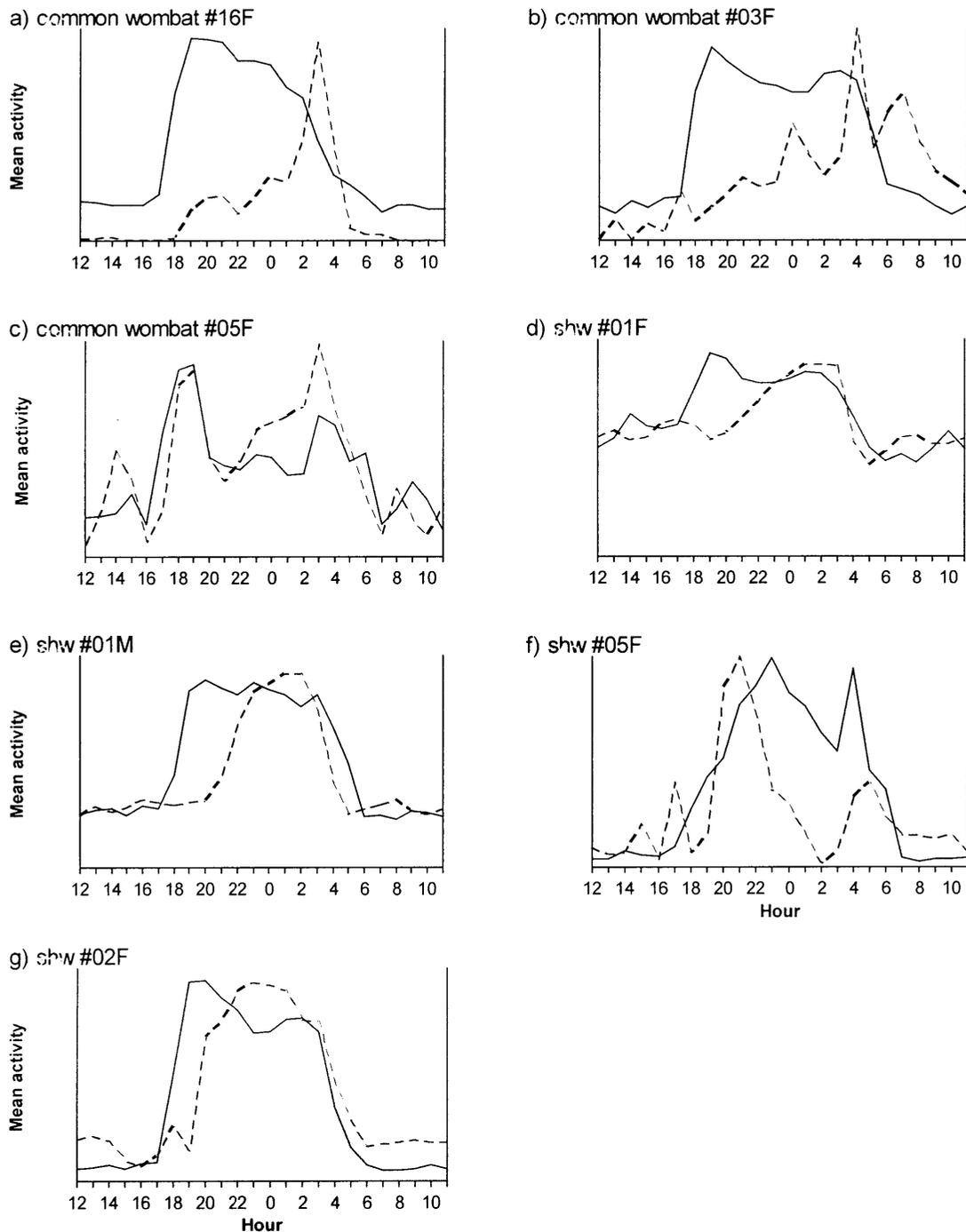
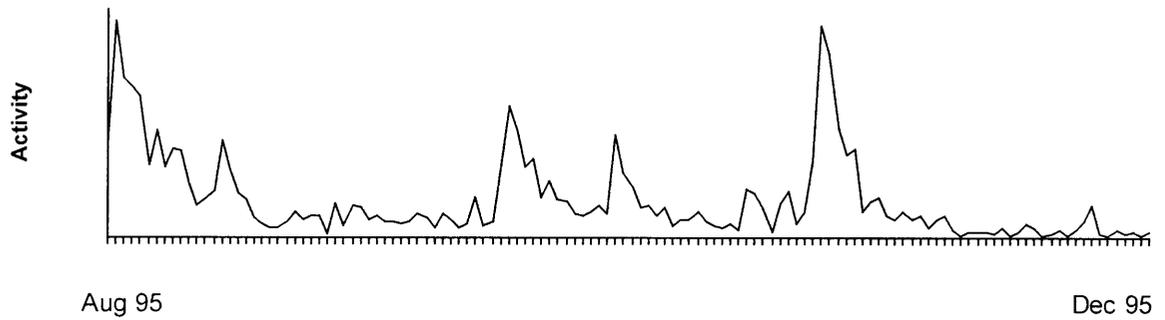
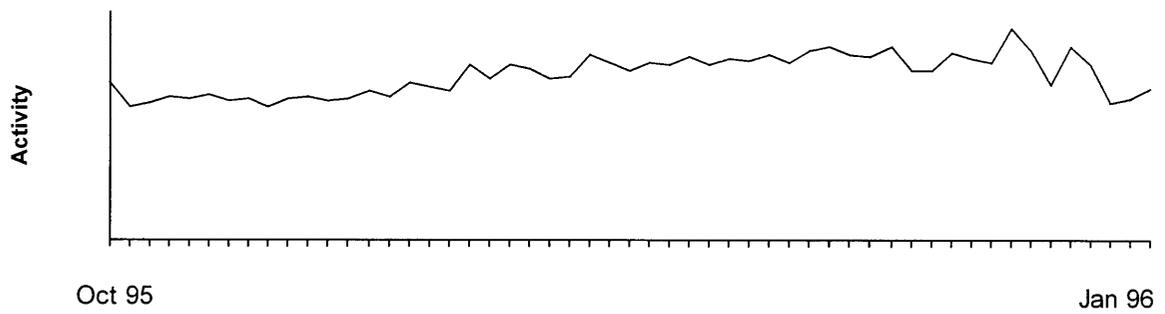


