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# The Biology of *Bettongia penicillata* Gray, 1837, and *Macropus eugenii* (Desmarest, 1817) in Relation to Fire

P. E. S. CHRISTENSEN

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# The Biology of *Bettongia penicillata* Gray, 1837, and *Macropus eugenii* (Desmarest, 1817) in Relation to Fire

by

P. E. S. CHRISTENSEN

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*Conservator of Forests*

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*FRONT COVER*

Woylie (*Bettongia penicillata*)
Photograph Darryl Blackshaw

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# Summary

The woylie (*Bettongia penicillata*) and the tammar wallaby (*Macropus eugenii*) live in a flammable habitat and it is to be expected that fire has been a force of evolutionary significance in the biology of both species. The presence of possible adaptations was tested by means of experimental burns.

Mortality during experimental burns was extremely low. Both species remained within their home range areas, escaping the fire by seeking refuge on small unburnt patches or by doubling back through the flames. Woylies generally remained within their burnt-out home range areas, living primarily on species of hypogean fungi. Despite considerable mortality during these periods, some individuals survived to reproduce. Re-colonisation was effected by these and other young animals from unburnt patches and from the unburnt surrounds.

After fire tammar wallabies, which feed largely on grasses, attempted to re-establish themselves in neighbouring colonies. Mortality was high and re-colonisation of the post-fire succession was slow. Although tammars from nearby thickets fed on the burn area, two years after the fire the regrowth thickets had not yet reached a seral stage suitable for re-colonisation.

An ordination study indicated that the areas occupied by both species may be defined in terms of site-vegetation types. Some of the underlying factors that determine the occurrence of the vegetation types are identified in broad terms. It is suggested that these factors limit the distribution of both the study species by their influence on the distribution of food and cover species.

Both species are well adapted to the environment in which they live. They survive fire and successfully re-colonise the post-fire succession without any obvious specific fire adaptations. Both species exhibit a marked degree of "fire dependence", in that the food and cover species on which they depend are adapted to certain specific fire regimes. In the prolonged absence of hot fires it is likely that colonies of both species would suffer severe reduction or even disappear altogether from the habitats studied.

SECTION I

# General Introduction

It is likely that fires have occurred since combustible materials first appeared on earth. Lightning, as an expression of the earth's electro-magnetic field, has been a constant source of ignition and a major fire agent in recent times (Komarek, 1967 and 1968), and there is every reason to believe that it was so in the past. American coal beds provide evidence of ancient fires during the Carboniferous and later epochs (Komarek, 1972), and there is also evidence of pre-historic fires from Mesozoic coals in Australia (Gill, 1973).

The role of fire in ecosystems has been extensively reviewed by Kozlowski and Ahlgren (1974), and there can be little doubt that it is a major force of selective adaptation in many ecosystems. Australian ecosystems have been influenced by fire for a very long time. *Eucalyptus,* the characteristic and dominant genus of many current Australian plant communities, is generally believed to have evolved some time before mid-Tertiary (Crocker and Wood, 1947). More recently, R. T. Lange* (personal communication) has produced definite evidence of *Eucalyptus* and other current genera in deposits believed to be either Oligocene or Mio-Pliocene in origin.

There is a close association between fire, eucalypts and their associated understoreys (Mount, 1964; Mutch, 1970; Webb, 1970). The extensive array of adaptations enabling eucalypts and their associated understoreys to survive fire has been reviewed by Gill (1975).

The little fossil evidence that exists suggests that the families and possibly also the sub-families of Australian marsupials were differentiated by the Miocene at the latest (Simpson, 1961; Tedford, 1974). In view of their long association it seems reasonable to suppose that, like the eucalypt communities which they inhabit, many of Australia's marsupials should exhibit fire adaptations. However, recent fire ecology studies of Australian mammals (Leonard, 1972; Recher *et al.,* 1974 and 1975; Christensen and Kimber, 1975) show little evidence of adaptations which may be directly attributed to fire.

It may be that mammals are adapted to combustible habitats (Kozlowski and Ahlgren, 1974) rather than fire *per se.* For example, Handley (1969) and Komarek (1962) regard such traits as the ability to run quickly, burrowing and storing food, migration and pressing flat to avoid detection, as features that are probably adaptations to flammable grassland habitats. The connection between such traits and fire is somewhat vague. They are more readily interpreted as the results of collective adaptive influences of many factors rather than of fire alone.

The question arises: do mammals in fact possess certain traits which may be confidently attributed wholly or partly to the adaptive influence of fire? If such traits exist they should be most obvious among populations living in highly flammable habitats. To investigate this possibility two marsupials living in the highly flammable dry sclerophyll forests of the Perup region in south-western Australia were chosen for study. The animals chosen were a rat kangaroo, *Bettongia penicillata* Gray, 1837 (the woylie), and a small wallaby *Macropus eugenii* (Desmarest, 1817) (the tammar). These two species were chosen because little or no information was available on the relationship between medium-sized animals and fire in Australia. Both species live in close association in the Perup, are easily trapped and are large enough to permit the use of radio telemetry. This choice provided a comparison of two species living in different habitats in the same locality. It also provided an opportunity of collecting data relevant to habitat management of these two uncommon species: the woylie is now listed as an endangered species in the Red Data Book (Simon, 1966).

In considering those aspects of the two species' biology most likely to be influenced by fire, useful parallels may be drawn from plants, which have been studied more fully. Plant adaptations to fire tend to centre around three life-history stages: (1) survival of the adult; (2) survival of the seed (propagule); (3) germination and establishment of the seedlings (Gill, 1975).

If fire adaptation in the first two stages exists in mammals, it is unlikely to manifest itself in the same manner as in plants. Whereas plants have become specialised in the area of protection, animals are mobile and can thus avoid the direct effects of fire in a variety of ways and move to unburnt areas after fire. Any adaptive influence of fire on mammals is more likely to exhibit itself in behavioural patterns and other aspects of movement. The third stage, establishment of the young, is one where fire adaptations may be expected to be similar in both animals and plants. In addition, fire may affect the distribution of mammals indirectly through the media of food and shelter.

Three hypotheses were formulated as a basis for a study of these specific areas of the species' biology.

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The first hypothesis formed the basis of a vegetation and site study dealing with the distribution of the study species. It was an indirect approach to see whether vegetation or edaphic factors influence distribution and whether fire is implicated either directly or indirectly.

The second and third hypotheses formed the basis of a population study concentrating particularly on aspects relating to movement during and after fire and to re-establishment of the population.

**Hypothesis 1**

Both woylie and tammar populations are centred around certain site types which may be defined by distinctive plant associations. Each plant association is indicative of certain site characteristics, some or all of which are identifiable.

**Hypothesis 2**

Woylies and tammars will survive within the burn, but they will fall prey to predators during the first weeks after fire. Re-population of the area will be effected by young animals from the unburnt surrounds and large unburnt patches within the burn area itself.

**Hypothesis 3**

Woylies remain within their home range area after fire, not because they are excluded from the unburnt surrounds by other home range owners, but because of an innate fidelity to their home range area.

Hypothesis 1 was based on personal observations made on woylie and tammar distribution obtained during spotlight surveys and from trapping results. Also, Havel (1975*a*) showed that plant associations are indicative of site characteristics. Hypothesis 2 was based on the results of an earlier study of the effects of fire on the southern bush rat (*Rattus fuscipes*) (Christensen and Kimber, 1975), which indicated that there was no emigration of resident *R. fuscipes* after fire had destroyed all vegetative cover on their home range areas. Hypothesis 3 was developed during the testing of the second.

The first hypothesis was tested by means of principal component analysis. Hypotheses 2 and 3 were tested using capture-recapture techniques and radio telemetry to track marked animals before and after two experimental areas were burnt. A study of the animals' food, in particular that of the woylie, was included at a later stage because of its relevance to the species' survival in relation to the fire cycle.

SECTION II

# Habitat Site-vegetation Studies

## INTRODUCTION

Both study species, once widespread, are now much reduced in numbers (Shortridge, 1909; Perry, 1971; Wood-Jones, 1924; Finlayson, 1958; Wakefield, 1967; Ride, 1970; Sampson, 1971). Clearing for agriculture has undoubtedly contributed to their decreased populations by reducing the area of suitable habitat. However, this factor alone cannot account for their disappearance from many uncleared areas where they were formerly reported to be common.

Among reasons advanced for their disappearance from these areas are predation by the introduced European fox (*Vulpes vulpes*) and domestic cat (*Felis catus*), and competition from other feral animals such as the rabbit (*Oryctolagus cuniculus*) and the goat (*Capra hircus*) (Wood-Jones, 1924; Troughton, 1967; Ride, 1970). Little or no proof is advanced to substantiate these claims, and the evidence is largely circumstantial. In one of the few population studies of native species, Sampson (1971) considers that predators play only a minor role in limiting the distribution of the woylie.

Suitable habitat is an important factor in species distribution, and large areas of dry sclerophyll forest habitat still remain in a comparatively undisturbed state. Why then do both species have such a restricted range? Trapping and spotlight surveys in the Perup area, where the largest known concentration of woylies is found and where the tammar is also common, suggested a clumped or discontinuous distribution. Both species appear to be associated with specific site-vegetation types: the distribution of woylie nests and diggings, both good indicators of woylie presence (see Section IV), in Dryandra Forest (Table 1), and trapping in Tutanning (Sampson, 1971) suggest associations with certain vegetation types.

In attempting to explain the present distribution of the study species it was necessary to find out whether there were any fundamental differences between populated and neighbouring unoccupied or little-used areas. Vegetation type has a marked influence on fire frequency and intensity (Christensen and Kimber, 1975), and a better understanding of the relationship between the study species and the vegetation may also assist in defining the role of fire in their ecology.

## CHOICE OF METHODS

Methods of vegetation analysis suitable for this type of study are reviewed by Havel (1968 and 1975*a*). Of the many methods available principal component analysis (P.C.A.) is the most likely to reveal any associations between the study species and site-vegetation types. The method uses the inter-relationship between plant species to detect the underlying factors which determine the vegetational pattern. The factors are mathematical abstractions which may or may not be identifiable with actual environmental factors. It has been used successfully in the study of vegetation associations and in the detection of the underlying factors which determine vegetation distribution (Goodall, 1954; Havel, 1968 and 1975*a*; Noy-Meir, 1971 and 1974). Less frequently, it has been used to study the factors influencing the distribution of

**Table 1**
DRYANDRA FOREST—NEST AND DIGGING TRANSECTS

| *Site-vegetation type* | *Transect length (m)* | *Nest numbers* | *Digging numbers* | *Nests per 100 m* | *Digging per 100 m* |
|---|---|---|---|---|---|
| 1. *Eucalyptus wandoo* and *E. accedens*. Lower to mid-slopes sandy loams to sandy gravels | 2575 | 9 | 322 | 0·35 | 12·50 |
| 2. As above—recently burnt | 1100 | 1 | 19 | 0·09 | 1·73 |
| 3. *E. accedens* and *Dryandra nobilis* + *Petrophile* also *E. drummondii*, ridge-tops lateritic | 1500 | 7 | 191 | 0·47 | 12·73 |
| 4. *E. accedens* and *D. nobilis*. Very dense thicket, ridge-top laterite | 200 | 11 | 4 | 5·5 | 2·00 |
| 5. *Casuarina huegeliana* thicket | 250 | Nil | 14 | Nil | 5·60 |
| 6. Sand plain, open low scrub on white sand | 1100 | Nil | 1 | Nil | 0·10 |

Data from a survey carried out in Dryandra forest during December 1975. Transects 12 m wide, located at random, were sampled in the main forest blocks.

animals; for example, zooplankton (Miracle, 1974), ants (Majer, 1976) and birds (James, 1971).

A major consideration in choosing P.C.A. was the fact that site-vegetation types similar to those in the study area have been defined and mapped successfully in the region immediately to the north (Havel 1975*a* and 1975*b*). It thus seemed certain that a P.C.A. of site and vegetation factors would be successful in the study area. It remained to establish whether woylie and tammar distribution could be successfully integrated into the site-vegetation framework and whether some of the underlying factors influencing their distribution could be identified.

In case other methods may have provided more valuable information a hierarchical linkage analysis (McQuitty, 1964) was also tried.

## METHOD

### The study area

An area of approximately 6000 km², including all known woylie and tammar populations within the State forest area east of Manjimup, was selected for the study (Figs. 1 and 2). The area is in the south coast drainage system within the mature to old drainage lines on the upper reaches of the Warren River (Bettenay and Mulcahy, 1972). Although it is further to the east, much of the eastern sector of the area is similar to the Perup association (McArthur and Clifton, 1975) of broad, flat, seasonally swampy drainage lines separated by low ridges. Yellow podsolic soils occur along the drainage lines while the ridges are sandy gravels with occasional boulders and sheets of laterite pavement. Open woodland of jarrah (*Eucalyptus marginata*) and wandoo (*E. wandoo*) with an understorey of low xeric scrub typically dominates the ridges. The broad flat drainage lines support occasional trees of paper bark (*Melaleuca preissiana*) and a tall open or closed xeric scrub layer.

The extreme south-western corner is occupied by the Nyamup association representing dissected laterite country with younger, more fertile soils (McArthur and Clifton, 1975). The valleys have steep sides with

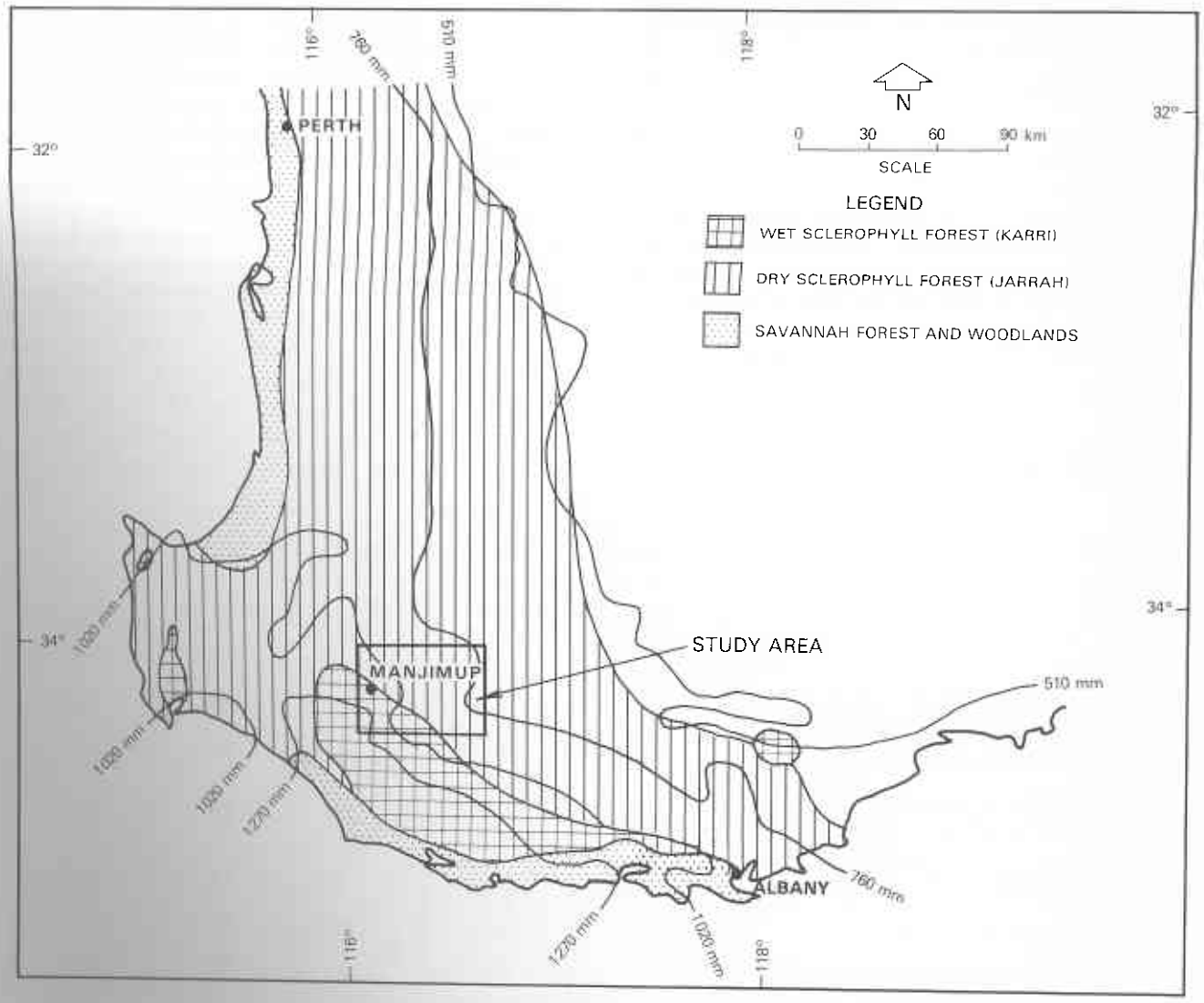



**Figure 1**

Map of the south-west of Western Australia showing location of study area.

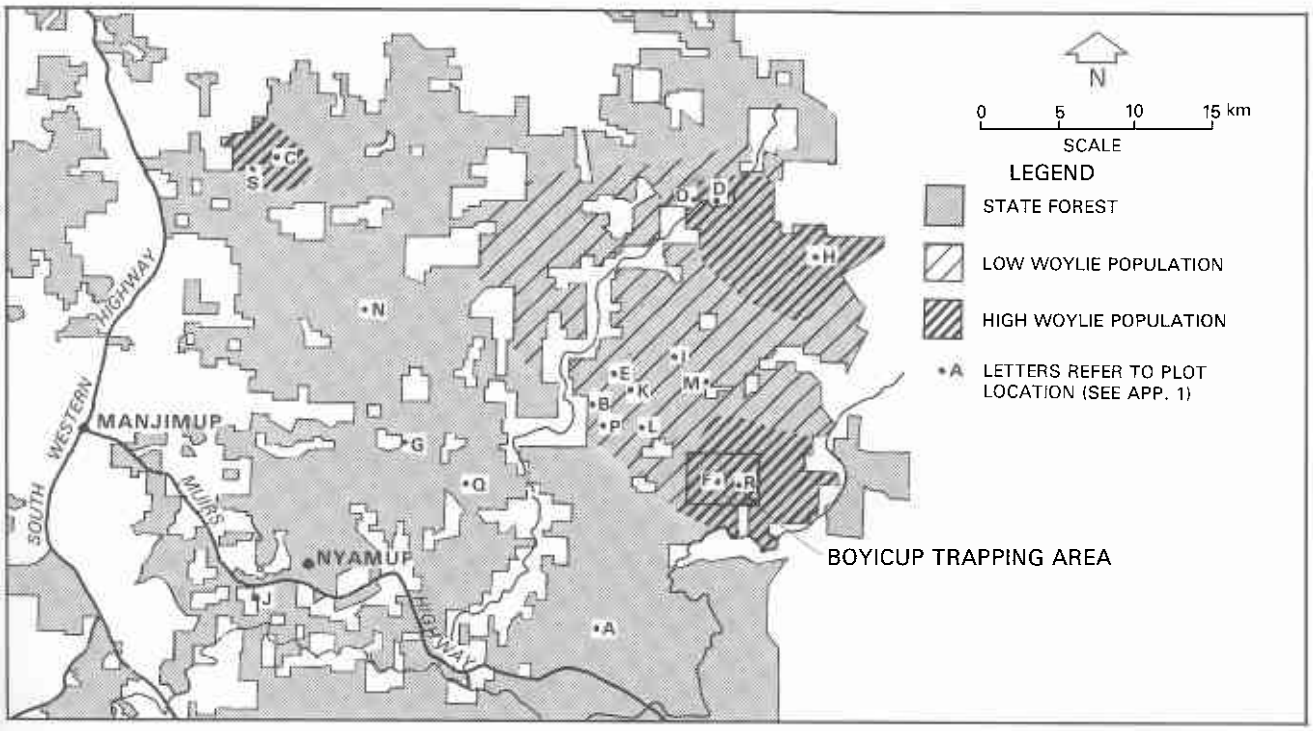



**Figure 2**

Map of study area showing location of Boyicup trapping area, vegetation site locations and woylie distribution.

yellow and red podsols and red earth predominating on the ridges and slopes, and the main streams have terraces of loamy alluvium. The main vegetation, high closed jarrah and marri (*E. calophylla*) forest with a dense xeric to mesic understorey, dominates the ridges. Valley bottoms often have stands of blackbutt (*E. patens*) and dense tall mesophytic scrub and understorey trees.

The range between these two extremes is occupied by associations very similar to the Balbarrup association of McArthur and Clifton (1975). The dry northeastern sector of the study area is similar to the Perup association but more xeric.

**Sampling method**

Data were collected for two separate analyses.

(1) An intensive study was carried out in an area of limited extent with high woylie and tammar populations. This comprised a total of 188 circular plots, 12 m in diameter, located systematically on the trapping grid in the 1975 burn area in Boyicup block (see Fig. 20).

(2) A wide-scale study was conducted covering a range of nineteen sites over an extensive area within and around the area of the main Perup woylie and tammar populations. A further 206 plots were located on these sites (see Fig. 2). Two criteria were used in choosing the sites to be sampled.

(*a*) They must represent the widest possible range of site-vegetation types within the study area.

(*b*) They should include sites with both high and low woylie and tammar populations as well as some in which neither species was present.

The nineteen selected sites are described in Appendix I. These sites are not the equivalent of Havel's (1975*a*) site-vegetation types and should not be confused with them.

For the analysis it was necessary to reduce the total number of plant species recorded to a list of those most likely to indicate habitat differences. The list (see Fig. 11) comprised all those left after rejecting rare species, species with very narrow site preferences, small perennials, species difficult to identify and species with weak habitat preferences (Havel, 1975*a*). Where possible, species represented in Havel's site-vegetation study were included.

The frequency of each "indicator" species on each plot was estimated using a five-point scale (Havel, 1975*a*). Other data relating to scrub structure, topography and soils were also recorded (Appendix II). Nest counts along 1-km transects in each locality and the numbers of diggings per plot were used as quantitative indicators of woylie presence. Nest counts (Christensen, unpublished data) and diggings (see Section IV) are both good indicators of woylie presence. Capture percentages were used to indicate tammar presence. In the Boyicup study woylie and tammar presence was measured more accurately using capture percentages per plot.

## ANALYSIS AND RESULTS

Principal component analysis of data from the intensive study in Boyicup block produced relatively little separation of the sample plots. The only clear pattern was the separation of upland and valley plots on Component 1. This result was not unexpected as the area sampled is small and, apart from the difference between upland and valley, is fairly

homogeneous throughout. Woylies occur uniformly throughout the area with the exception of the denser parts of the heartleaf (*Gastrolobium bilobum*) thickets occupied by the tammar in the valleys. These results strengthen the hypothesis that woylies occur on certain site types.

Accordingly, the main results are not presented, but some of the data showing correlations between woylie nests and scrub structure are presented later.

Similarly, results of McQuitty's (1964) analysis carried out on the wide-scale study data are not presented. The analysis was quite successful and achieved a reasonable hierarchical assemblage. However, some "unnatural" groupings occurred; for example, species recorded infrequently tended to be grouped together regardless of the lack of any ecological affinity. Further, the method does not allow interpretation of the underlying factors responsible for the observed groupings. Apart from confirming some of the affinities between the species it contributed nothing new to the analysis.

The results presented below are the results of P.C.A. of the wide-scale study area.

**Distribution of plots within the component space**

*Distribution of the sample plots*

Ordination of the plots was accomplished using the programme FACVA (Havel, 1975*a*). This programme combines the loadings of the vegetation species on the component axes with their cover values on individual plots to obtain scores which can be used as plot co-ordinates. The plot co-ordinate (score) on any component axis is the sum, for all species, of the products of their loadings on that component and the deviation of their cover value on that plot from their mean cover value in the study as a whole. Varimax rotation was used to obtain the best alignment of the component axes.

Good separation of both plots and sites has been achieved on both Components 1 and 2 (Fig. 3). These two components represent 14·0 and 8·9 per cent of the variance respectively. The plots on any particular site tend to fall within the same general area of component space. Exceptions to this occur on heterogeneous sites which cover a range of site-vegetation types, for example, the Moopinup (H) site.

Component 1 (C1) separates the well drained sites, concentrated towards the negative end of the axis, from the wet and seasonally wet sites which occur towards the positive end. Component 2 (C2) separates sites in the western deeply dissected, high-rainfall country (negative end) from those in the eastern lower-rainfall area (positive end).

Components 3 (C3) and 4 (C4) account for only 7·3 and 5·4 per cent of the total variance respectively. Hence separation is not as good, and plots tend to be

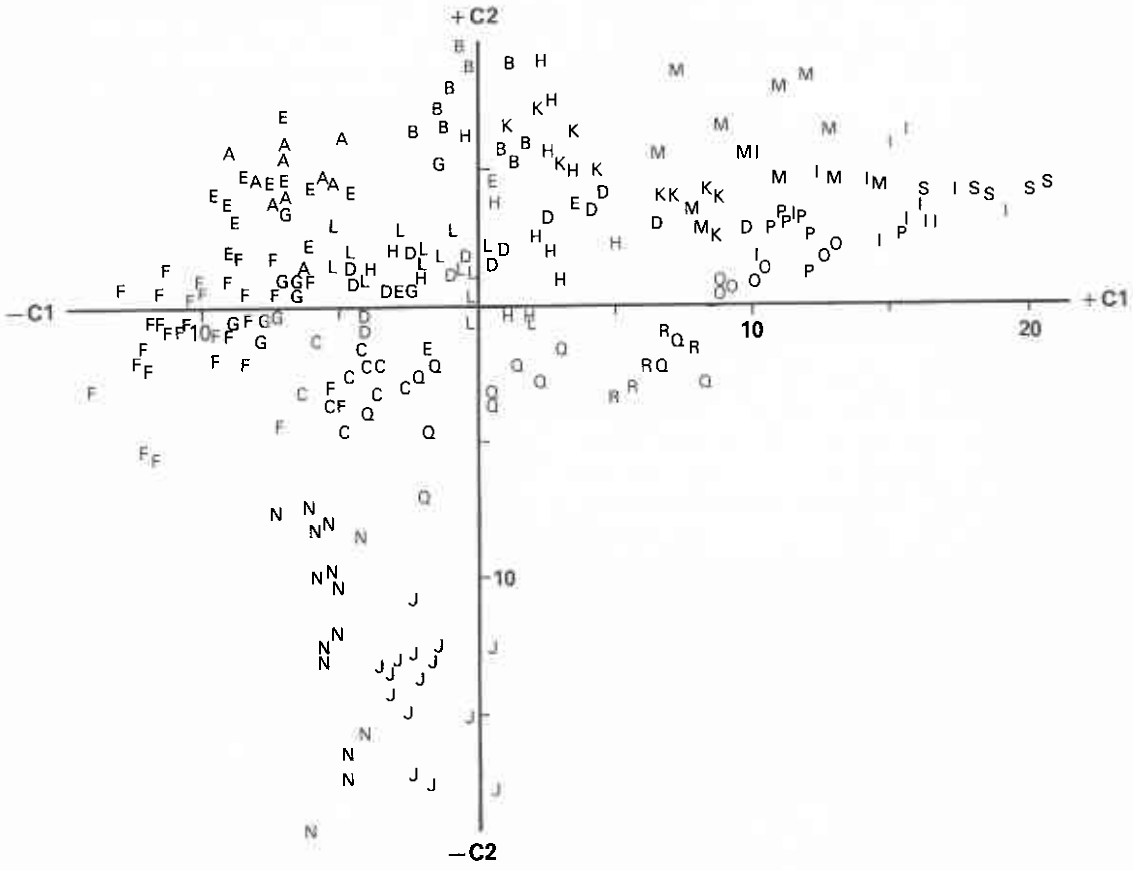



**Figure 3**

Distribution of 236 sample plots within component space derived by P.C.A., varimax loadings, 64 vegetation species, Components 1 and 2. Letters refer to sites, see Appendix I.

clustered about the intersection of the axes. To avoid confusion, only plots from some selected sites are shown in Fig. 4.

Open treeless plots with very shallow soils from the granite outcrop site (K) occur towards the positive end of the C3 axis, while the plots from sites on deeper soils are clustered at the negative end. Plots from seasonally droughty upland sites in the eastern sector occur towards the positive end of the C4 axis, while plots on moist to wet sites in depressions occur towards the negative end.

**Distribution of woylies within the component space**

To see whether there was any correlation between woylie distribution and vegetation plots, numbers of diggings and nests per plot were plotted within the component space using the plot scores (Figs. 5 and 6). High values for both nests and diggings show a distinct concentration at the negative end of the C1 axis; on C2 the diggings tend slightly towards the negative end also. These are the well drained upland sites tending towards the western sector. Lesser concentrations of diggings and some nests occur towards the positive end of both C1 and C2 on the seasonally wet, more fertile red earths and podsols of the wandoo sites.

Owing to the cluster of plots at the intersection of the axes, nests and diggings are shown differently on C3 and C4. The component framework has been sectioned into squares of one unit each, and the mean number of nests or diggings per square is plotted (Figs. 7 and 8). The highest concentration of both nests and diggings occurs at the extreme negative end of C3 tending towards the negative end of C4. These are sites with deep soils towards the moister end of the spectrum. Some nests and diggings also occur on the shallow soils of the granite outcrop at the negative end of C3.

Distribution of woylie nests on plots within the component space is best visualised using a four-dimensional model (Havel, 1975*a*). The concentration of plots with high densities of woylie nests is obvious and very striking (Plate 1).

**Distribution of tammars within the component space**

Capture percentages are plotted within the component space in a manner similar to that used for the woylie nests (Figs. 9 and 10).

The tammar occurs in a very definite area, situated towards the positive end of the C1 axis and rather more towards the negative end of C2 than the woylie. These are the moister, sometimes seasonally wet valley sites tending towards the more fertile western sector.