Figure 5.14 Mean hourly activity for common wombats and southern hairy-nosed wombats (shw). These hourly patterns show a diel cycle of nocturnal ranging (higher activity) and daytime resting (lower activity). Solid line = September, dashed line = December. Note that absolute levels of activity cannot be directly compared between individuals or between seasons for the same individual in this figure because the scales differ.

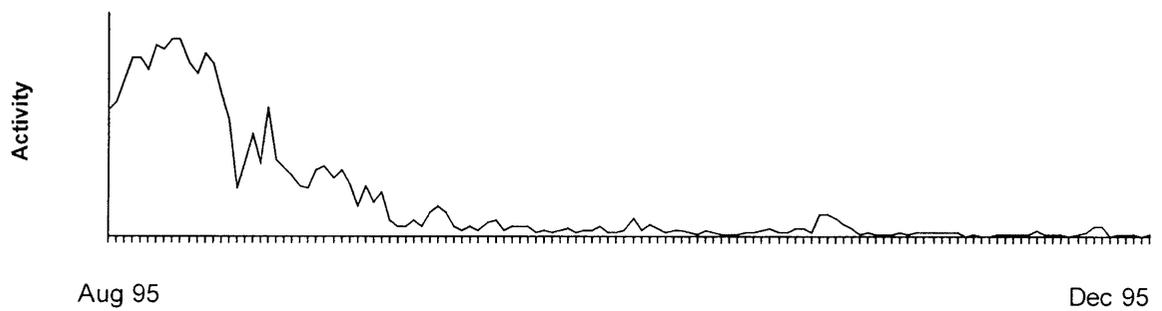
a) common wombat #05



b) common wombat #13