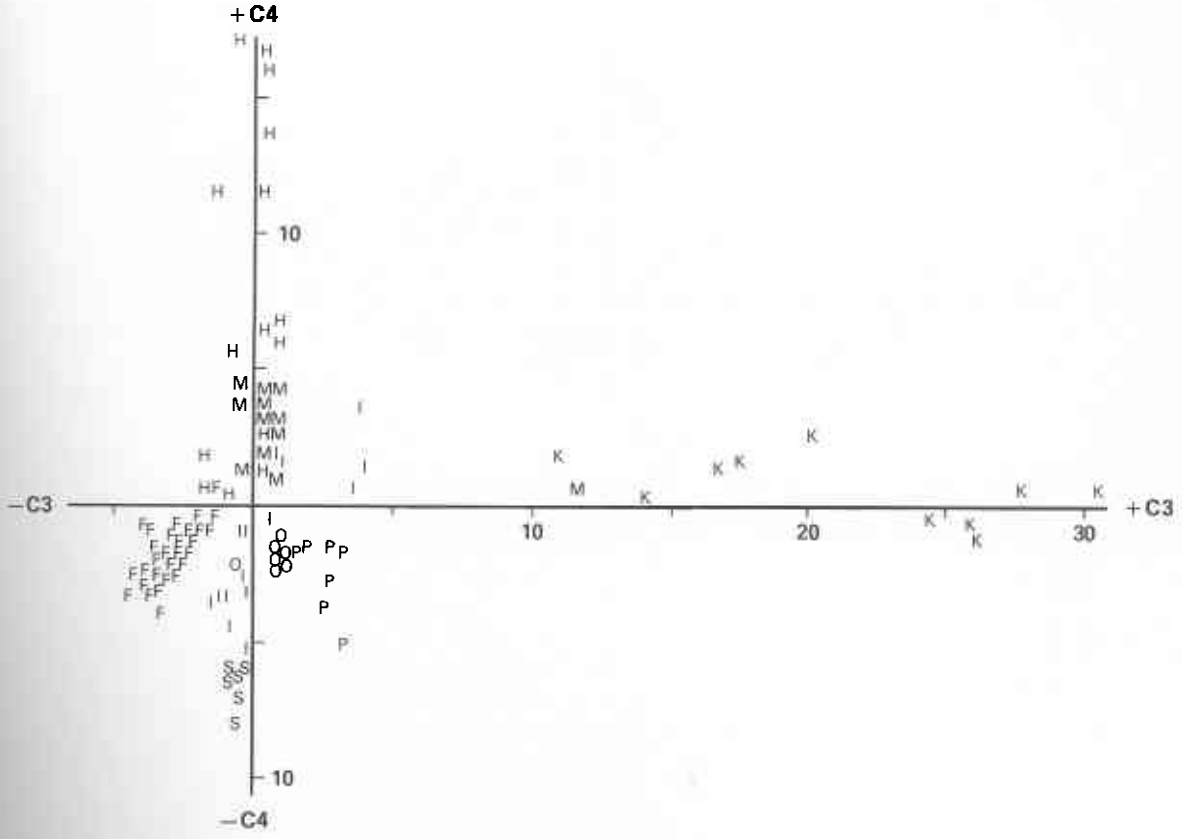



**Figure 4**

Distribution of 103 sample plots within component space derived by P.C.A., varimax loadings, 64 vegetation species, Components 3 and 4. Letters refer to sites, see Appendix I.

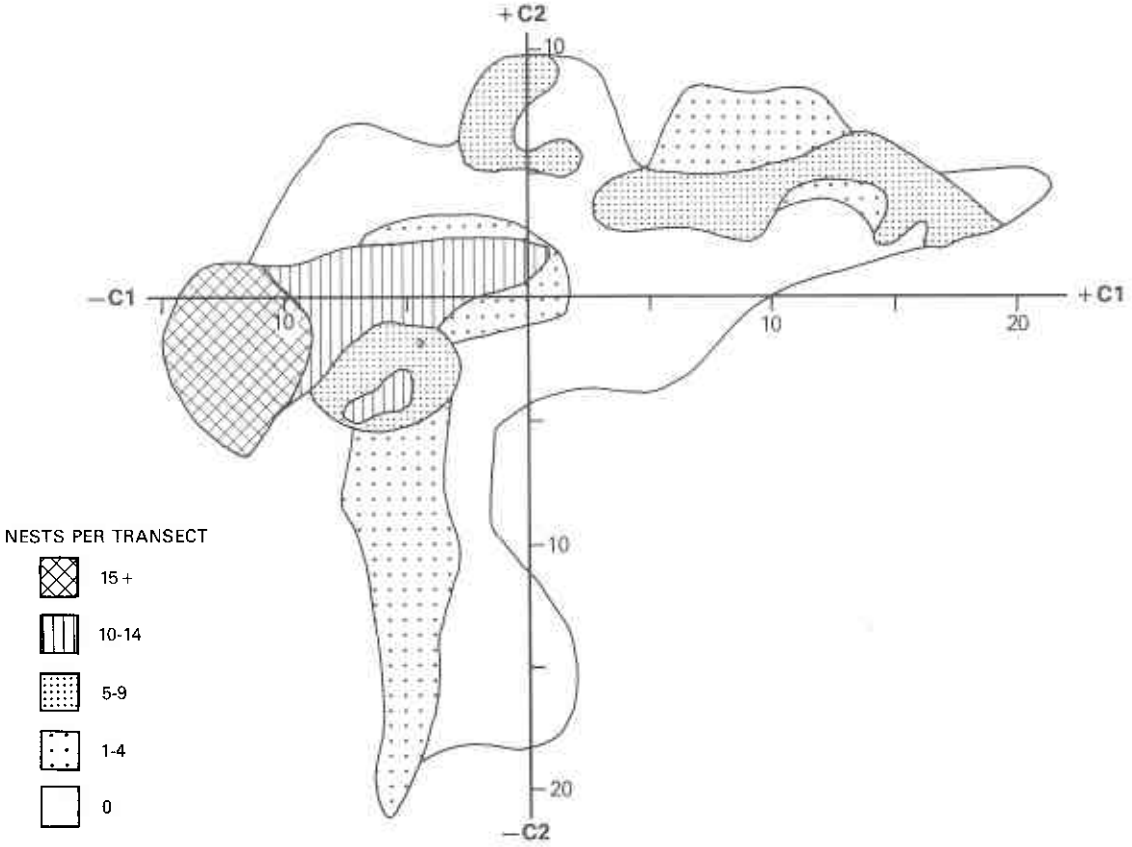



**Figure 5**

Distribution of woylie nests on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 3), Components 1 and 2.

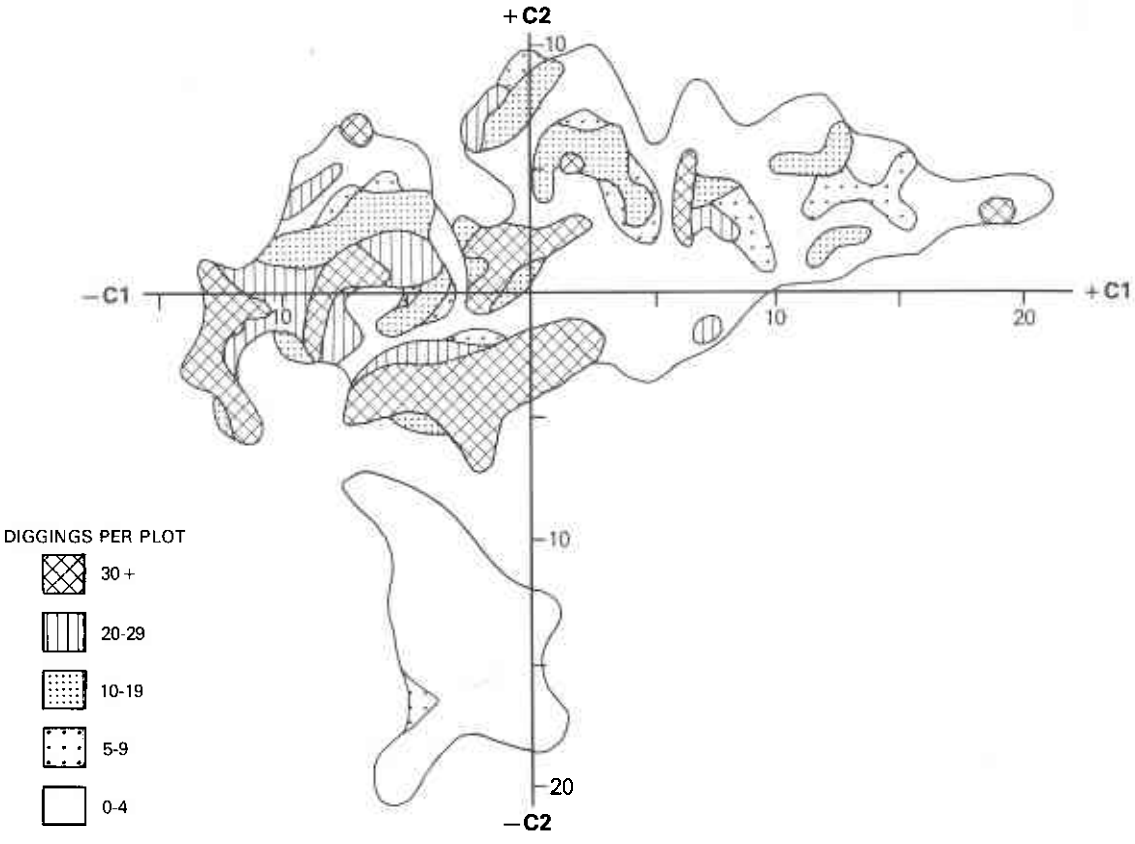



**Figure 6**

Distribution of diggings on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 3), Components 1 and 2.

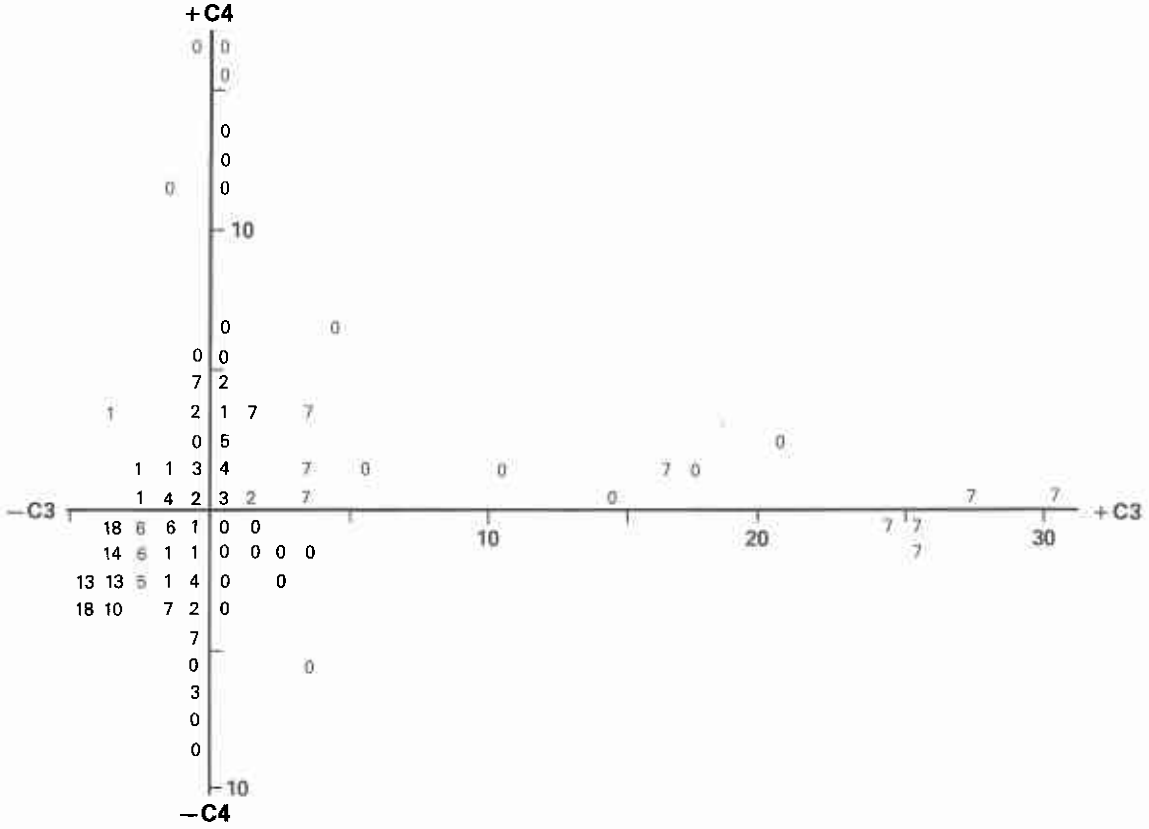



**Figure 7**

Distribution of woylie nests on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 4), Components 3 and 4. The component framework has been divided into segments of one unit each. The numbers in each represent the mean number of nests per plot for the plots within each segment.

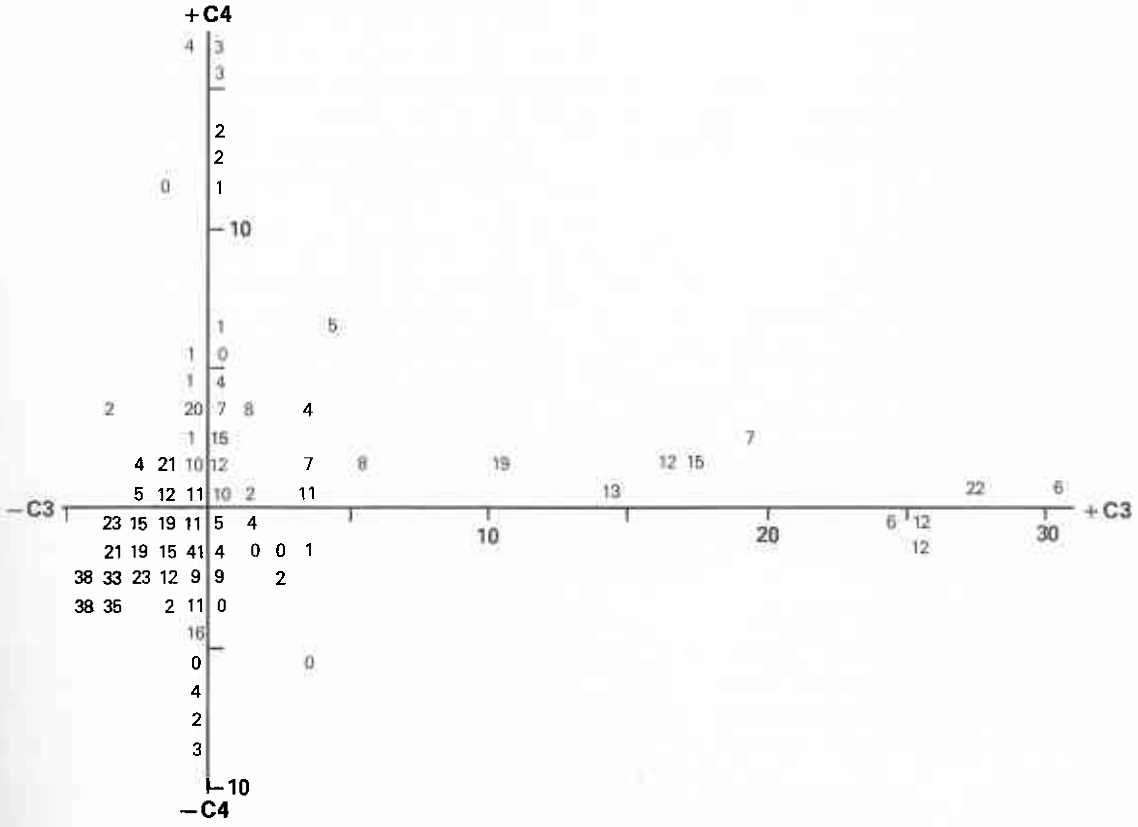



**Figure 8**

Distribution of diggings on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 4), Components 3 and 4. The component framework has been divided into segments of one unit each. The numbers in each represent the mean number of diggings per plot for the plots within each segment.

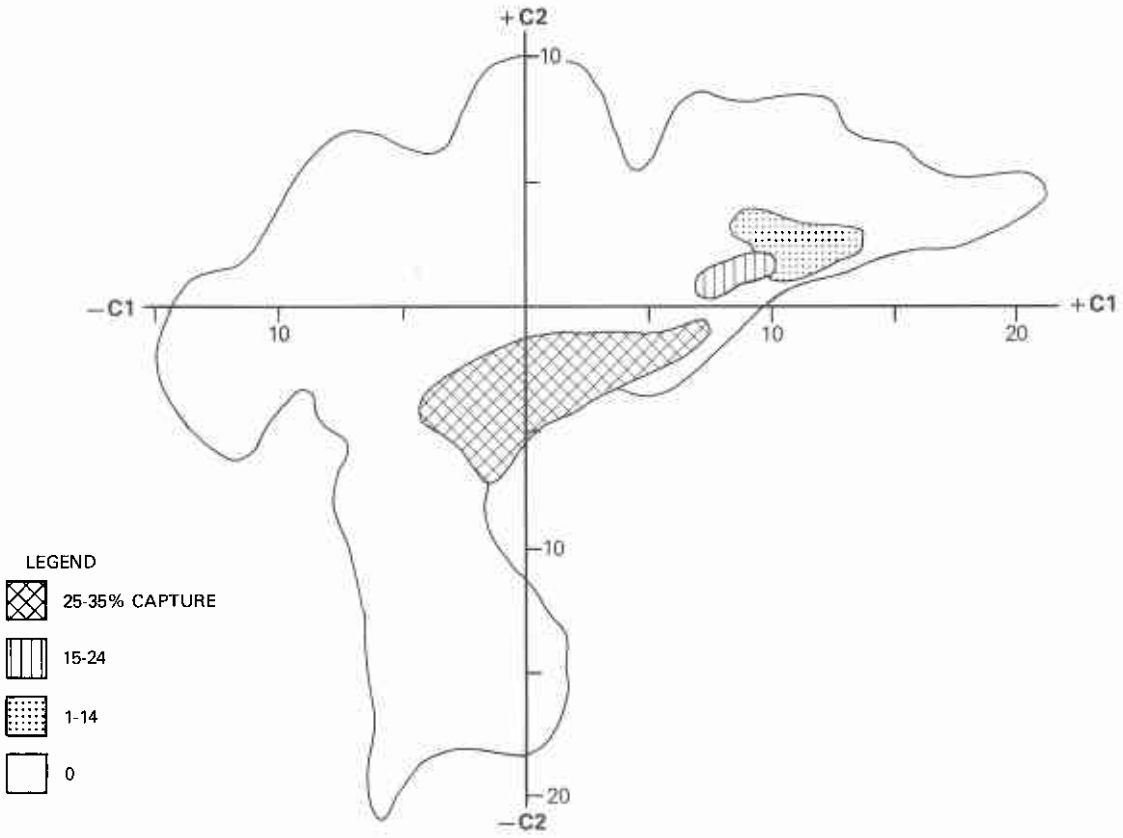



Figure 9

Distribution of tammars on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 3), Components 1 and 2.

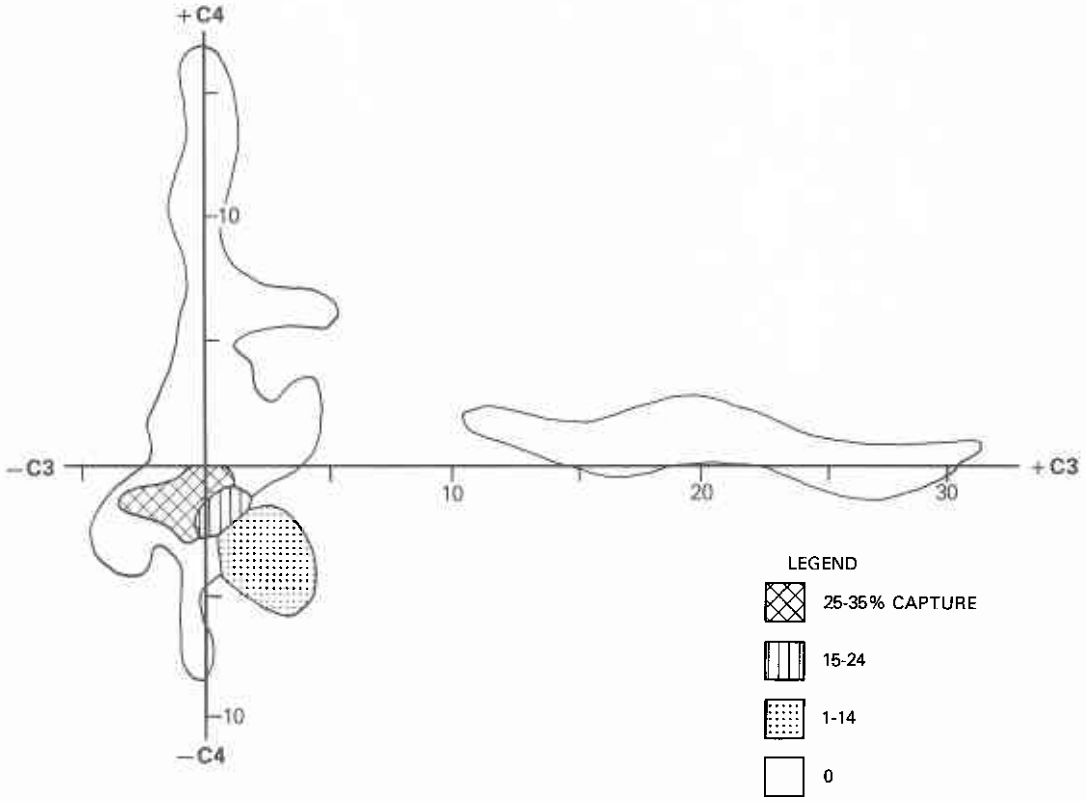



**Figure 10**

Distribution of tammars on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 4), Components 3 and 4.

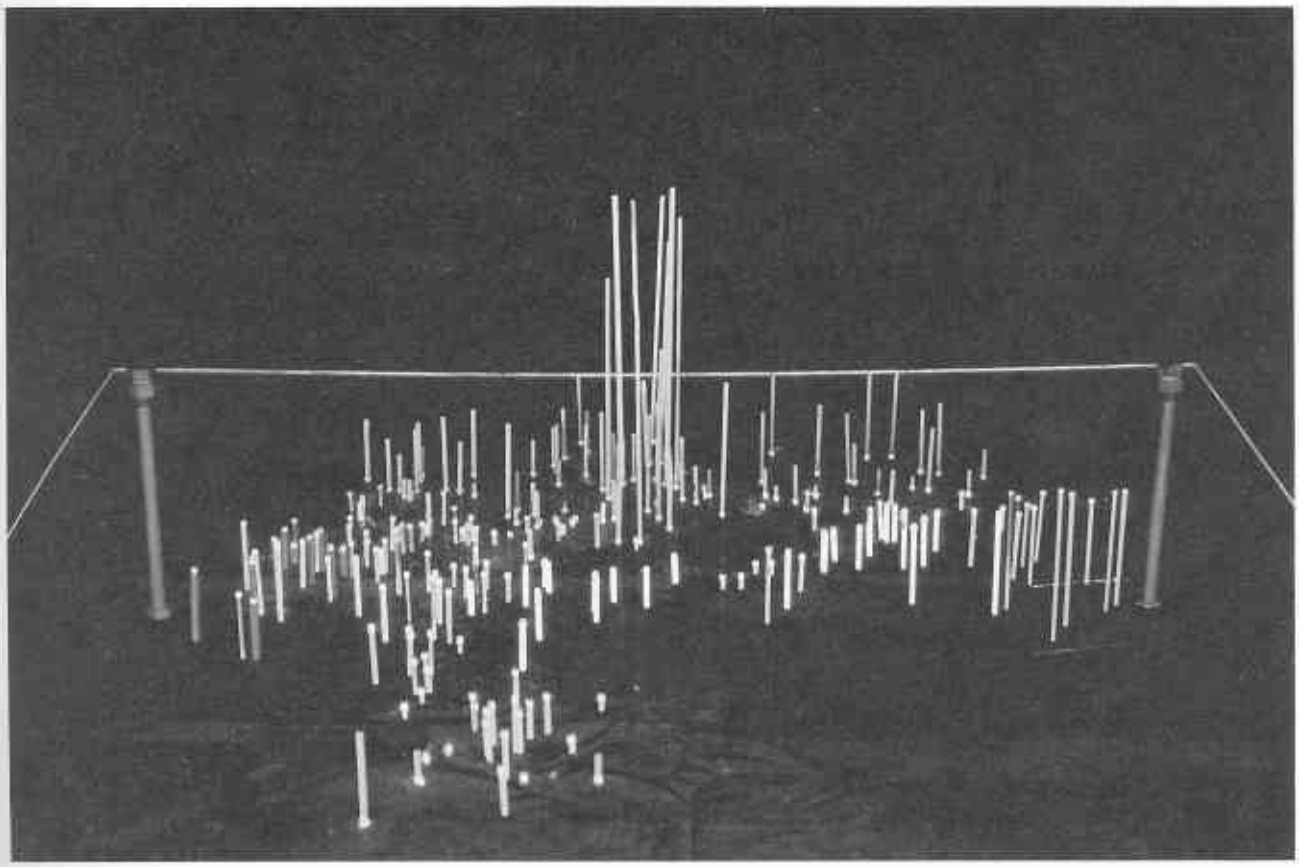


**Plate 1**

Four-dimensional model of ecological relationships in the study area. Each coloured stick represents an ecological sample plot. The arrangement of components derived by P.C.A. is as follows:

Left to right: —C1 to +C1. Front to back: —C2 to +C2. Up: +C4. Down: —C4.

The colours represent the concentration of woylie nests per plot and tammar presence on plots.

| | | | |
|---|---|---|---|
| White sticks | = Tammar present | Blue sticks | = 1 to 9 woylie nests per transect |
| Red sticks | = 15+ woylie nests per transect | Green sticks | = No woylie nests per transect |
| Yellow sticks | = 10 to 14 woylie nests per transect | | |

Within the framework of the third and fourth components they occupy the sites towards the negative ends of both axes (the deeper soils), but tending more towards the seasonally wet sites than the woylie sites.

Again, their restricted area of distribution is most striking on the four-dimensional model (see Plate 1).

**Interpretation of the principal components**

Woylie and tammar sites fall into distinct and definable areas within the component space based on the vegetation plot scores. If the principal components can be identified with specific environmental factors, some of the underlying factors determining woylie and tammar distribution may be revealed.

Two approaches were tried.

(1) The use of indicator species—thirty-three of the species used in the analysis occur in the area covered by Havel's (1975*a*) survey. Soil analysis data including both chemical and physical properties are available for the sites on which these species occur. These data were used in the interpretation of the principal components.

Distribution of the vegetation species within the component space is shown in Figs. 11 and 12. Varimax loadings were used since they show the relationship between the components and vegetation species better than normal loadings (Havel, 1975*a*).

Species occurring at the extremities of each axis are listed below.

—C1 *Leucopogon capitellatus, Eucalyptus marginata, Hakea lissocarpha, Leucopogon verticillatus, Macrozamia riedlei*—species occurring on well drained upper slopes with deep sandy gravelly loams (Plate 2).

+C1 *Drosera bulbosa, Acacia cyanophylla, Hakea prostrata, Hypocalymma angustifolium, Melaleuca preissiana*—species typically associated with broad, flat, seasonally swampy drainage lines (Plate 3).

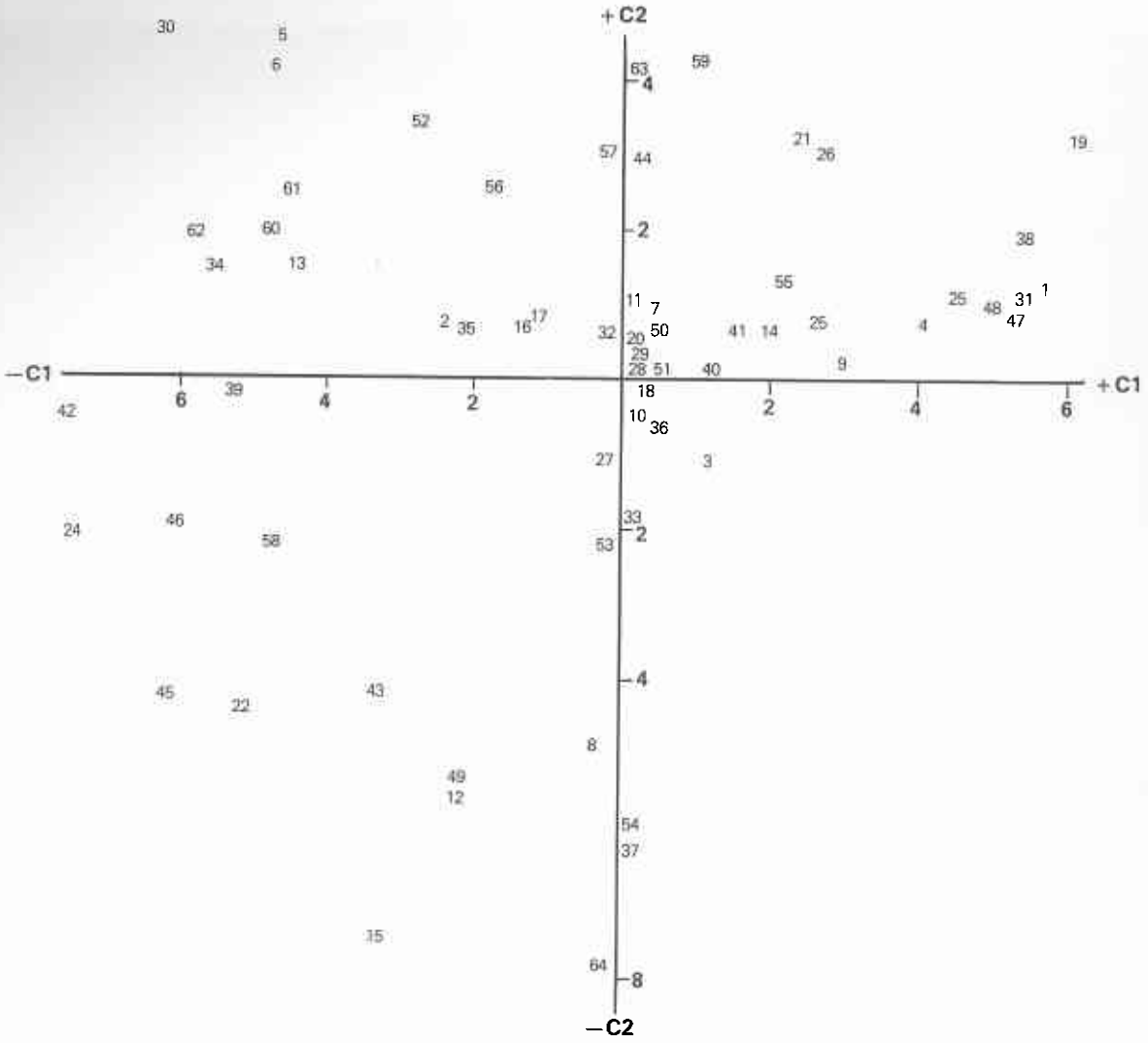



**Figure 11**

Distribution of 64 individual plant species within component space derived by P.C.A., Components 1 and 2.

1. *Acacia saligna*
2. *Acacia* sp.
3. *Agonis parviceps*
4. *Astartea fascicularis*
5. *Astroloma pallidum*
6. *Astroloma ciliatum*
7. *Baeckea camphorosmae*
8. *Banksia grandis*
9. *Banksia littoralis*
10. *Banksia sphaerocarpa*
11. *Bossiaea eriocarpa*
12. *Bossiaea linophylla*
13. *Bossiaea ornata*
14. *Casuarina humilis*
15. *Clematis pubescens*
16. *Conostylis setigera*
17. *Daviesia preissii*
18. *Pultenaea ericifolia*
19. *Drosera bulbosa*
20. *Dryandra armata*
21. *Dryandra nivea*
22. *Eucalyptus calophylla*
23. *Eucalyptus decipiens*
24. *Eucalyptus marginata*
25. *Eucalyptus rudis*
26. *Eucalyptus wandoo*
27. *Gastrolobium bilobum*
28. *Gastrolobium spinosum*
29. *Hakea incrassata*
30. *Hakea lissocarpha*
31. *Hakea prostrata*
32. *Hakea undulata*
33. *Hibbertia cuneiformis*
34. *Hibbertia cunninghamii*
35. *Hibbertia glaberrima*
36. *Hibbertia quadricolor*
37. *Hovea elliptica*
38. *Hypocalymma angustifolium*
39. *Leptomeria cunninghamii*
40. *Leptospermum ellipticum*
41. *Leucopogon australis*
42. *Leucopogon capitellatus*
43. *Leucopogon propinquus*
44. *Leucopogon pulchellus*
45. *Leucopogon verticillatus*
46. *Macrozamia riedlei*
47. *Melaleuca viminea*
48. *Melaleuca preissiana*
49. *Persoonia longifolia*
50. *Petrophile serruriae*
51. *Phyllanthus calycinus*
52. *Pimelea suaveolens*
53. *Podocarpus drouynianus*
54. *Ranunculus lappaceus*
55. *Synaphea petiolaris*
56. *Thomasia grandiflora*
57. *Trymalium ledifolium*
58. *Xanthorrhoea gracilis*
59. *Xanthorrhoea preissii*
60. *Xanthosia atkinsoniana*
61. *Xanthosia candida*
62. *E. marginata*—regrowth
63. *Acacia pulchella*
64. *Pteridium esculentum*

−C2 *Pteridium esculentum, Clematis pubescens, Hovea elliptica, Ranunculus lappaceus, Bossiaea linophylla, Persoonia longifolia*—species associated with well drained, fertile upper slopes in the high rainfall western sector (Plate 4).