c) common wombat 16



d) common wombat #03

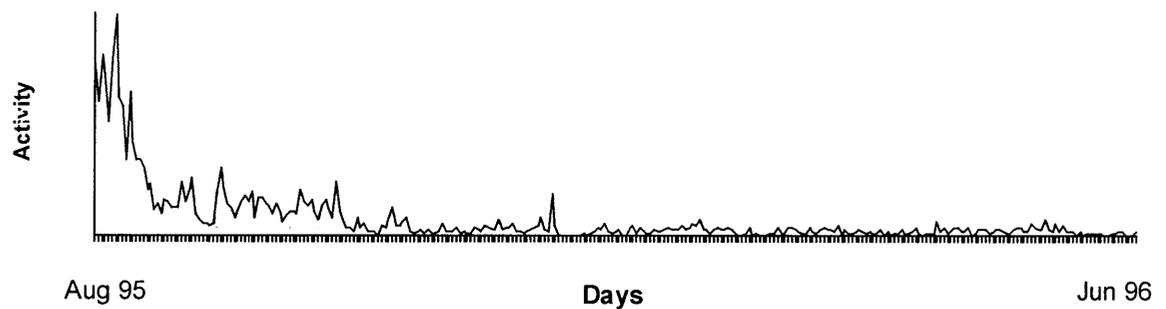


Figure 5.15 Daily activity levels for common wombats. Activity levels were recorded by data logging computers attached to collars. Axes scales differ between graphs. The rectangle encloses the period shown in Figure 5.13.

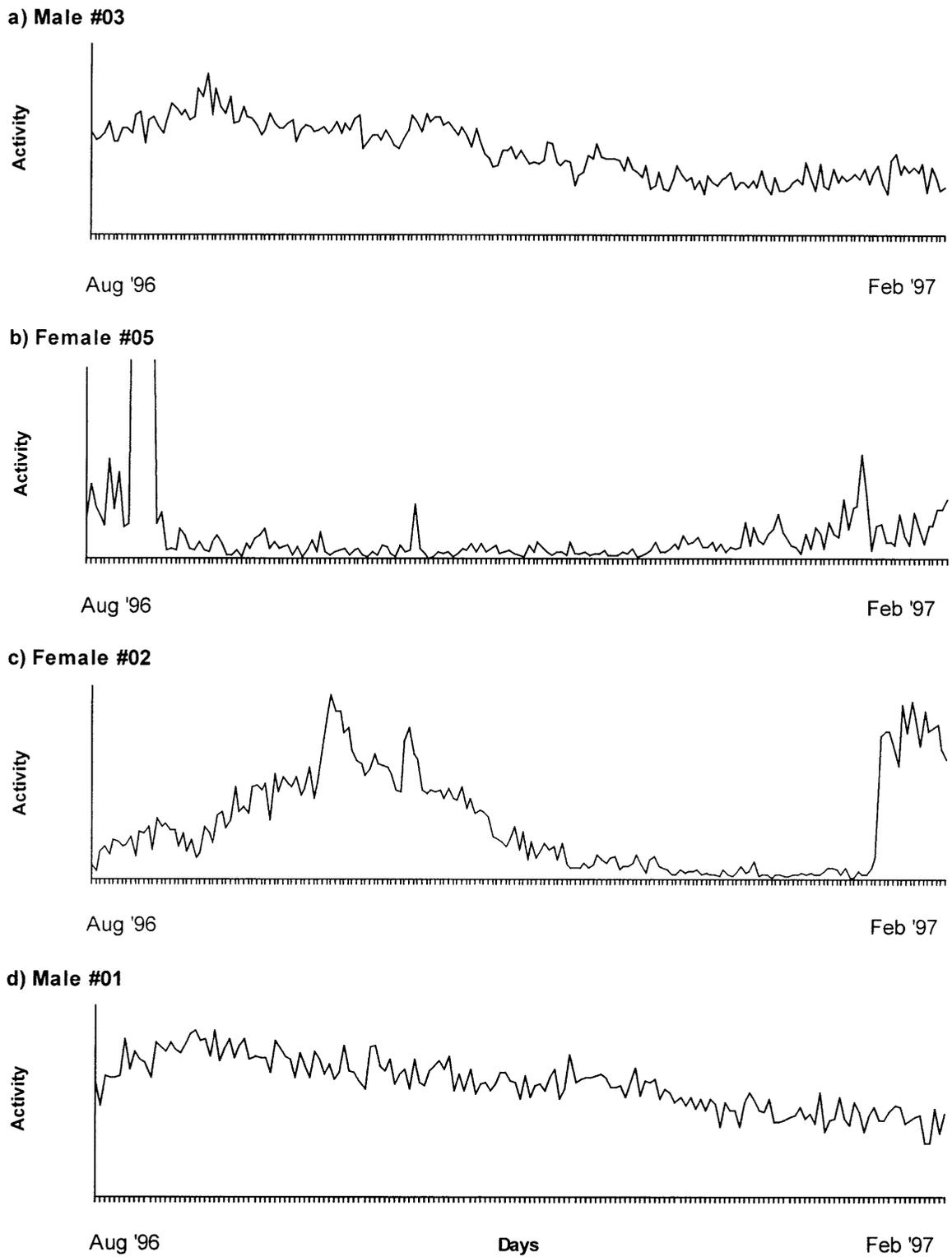


Figure 5.16 Daily activity levels for southern hairy-nosed wombats. Activity levels were recorded by data logging computers attached to collars. Axes scales differ between graphs.