+C2 *Xanthorrhoea preissii, Acacia pulchella, Pimelea suaveolens, Dryandra nivea, Trymalium ledifolium, Leucopogon pulchellus, Thomasia grandiflora*—species more common in the eastern sector, often on poor, infertile sites supporting low-quality forest (Plate 5).

−C3 *Eucalyptus marginata, Macrozamia riedlei, Leucopogon propinquus, Hakea lissocarpha, Leucopogon verticillatus*—species commonly occurring on deep soils, very similar to −C1.

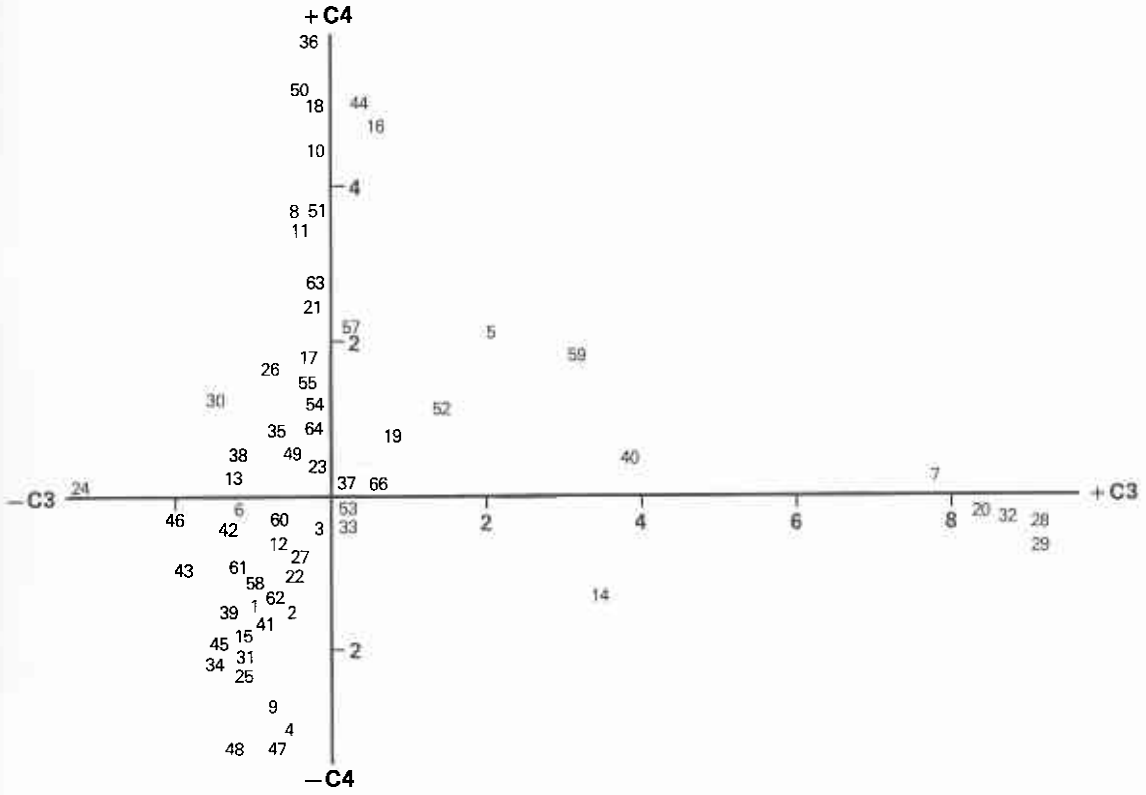



**Figure 12**

Distribution of 64 individual plant species (see Fig. 11) within component space derived by P.C.A., Components 3 and 4.

+C3 *Gastrolobium spinosum, Hakea incrassata, Hakea undulata, Dryandra armata, Baeckea camphorosmae*—species common on soils too shallow for tree growth and often overlying massive granite (Plate 6).

−C4 *Melaleuca preissiana, M. viminea, Astartea fascicularis, Banksia littoralis, Eucalyptus rudis*—species occurring on moist to wet sites in depressions (Plate 7).

+C4 *Hibbertia quadricolor, Petrophile serruriae, Pultenaea ericifolia, Leucopogon pulchellus, Conostylis setigera, Banksia sphaerocarpa*—species occurring on dry upland sites in the eastern sector, which is subject to drought (Plate 8).

A refinement of the vegetation species approach to the identification of the component axes is to examine the patterns formed by individual species within the co-ordinate framework based on vegetation, using the CORD programme (Havel, 1975*a*). The pattern of distribution of each of the sixty-four species used was thus examined and the results confirmed the conclusions reached above.

(2) Plotting of soil data within the component space.

Although a fairly detailed soil analysis was carried out on sixteen of the sites, it was difficult to associate component axes with individual soil factors. Fine sand showed a general correlation with woylie site distribution (Fig. 13). There is a tendency towards a high fine sand content in the soils on sites towards the negative end of the C1 axis, the area with the highest woylie density. Other data relating to soil structure and composition, clay content and coarse sand, showed no correlation with woylie distribution.

Similarly, definite associations with soil fertility factors, phosphate content, cation exchange capacity and nitrogen content were difficult to detect. The best correlation, total phosphate, is shown in Fig. 14. There is a general trend towards higher phosphate levels near the negative end of the C1 axis. Although the wandoo sites do not conform, they correlate with woylie distribution (see Figs. 5 and 6).

It was not possible to identify C3 and C4 with any of the soil factors recorded. Soil analysis was not carried out on the tammar sites.

In summary, the four principal components may be identified as follows:

C1—Mainly a topographical factor, separating well drained upland sites with deep soils and good to reasonable soil water retention capacity from low-lying valleys and depressions which are moist to seasonally wet, often poorly drained and of low water retention capacity.

C2—Largely a geographical factor, separating the eastern plots from the western ones. Several factors are closely related to this east-west alignment (McArthur and Clifton, 1975). Rainfall increases approximately 8 mm per annum per kilometre from east to west. A topography of broad flat valleys and

## Site-vegetation types representative of the extremities of the P.C.A. axis

**Plate 2**
Extremity —C1 axis; deep sandy gravels on well drained upper slope.

**Plate 3**
Extremity +C1 axis; broad flat seasonally wet drainage line.

**Plate 4**
Extremity —C2 axis; well drained fertile upper slopes in high rainfall western sector.

**Plate 5**
Extremity +C2 axis; poor infertile site in the low rainfall eastern sector.

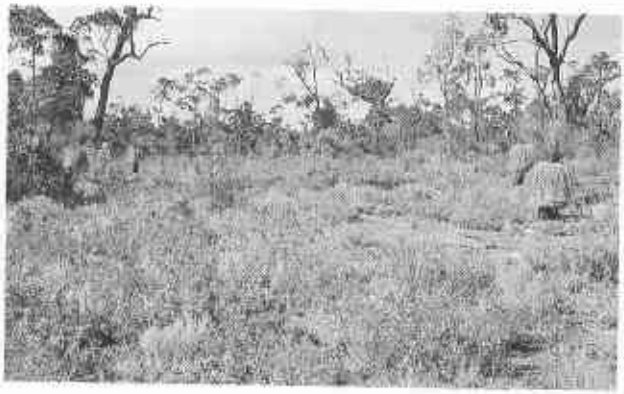


**Plate 6**
Extremity +C3 axis; soils too shallow for tree growth overlying massive granite.

**Plate 7**
Extremity —C4 axis; moist wet site in a depression.

**Plate 8**
Extremity +C4 axis; dry upland site in eastern sector subject to drought.

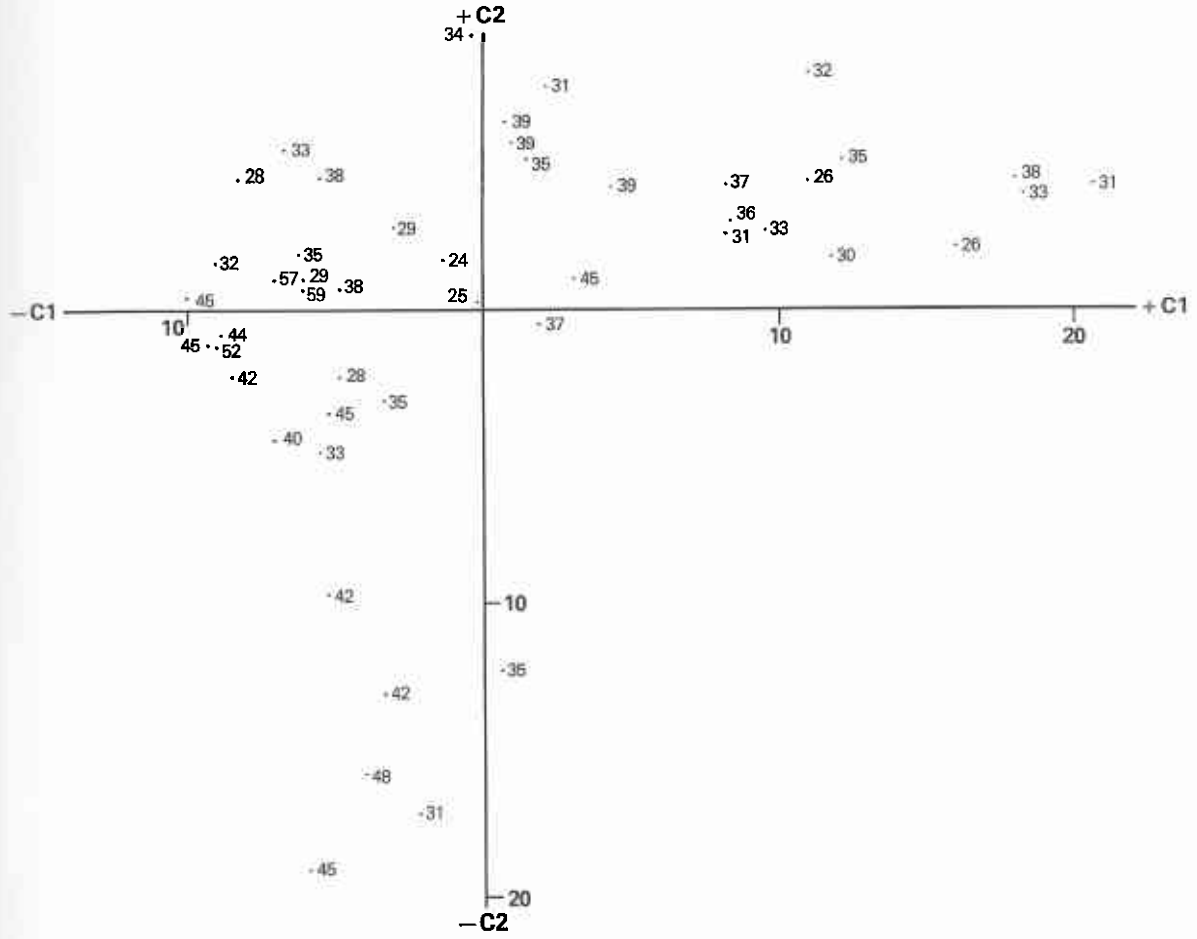



**Figure 13**

Distribution of percentage fine sand on 48 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 3), Components 1 and 2.

low ridges changes to one of deeply incised valleys and high ridges. Soil fertility is generally low in the old eroded soils of the eastern sector and high in the younger soils of the dissected western landscape.

C3—A soil depth factor—plots with deep soils are separated from sites with shallow soils overlying massive granite and from those with impermeable layers in broad, flat, seasonally wet valleys.

C4—A drought factor—plots on drought-prone eastern sites are separated from moist valley sites with deep soils not subject to seasonal drought.

## Correlation of individual variables with woylie and tammar occurrence

*The woylie*

Examination of the correlation matrix from the P.C.A. of the Boyicup trapping area, where nests were counted on each individual plot, revealed a correlation between nests and scrub density at 0 to 60 cm ($r = +0{\cdot}347$) and between nests and bare ground ($r = +0{\cdot}283$). The correlation co-efficients are not high, but they are significant at the 0·001 level. These two factors show a high negative correlation with one another: $r = -0{\cdot}787$ in the wide-scale survey and $r = -0{\cdot}831$ in the Boyicup survey. When plotted within the component space on C1 and C2 (Fig. 15), ground cover density (scrub density 0 to 60 cm/bare ground) forms a pattern very similar to the woylie nest distribution (see Fig. 5). The highest nest densities occur in areas with a scrub density of more than 50 per cent at 0 to 60 cm and bare ground of 20 to 40 per cent. Dense cover is a requirement for nesting, but a certain percentage of bare ground appears to be essential to the woylie, to allow it to move through the scrub.

The broad correlation between a high fine sand content of the soil and woylie sites was noted earlier. Further evidence of a preference for sandy gravels is evident in the correlation of individual plant species with woylie diggings. Plant species showing the highest correlations with diggings are: *Hakea lissocarpha* ($r = +0{\cdot}490$), *Leptomeria cunninghamii* ($r = +0{\cdot}322$) and *Hibbertia cunninghamii* ($r = +0{\cdot}322$). These species all have moderately high negative correlations with soil type and moderately high positive correlations with stoniness, showing that they prefer sandy gravels. High negative correlation with diggings are shown by *Persoonia longifolia* ($r = -0{\cdot}381$) and *Pteridium esculentum* ($r = -0{\cdot}310$), both on the heavier soils in the western sector. Diggings also show weaker negative correlations with *Banksia grandis* and *Drosera bulbosa,* species which are typical of

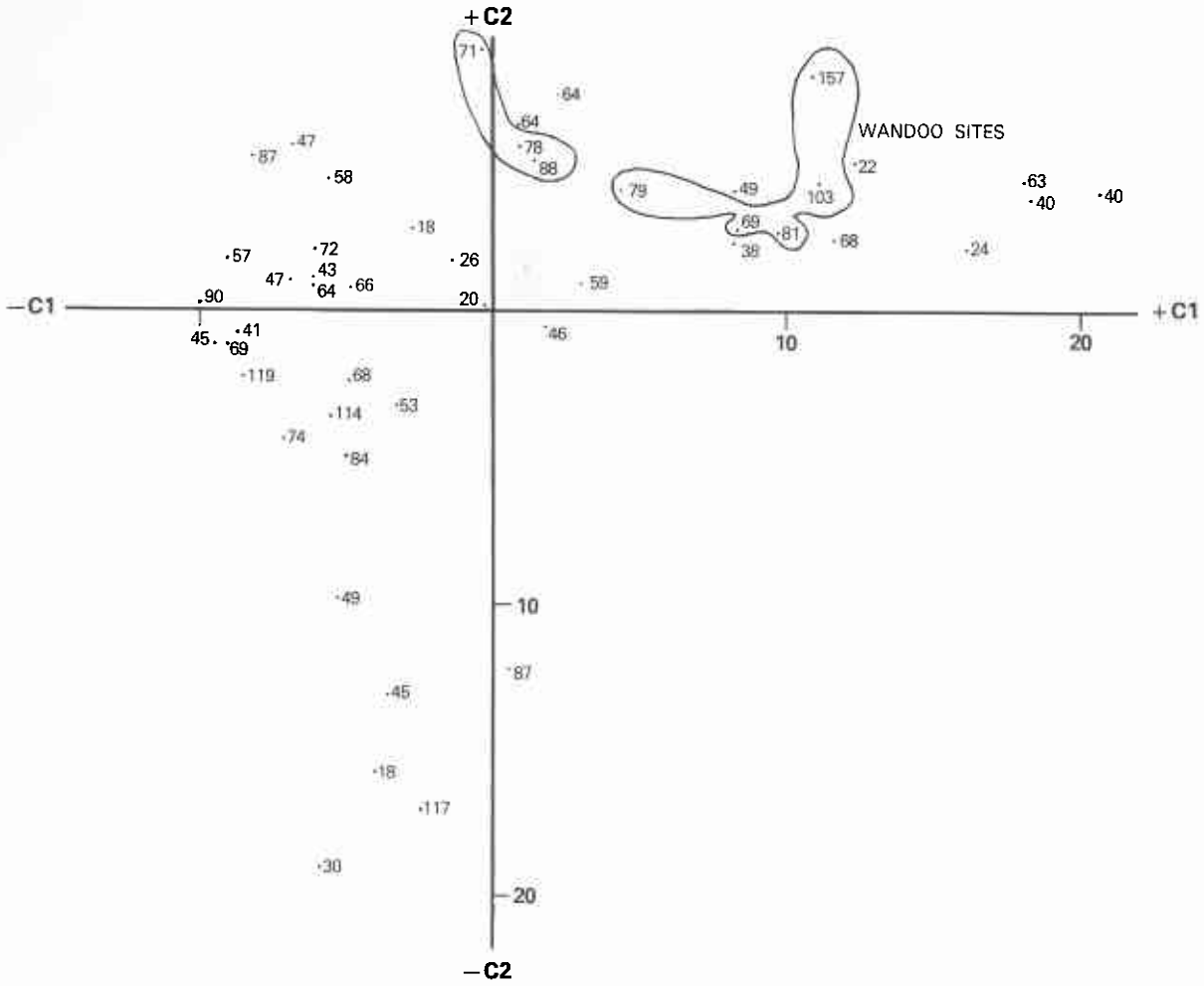



**Figure 14**

Distribution of total phosphates (p.p.m.) on 48 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 3), Components 1 and 2.

massive lateritic ridges and of seasonally wet gullies and depressions with coarse sandy soils respectively.

There is no correlation with time since fire, or with either diggings or nest numbers.

*The tammar*

The scrub density at 120 cm+ (mean of 120 to 240 cm and 240 cm+) plotted with percentage bare area within the component space on C1 and C2 (Fig. 16) shows a correlation with tammar distribution (see Fig. 9). Tammar distribution is limited to those areas with 21 to 50 per cent overhead scrub cover and with 80 to 100 per cent bare ground beneath. In the study area, such thickets are formed by only three species, *Gastrolobium bilobum* (heartleaf), *Melaleuca viminea* and, to a lesser extent, *Casuarina humilis.*

## CHARACTERISTICS OF WOYLIE AND TAMMAR SITES

### The woylie

Woylies occur on quite distinct site types characterised by specific plant species and centred on a specific area within the component space (see Plate 1). Specific identification of the principal components has not been possible owing to the limitations of the experimental technique and the extreme complexity of the site-vegetation complex. However, a broad description of woylie sites is possible.

Woylies occupy well drained sites with deep soils in areas tending very marginally towards the more deeply dissected topography of the Nyamup association of McArthur and Clifton (1975). Good woylie sites, such as the Boyicup study area, are more deeply dissected than the more typical Perup association with low ridges and broad shallow valleys. Hence, the soils appear to be marginally more fertile than those of the Perup association and other localities in the area. It is of note that what was once the woylies' main habitat, an area to the east of State forest, is today a fertile farming area.

They appear to prefer the sandier soils, avoiding areas of massive laterite and the heavier soils of the Nyamup association in the western sector. The broad, shallow valleys typical of the Perup association are also avoided.

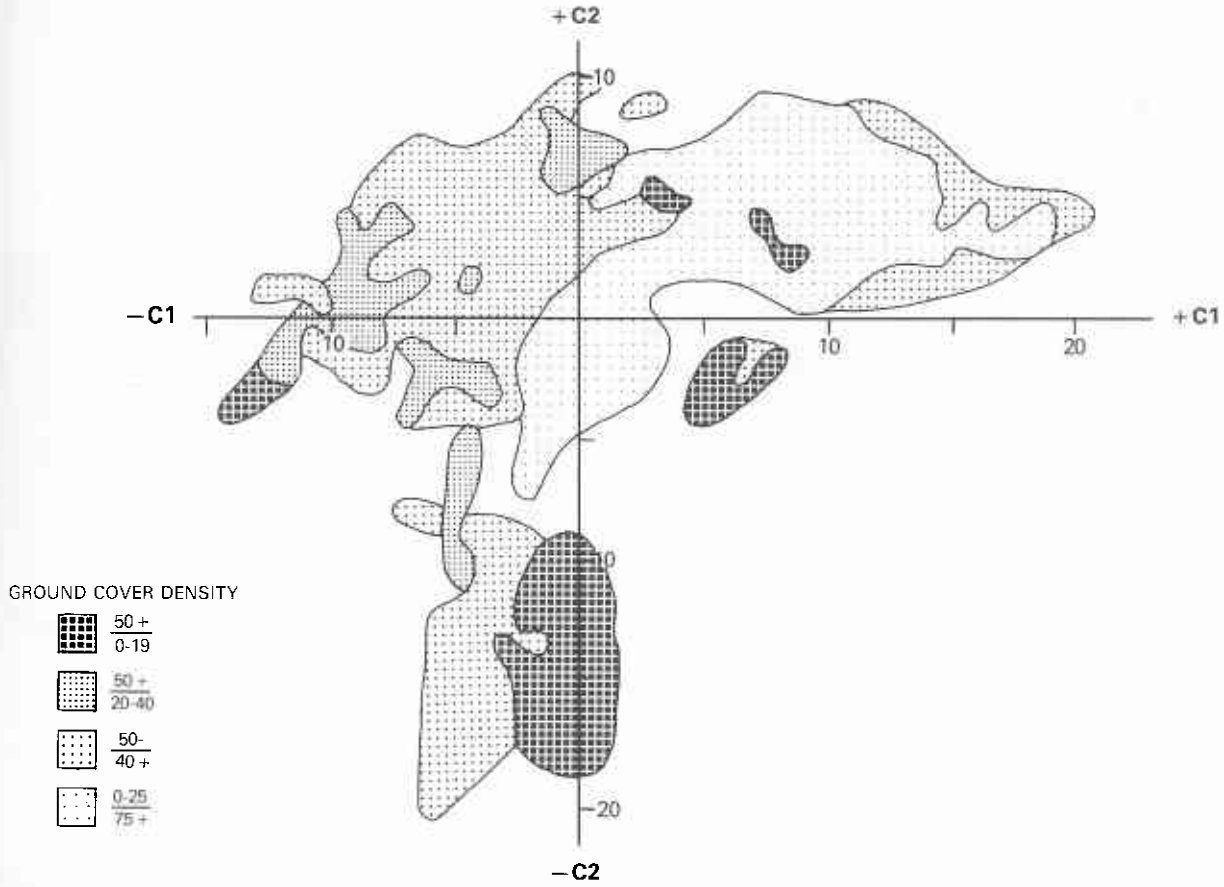



**Figure 15**

Ground cover density = $\frac{\text{scrub density 0 to 60 cm}}{\text{percentage bare ground}}$ on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 3), Components 1 and 2.

Scrub density, more particularly the percentage of bare ground, appears to be important. The woylie is absent from very open areas as well as from areas with a very dense ground cover. A ground cover density of between 50 and 80 per cent together with 20 to 40 per cent bare ground in the vicinity of nesting areas, may represent an ideal density required for efficient escape from predators (Plate 9).

There is no evidence that fire is a limiting factor in the study area. Foxes are an important predator in the area (see Section III, Mortality Factors) but the woylie still survives (see Section V, General Discussion). It appears that edaphic factors and scrub cover are prime factors contributing to the present distribution of the woylie.

### The tammar

The tammar occupies very distinct site types characterised by a few specific plant species. These sites are centred in a very restricted area within the component space (see Plate 1).

Prime sites occur in close proximity to woylie areas but extend considerably further towards the moister positive end of the C1 axis. Soils are sands or sandy loams but unlike those on woylie sites they may be shallow and subject to seasonal drought where they occur on the broad shallow valleys in the Perup association.

Thickets providing a minimum of 20 per cent cover, and with 80 to 100 per cent bare ground beneath, are prime requirements. Overhead protection may be essential to a social species living in groups, while the stems of the thicket-forming species may be a help when eluding ground predators. The wedge-tail eagle (*Aquila audax*) and the European fox (*Vulpes vulpes*) are both major predators of the tammar (see Section III, Mortality Factors).

Although not included in the P.C.A., observation indicates that grasses and small grass-like sedges are invariably found in close association with "tammar thickets" (Plate 10). Grasses are a major food item of the tammar (see Section IV, Stomach Content Analysis). In the Boyicup study area, six species of grass, three of them introduced, are found in association with the heartleaf thickets. A lush, lawn-like growth appears in spring (see Plate 31) and the grass persists as a dry food source throughout the summer.

Grasses are relatively rare in south-western ecosystems (Diels, 1906; Gardner, 1952), and a dense growth of grass may be an essential factor of the tammar's habitat. It is perhaps the only food source capable of sustaining groups of medium-sized

**Plate 9**
Typical woylie nesting area. Fairly dense understorey of *B. ornata* with 20 to 40 per cent bare ground.

**Plate 10**
Typical heartleaf "tammar thicket", a closed canopy but open at ground level. Note the well grazed grassy understorey.

**Plate 11**
Vigorous heartleaf seedlings forming a dense thicket on ashbed created following a hot fire.

**Plate 12**
Within minutes of ignition under hot dry conditions, flames leap from *Melaleuca viminea* thicket fanned by strong winds.

**Plate 13**
Heartleaf thicket fifteen to twenty years old in early stages of "degeneration". Note the large numbers of dead and collapsing bushes.

**Plate 14**
Funnel trap. The hanging wire trip mechanism is barely visible at the rear end of the enclosure.

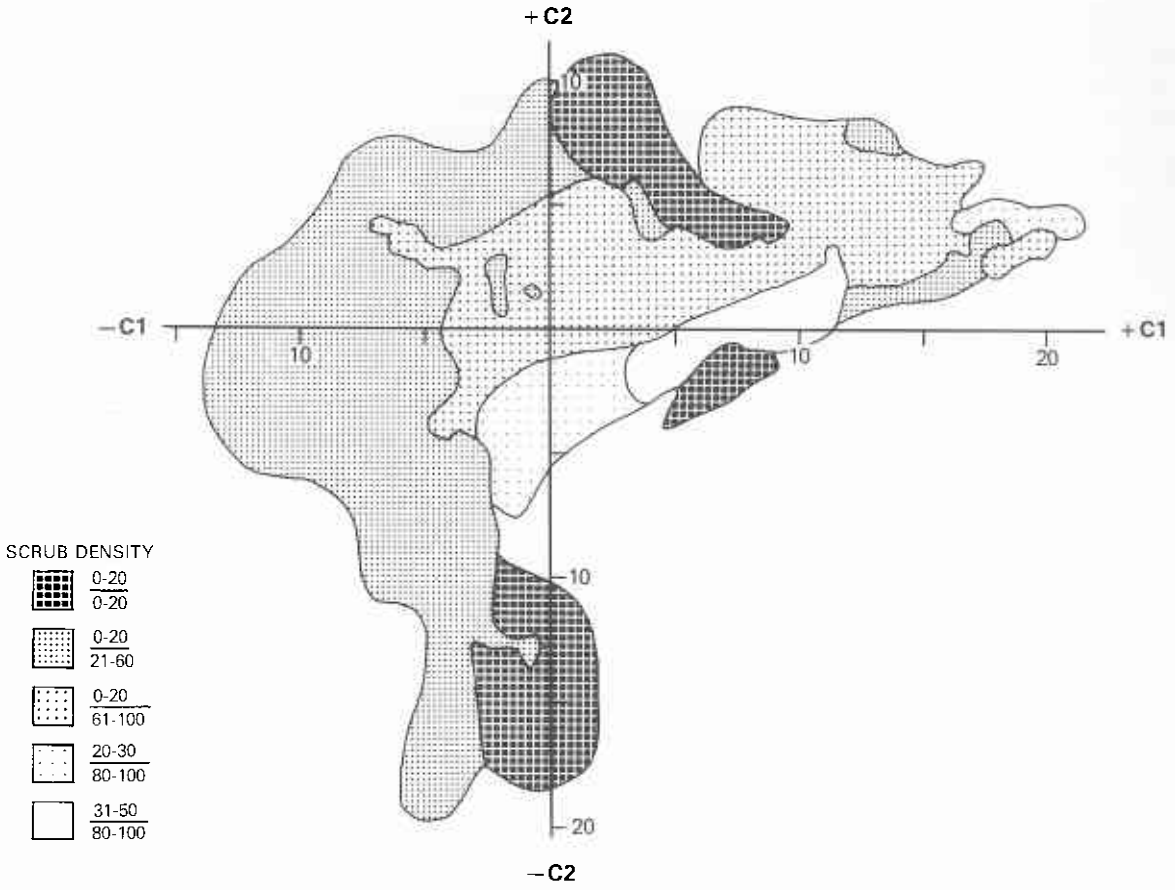



**Figure 16**

Scrub density = $\frac{\text{percentage density 120+ cm}}{\text{percentage bare ground}}$ on 236 plots within component space derived by P.C.A., varimax loadings, 64 vegetation species (see Fig. 3), Components 1 and 2.

herbivores crowded into a restricted area. Nitrogen fixation by native legumes (Shea and Kitt, 1976) may improve the soil, so that the legume heartleaf may be essential to maintain the lush growth of grasses on these sites.

Once again, it appears that soils and vegetation, rather than predation (see Section V, General Discussion), are the prime factors contributing to the current distribution of the tammar.

## EFFECTS OF FIRE ON VEGETATION TYPES INHABITED BY THE WOYLIE AND THE TAMMAR

This study provided no direct evidence of fire as a factor in woylie and tammar distribution. The study area is control-burnt by the Forests Department (Peet, 1967) on a five- to seven-year-cycle. Although the mosaic effect (Christensen and Kimber, 1975) contributes to the variety, it is rare to find areas of unburnt understorey over the age of twenty-five years. But it is possible that fire more frequent than every five to seven years or less frequent than every twenty-five years may have a significant effect on the distribution of the study species.

### The woylie

In the dry sclerophyll forests of the study area, understorey vegetation regenerates rapidly, chiefly from subterranean organs (Christensen and Kimber, 1975). On some woylie sites, particularly in wandoo (*Eucalyptus wandoo*) forest (the major habitat in Dryandra State forest) the understorey cover species regenerate largely from seed. These species, such as *Acacia pulchella*, *Gastrolobium oxylobioides* and *G. calcycinum*, are short-lived, hard-seeded species which require hot fires for germination (Fig. 17). In the prolonged absence of fire such species disappear. Similarly, too frequent mild fires do not stimulate their germination (Christensen and Kimber, 1975) and they may vanish. Thus on such sites dominated by hard-seeded "fire-weeds" the woylie's distribution could be influenced by the effect of fire on its cover.