able to burrow through the underlying softer substrate, the calcrete layer is generally impenetrable to the burrowing efforts of wombats. Burrow entrances are restricted to natural fissures and faults in the calcrete layer, which leads to 'warren' systems with a number of wombats using the same entrance. It is possible individuals avoid each other to some extent while in the warren by using different tunnels. The limited trapping and radio-tracking data for southern hairy-nosed wombats indicates that individuals used more than one warren, and these warrens were usually adjacent to each other. Adjacent warrens at the study site were up to 300 m apart. The community structure of burrows of northern hairy-nosed wombats appears to be intermediate to that of the other two species. Burrows of northern hairy-nosed wombats tend to be loosely aggregated into clusters, though burrows within clusters are not interconnected (pers obs). Burrows of this species appear to be more complex than those of common wombats in generally having two to several entrances. Individuals of this species do not use as many different burrows as common wombats, but northern hairy-nosed wombats appear to share burrows at the same time more often than do common wombats (pers obs).

5.4 DISCUSSION

5.4.1 Home-ranges

Common wombats ranged through all three habitat types at the Riamukka State Forest study site. Forest habitat was clearly important to wombats, as all home-ranges included this vegetation type. Almost all home-ranges included Cleared pasture, and only about half of the home-ranges included Woodland. Most core areas included both Forest and Cleared pasture, with relatively few core areas including Woodland. The relative level of use of the three habitat types was similar between summer and winter, indicating that common wombats did not markedly change their feeding areas between seasons. This suggests that wombats were not employing area selectivity as a feeding strategy to cope with seasonal differences in food availability or quality. It is possible that the lack of seasonal difference in the relative use of each habitat indicates that relative differences between habitats in terms of food availability or quality vary little between seasons. Intensity of use within the home range was remarkably uniform.

Home-ranges extensively overlapped between and within sexes, indicating that ranges are undefended. There is some evidence, however, that individuals mark their ranges.

Inter-seasonal differences in home-range size and ratio of core area to home-range area were not significant, indicating that wombats did not markedly vary their ranging behaviour between seasons. Ranging behaviour was also similar between sexes. From an energetics viewpoint, this suggests that common wombats do not conserve energy during the poor season (winter) by restricting movement to a smaller area than during the good season. Conversely, these animals do not appear to expand their home-ranges or core areas during the poor season in response to poorer food quality. Although wombats did not appear to vary their ranging behaviour between seasons, it is possible that activity levels varied seasonally (discussed below). Sample sizes (numbers of individuals) for comparing home-range areas and proportions of habitat types in home-ranges may have been insufficient to detect significant seasonal differences in these parameters. Any seasonal differences, therefore, would be expected to be subtle rather than marked.

There have been few studies of home-ranges or ranging behaviour for any of the three wombat species. The generally conservative ranging behaviour of wombats in this study is consistent with the results of other studies. McIlroy (1976) found home-ranges of common wombats in *Pinus radiata* plantations varied from 5 ha to 23 ha. Taylor (1993) found home-ranges of two male common wombats in largely cleared agricultural land in Tasmania were 8.3 ha and 13.3 ha. Annual home-ranges of northern hairy-nosed wombats averaged 27.3 ha and their size increased significantly by winter (Johnson 1991a). To my knowledge there have been no published studies of home-ranges of southern hairy-nosed wombats.

5.4.2 Activity

There is some evidence that capture, handling and collaring may have disrupted normal behaviour in some individuals. Behaviour may have been disrupted before capture, following capture, or both, and the change in behaviour was characterised by elevated levels of activity recorded by activity sensors. The duration of the possible effect on 'normal' behaviour from trapping, handling and collaring was difficult to determine for some individuals because of consecutive trapping events occurring within a

short period. Some individuals appeared to return to 'normal' activity levels within a week, whereas others apparently remained 'disturbed' for 2 or more weeks. I was unable to determine how much of the activity recorded by activity sensors was due to possible 'scratching' at a new collar by wombats, rather than elevated levels of 'whole-animal' movement.