### The tammar

Tammar distribution can be influenced through the effects of fire, or the lack of it, on the main components of its habitat. The main thicket species, heartleaf and *Melaleuca viminea*, depend on fire for regeneration. Heartleaf requires hot fires to germinate its seed and compares with *A. pulchella*, a known "fire-weed" species, in its response to heat treatment

(see Fig. 17). A hot fire is also essential for optimum growth and survival (Table 2 and Plate 11). Similarly, like some species of eucalypts (Christensen, 1971) *M. viminea* requires a hot fire to release the seed from the capsules and create the clean ashbed necessary for the germination of these tiny seeds.

Stem sectioning shows that, despite regular burning of the surrounding ridges, thickets of both species often reach the age of twenty to twenty-five years. The high percentage of bare ground underneath, contributed to by the tammar's own activities, reduces the fire risk to almost negligible proportions. Only under exceptional conditions of extreme winds and high temperature will they burn (Plate 12). After the age of about twenty years they start to degenerate and collapse (Plate 13), and the tammars leave the area (personal observation). Only another fire will rejuvenate them.

Grasses grow best after fires of moderate intensity, and germinate in patches on the most favourable sites after a hot fire in the thickets (see Table 2). Frequent cool grass fires would eliminate the thicket-forming species and encourage the grasses. Grazing by tammars and kangaroos (*Macropus fuliginosus*) helps reduce the grass fire hazard during the first few critical years after fire (see Plate 31).

Tammar distribution may be seriously influenced by the effect of fire on its cover and food species. The balance between the tammar, tammar thickets, grasses and fire is therefore extremely delicate and could easily be upset.

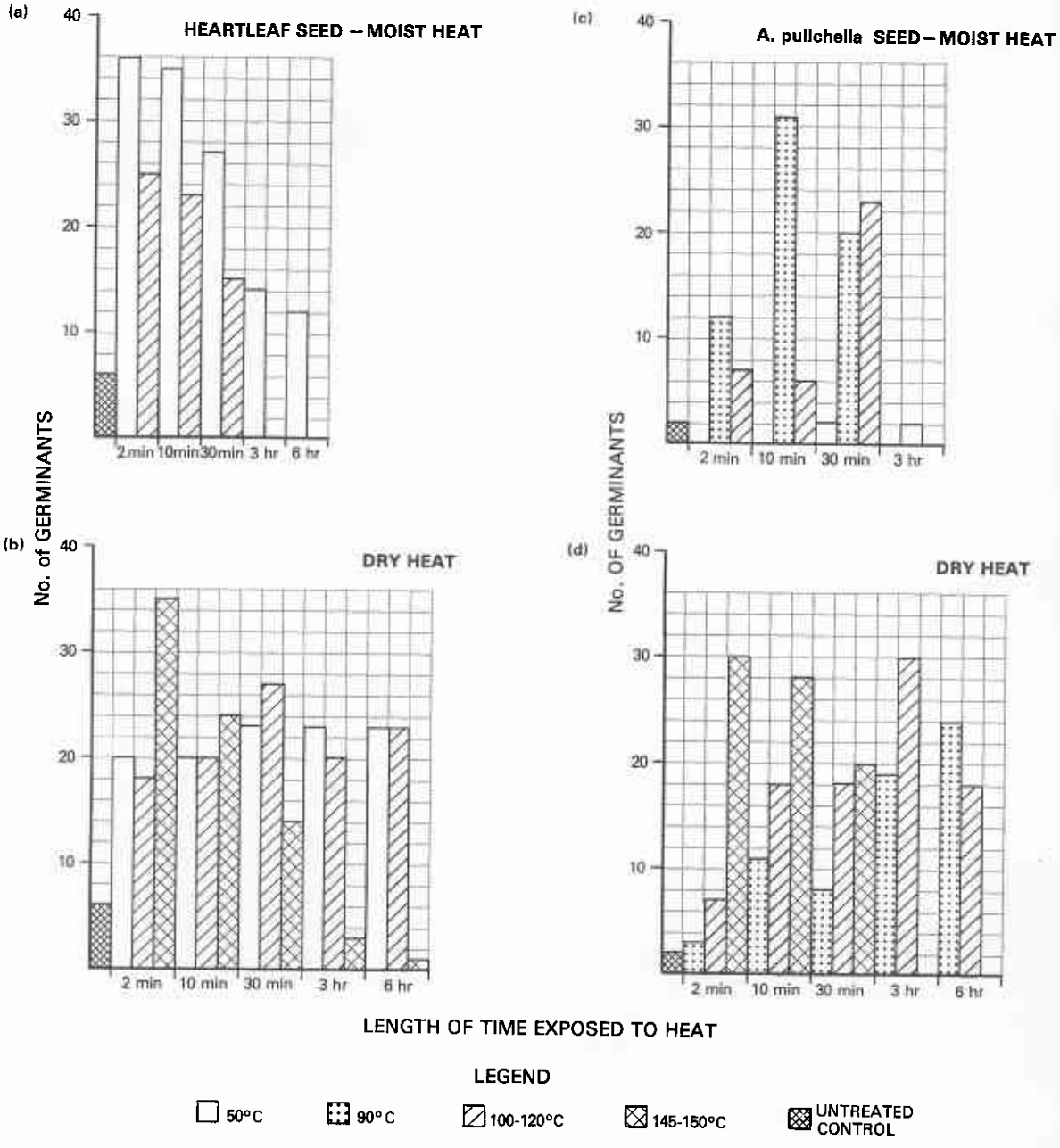



**Figure 17**

Laboratory seed germination trials (50 seeds per treatment) showing the effects of various heat treatments on germination.

**Table 2**

GROWTH AND SURVIVAL OF HEARTLEAF SEEDLINGS ON SITES BURNT WITH DIFFERENT FIRE INTENSITIES

| *Parameter measured* | *Gully site* | | *Significance** | *Upper slope* | | *Significance** |
|---|---|---|---|---|---|---|
| | *Tree canopy scorch* | *No scorch* | | *Tree canopy scorch* | *No scorch* | |
| Seedings per quadrat | 29·16 | 14·60 | 0·01 | 18·16 | 4·48 | 0·001 |
| Dead seedlings per quadrat | 0·24 | 0·40 | NS | 1·48 | 2·52 | NS |
| Height of seedlings (cm) | 32·44 | 14·40 | 0·001 | 16·88 | 11·08 | 0·001 |
| Grass cover | No grass present | Dense cover on all plots | | Light cover on two plots only | Light cover on all plots | |

Figures represent means for 25 1-m² quadrats. * Students *t* test.

SECTION III

# Population Studies

## INTRODUCTION

There have been relatively few detailed studies of the effects of fire on mammals (Kozlowski and Ahlgren, 1974; Recher and Christensen, in press). Most workers have concentrated on small mammals, and in only a few cases have population parameters been studied in any detail (for example, Christensen and Kimber, 1975; Lawrence, 1966; Leonard, 1972; Neal, 1967; Recher *et al.*, 1974).

One important characteristic of mammalian populations which has received little or no attention in relation to fire is the phenomenon of territoriality and home range attachment. This is a characteristic unique to animals because it is based on mobility, and it may therefore be expected to be an important factor in mammalian fire ecology.

Several investigators have found that many small mammals survive fire. Christensen and Kimber (1975) recorded no exodus of *Rattus fuscipes* from the trapping area after a hot fire. The rats stayed in the burnt area, showing a remarkable attachment or fidelity to their devastated home range areas.

The attachment to home range is so strong that destruction of most of the physical characteristics of the site fails to induce the animal to leave. This behaviour may have far-reaching consequences, particularly on primary population parameters. Natality, mortality, immigration and emigration (factors which affect re-population of burnt areas) would be profoundly influenced by such behaviour. Fire adaptations may be related to these aspects of the species' biology.

This study uses an experimental approach, comparing population parameters of pre- and post-fire populations with those of an unburnt control area. It is specifically designed to test Hypotheses 2 and 3 proposed in the Introduction.

## DESCRIPTION OF THE STUDY AREA

The Boyicup study area is located approximately 50 km due east of Manjimup in the south-east corner of the general study area (see Fig. 2). The area is within the headwaters of a number of small seasonal tributaries of the Tone River. It is not readily assigned to any of the associations of McArthur and Clifton (1975). The ridges are well defined and the valleys are moderately incised, the former represented by site F (see Plate 9) and the latter by site R (see Plate 10) in the wide-scale survey (Appendix I). The major understorey communities are shown in Fig. 18.

There is no permanent surface water in the area, and streams flow for only a brief period towards the end of winter. Selective logging has occurred over most of the area and there are numerous tracks. As a part of State forest the area has been subject to regular prescribed burning (Peet, 1967) on a five- to seven-year basis since 1955. This has resulted in a mosaic pattern of different ages of understorey scrub (Fig. 19). Such a pattern is a natural consequence of frequent fires, but the network of logging tracks has accentuated it.

## METHOD

Two separate experimental burns were carried out.

(1) The 1975 burn was designed to test Hypothesis 2, viz. woylies and tammars will survive within the burn but will fall prey to predators during the first weeks after fire. Repopulation of the area will be effected by young animals from the unburnt surrounds, and from large unburnt patches within the burnt area itself.

(2) The 1976 burn was designed to test Hypothesis 3, viz. that woylies remain within their home range area after fire, not because they are excluded from the unburnt surrounds by other home range owners but because of an innate fidelity to their home range area.

Trapping and radio-tracking of both species was carried out before, during and after each burn. Cage traps (Sampson, 1971) were used to trap the woylie, and funnel traps (Plate 14) were used for the tammar. The tammar traps initially had wire funnels, but woylies which entered them escaped through them, dug under the wire or climbed out using the corners. After considerable experimentation a design incorporating a sliding door set off by a mechanism similar to that of the cage traps, a wire bottom and wired-over corners proved successful for both species.

A mixed bait based on peanut butter, raisins and oatmeal (Giles, 1971) was used for the woylie. Wheat bait was used for the tammar. All animals were ear-tagged (Sampson, 1971) and weighed to the nearest gram on a beam balance; measurements of ears, head, pes and tail were also recorded. In addition, all animals were aged (see Appendix III), and joeys were weighed, measured and tagged when possible.

In addition to the trapping, certain individuals were tracked over a period before, during, and after each burn, using radio telemetry. A twelve-channel AVM Model LA12 portable receiver, operating on the 150.850 to 151.150 MHZ band, was used with a

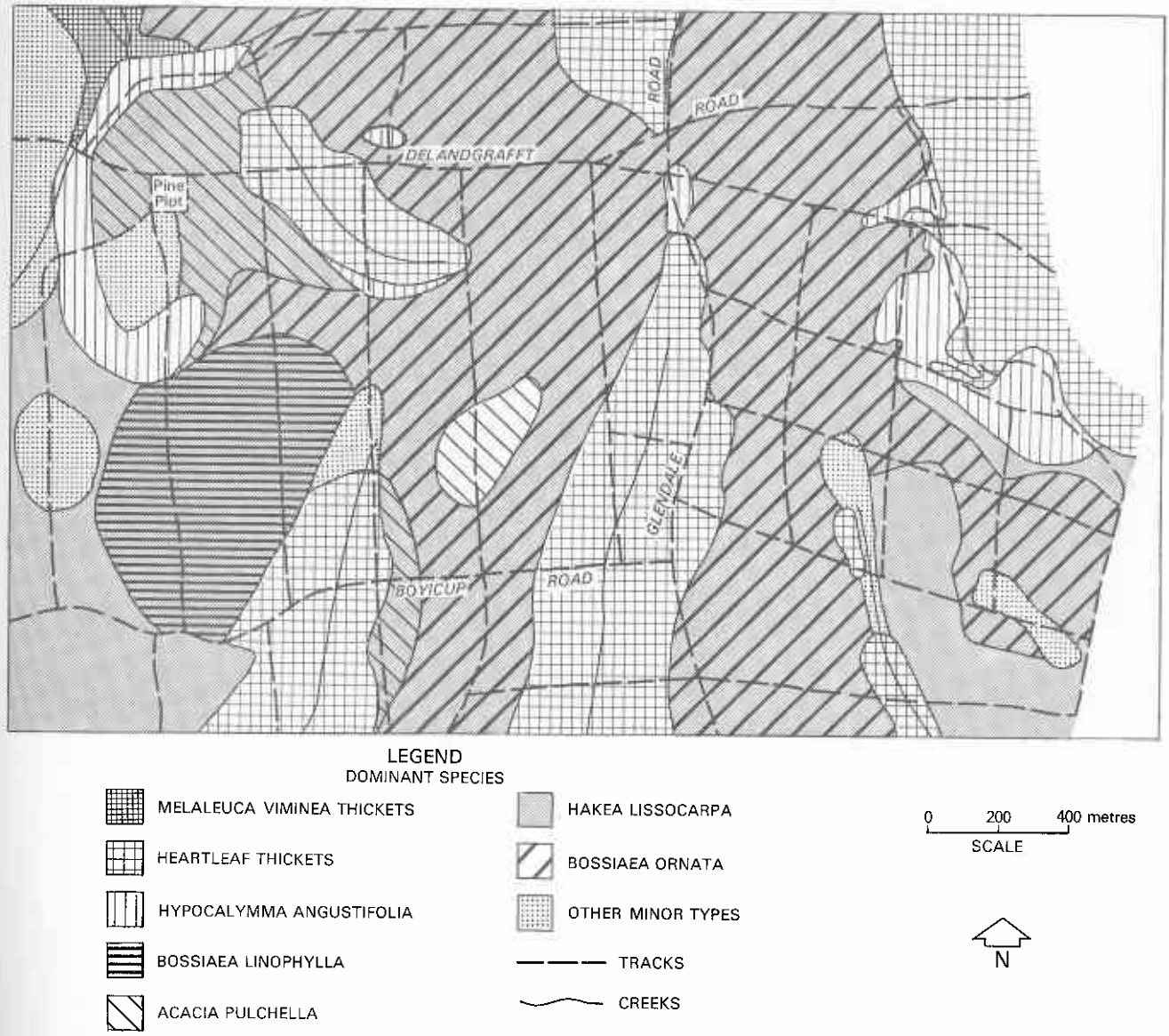



**Figure 18**
Boyicup trapping area—distribution of major understorey scrub communities.

hand-held yagi antenna (Plate 15). AVM transmitters were attached to the animals by means of a collar (Plate 16, and *Radio telemetry equipment and techniques,* AVM publication).