The activity pattern was characterised by a strong diel cycle with limitation of most activity to the night. Activity occurred throughout the night, with the pattern consistent with a 'travel out, graze, travel back' pattern (higher activity levels at the start and end of the night's foraging). Nightly activity was highly variable within and between individuals. Nightly activity showed some similarity between nights with a gradual change between sequential nights, occasionally punctuated with markedly higher activity 'spikes' in some individuals. Loggers on some wombats showed huge changes in levels of activity that persisted over many days or weeks. It is probable that nightly activity levels are correlated with variations in local rainfall and temperature, though I have not extended the analysis of activity to include daily fluctuations in environmental variables. Three of the four southern hairy-nosed wombats showed lower daily activity levels during summer than during winter, suggesting energy conservation during the poor season. Because of the high rate of malfunction in loggers used for common wombats, and the characteristic 'fading' of activity to zero when loggers failed, I was uncertain whether the initial decline in activity observed for some common wombat individuals was real or was due to logger malfunction. For this reason I have not directly compared activity levels between seasons for common wombats. In addition, it is possible that activity sensors inherently differed in their sensitivity to movement, and this might account for the different levels in activity between individuals. Therefore, I have restricted direct comparisons of activity between individuals to patterns and trends rather than absolute levels.

Most of the individuals that wore activity sensors during late winter and summer showed a shorter mean period of 'higher' nocturnal activity in spring than in summer. This suggests that wombats were spending more time outside the burrow during the poor season than during the good season. The use of activity sensors in this study provided useful information on hourly, daily and seasonal patterns of activity. Activity data for

southern hairy-nosed wombats suggests that the answer to the question “Are activity levels lower during poor seasons than during good seasons?” is ‘yes’. Unfortunately, the high rate of logger malfunction, and the possibility of data being derived from loggers that were malfunctioning, precludes answering this question for common wombats.

5.4.3 Burrow-use

The burrow-use data for all three species indicate that a wombat may use more than one burrow, and that a burrow may be used by more than one wombat. Burrows are clearly not defended for exclusive use, yet there is evidence that wombats avoid sharing burrows (during the less active daytime). Such pattern of burrow use supports the notion that home-ranges are also not exclusive and are not defended (section 5.4.1). Common wombats change burrows frequently, with the frequency being days rather than weeks. Multiple-use burrows appear to be maintained by more than one individual. Maintaining and using a number of burrows throughout a home-range would ensure that a wombat always has ready access to a predator-safe refuge. This might be important for young age classes that are presumably more susceptible to predation (such as sub-adults or young-at-foot) than are adults. Maintaining a number of burrows throughout a home range is likely to be energetically less expensive in terms of ranging, as this alleviates disproportionate time being spent returning to a single fixed location within the home range. In addition, the use of burrows by multiple individuals means that maintenance costs of the burrows are also spread across more than one individual. For common wombats, what determines frequency of burrow-swapping or why individuals appear to restrict burrow-use to certain burrows (rather than random use of all burrows in the home range) is unknown. Relatedness amongst individuals might influence burrow-use. For example, sub-adult females might continue to use the burrows that their mother used. Clearly, more information is needed before the reasons underlying burrow-use behaviour can be fully understood.

5.5 SUMMARY

Home-ranges of common wombats were typically almost circular with a relatively uniform intensity of use within the range. There was no intersexual distinction in ranges (though statistical power was limited by small sample sizes). Ranges and core areas extensively overlapped between and within sexes indicating undefended ranges. Forest and Cleared pasture were clearly important habitats for wombats at the Riamukka Forest site. Despite occurring in a seasonal environment, wombats at Riamukka SF appear to be remarkably invariant in the location of their ranges, where they range and the distribution of activity within the range. Burrow-use was not exclusive, with some burrows being used by a number of individuals at different times.

Activity was characterised by a strong diel cycle with limitation of most activity to the night. Activity occurred throughout the night, with a pattern consistent with a travel out-graze-travel back pattern. Nightly activity was highly variable, even within short periods. Most individuals showed a shorter mean nocturnal activity period in winter than in summer. Southern hairy-nosed wombats were less active during the hot, dry summer than winter when plants grew. Trapping, handling and collaring possibly disrupted normal behaviour of some individuals, as evidenced by apparently high levels of activity recorded during these periods. Logger malfunctions precluded seasonal comparison of activity levels for common wombats.