**Plate 15**
AVM receiver with hand-held yagi directional antenna.

Radio-tracked animals were located by means of triangulation both during the day and at night. The trapping grid (Fig. 20) was used for the triangulation: bearings were taken from fixed points so that for every location a minimum of three bearings were taken in such a way as to intersect when plotted on a

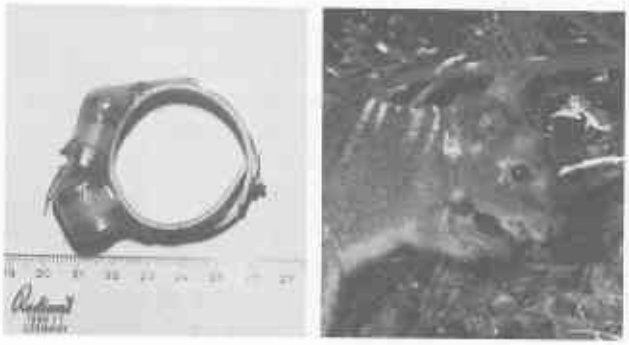


**Plate 16**
AVM collar type transmitter showing size and attachment to woylie.

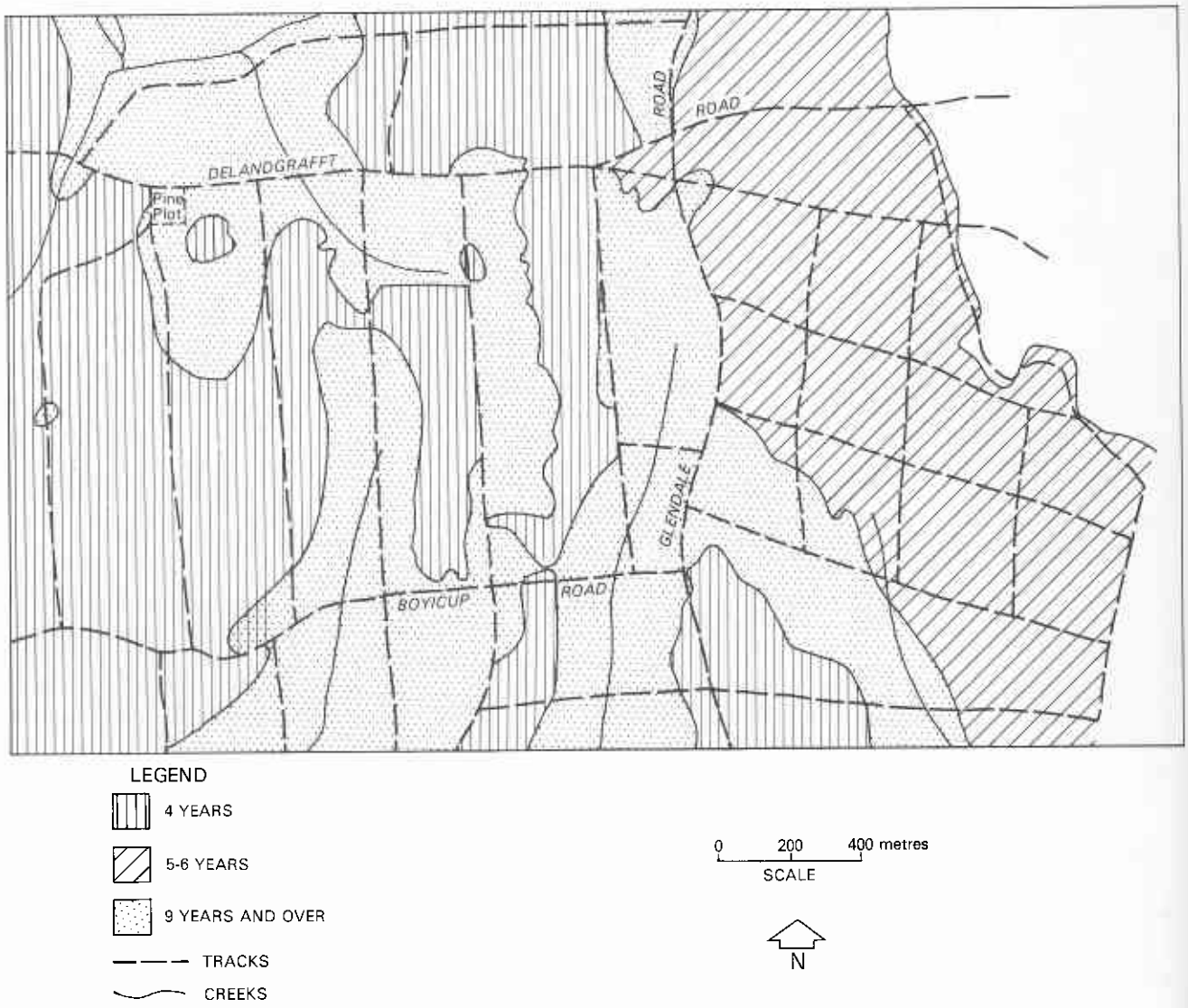



**Figure 19**

Boyicup trapping area—burn age map, showing the number of years since the understorey scrub was last burnt.

map. Animals were first located with the hand-held yagi attachment used from the back of a vehicle. Two observers were then used, one to accurately locate the direction of the signal from a trap point, and the second to take bearings along the main beam of the yagi antenna. Location of the animals was established by plotting the intersecting bearings on a grid map of the area. Tests carried out in the study area showed the average error of locations plotted in this way to be approximately 15 to 20 m.

A Rustrak continuous drum recorder plugged into the receiver using a ground plane antenna was used for continuous recording of nocturnal activity. Animal movement was recorded continously (Plate 17) while the animal was within range of the recorder (approximately 200 to 250 m).

### The 1975 burn

Permanent trap points for cage traps were located at 100 m intervals along the existing network of tracks which are spaced approximately 400 m apart. A central area of 225 ha (the area to be burnt) was surrounded by an unburnt control perimeter 800 m wide. To have as many animals tagged as possible, the entire area was first trapped. One hundred and twenty cage traps were used on a weekly rotation requiring three weeks trapping to cover the entire area. From the second month after the fire trapping was confined to the central burn area and a portion of the control area immediately to the south (see Fig. 20).

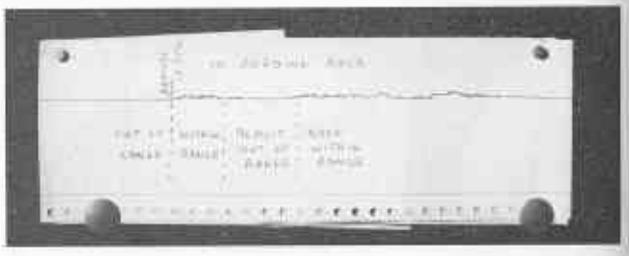


**Plate 17**

Typical trace on Rustrak recorder showing transmitter animal within and out of range of the recorder.

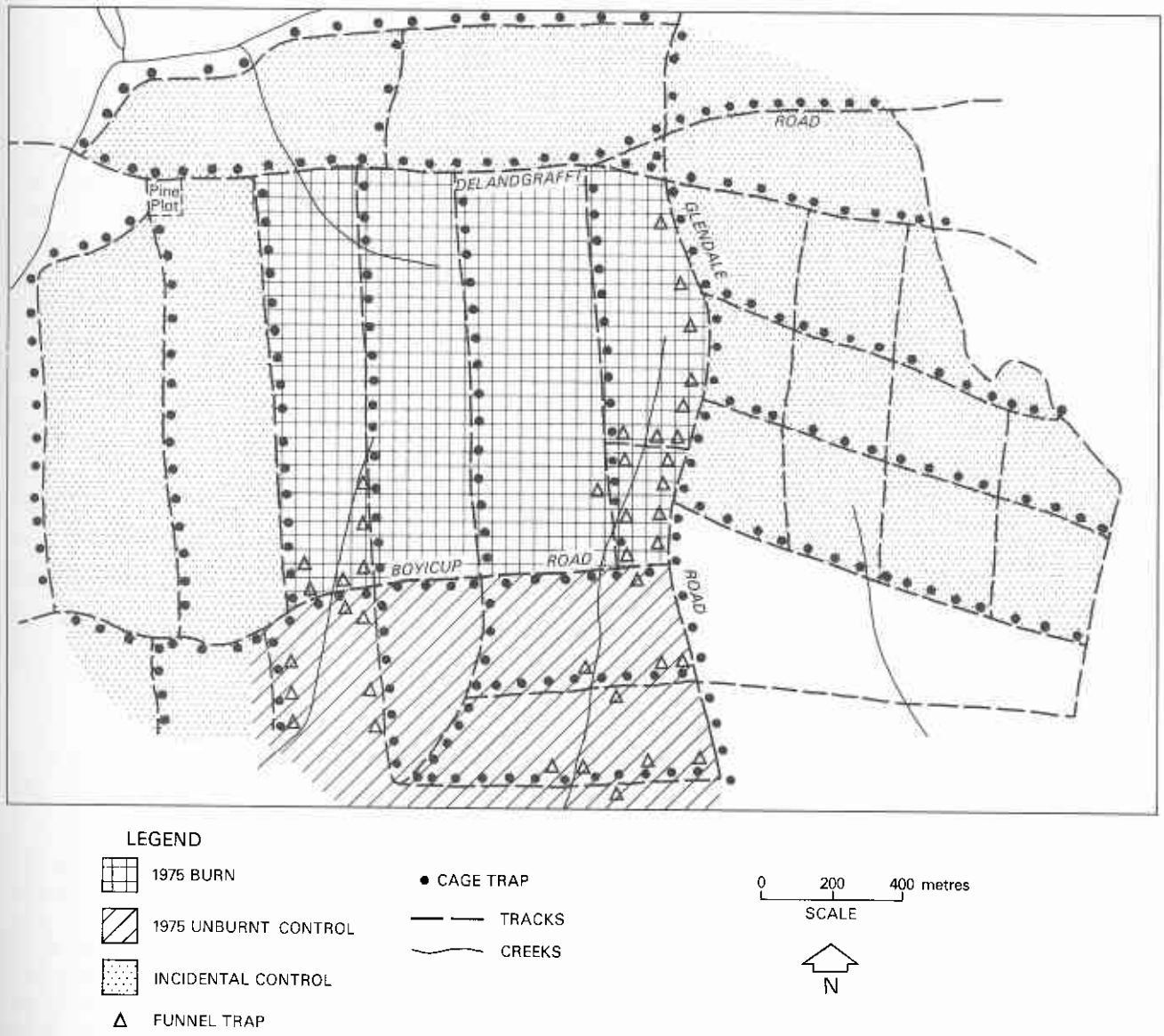



**Figure 20**
Boyicup trapping area—trap layout, 1975 burn area.

Tammars were trapped in a separate grid of thirty-nine permanently located funnel traps in heartleaf thickets in two adjacent valleys (see Fig. 20).

### The 1976 burn

An area of 190 ha, adjacent and to the east of the burn, was selected for this study. The western portion was set aside for burning while the eastern sector served as an unburnt control area (Fig. 21). Thirty-six permanently located funnel traps on a 400 × 200 m grid were used for trapping in the area. Experience from the 1975 burn had shown the funnel traps to be more efficient than the cage traps for trapping woylies (see Table 4). To ensure that all trappable animals were captured, two cage traps were also set next to each of the funnel traps.

Trapping commenced in November 1975 and continued at intervals until January 1976 when it was considered that all trappable animals had been caught. By mid-January all animals whose home range areas were judged to lie within the unburnt control sector and immediate surrounds were trapped and removed from the area. To obtain information on the distance from which transported woylies would return to their home range areas, individuals were released at distances varying between 2500 and 6000 m from their home range areas. The areas continued to be trapped for removals at intervals until the burn on 18 March 1976.

During mid-February eighteen woylies, comprising almost the entire trappable population within the area to be burnt and including some control animals from the surrounds, were fitted with radio transmitters. The activities of these animals were closely monitored before, during and for some months after, the burn. The primary objective was to see whether any animals changed their home range after the burn and moved into the now empty control area from which the resident woylie population had been removed.

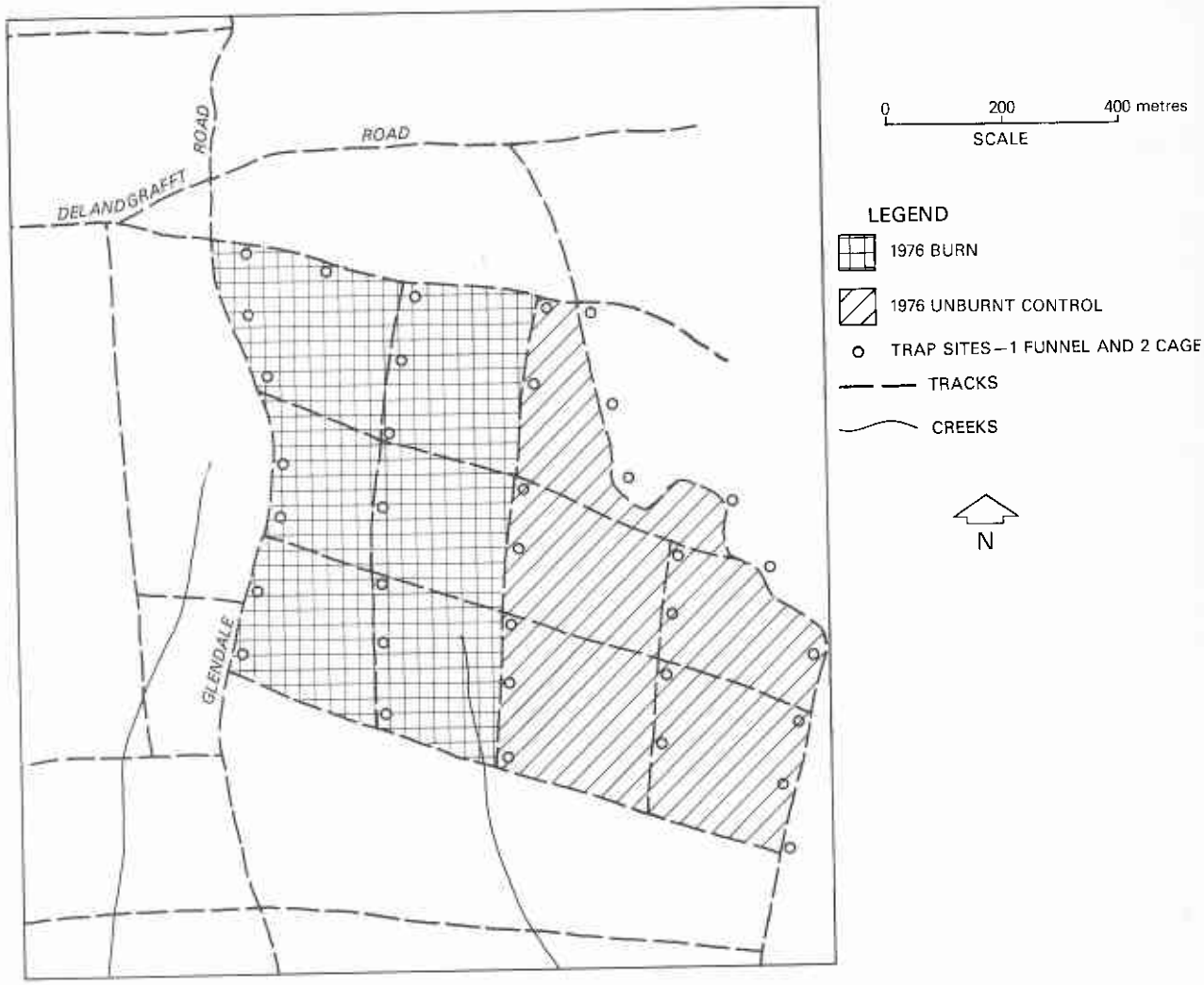



**Figure 21**

Boyicup trapping area—trap layout, 1976 burn area.

### Data analysis and presentation

Certain problems were experienced with the analysis and presentation of the data.

(1) The initial trapping grid was planned in an attempt to obtain the best possible data on movement but was found to be too large. This resulted in unequal trapping effort in different sectors during the pre-burn period of 1975.

(2) Woylie captures in the funnel traps set for the tammar were exceedingly high (Table 3). This meant dividing the woylie data according to trap types, or using relative comparison where possible.

These two factors precluded the use of many conventional techniques for estimation of population parameters such as those of Leslie and Chitty (1953) and Jolly (1963) as well as the compilation of life tables (Giles, 1971).

(3) With regard to written presentation, repetition of experimental details as a result of two separate burns, with pre- and post-burn populations of two species, was a major difficulty. Added to this was the necessity of having to divide the woylie data according to trap types. In the interests of a concise presentation it has therefore been found necessary to pool data from the two burns, especially since, for the purposes of this thesis, there was no great advantage in keeping them separate.

## THE PRE-BURN POPULATION—THE WOYLIE

A summary of trapping results over the three-year period of the study is presented in Table 3.

### Ageing the population

Details of the methods used are presented in Appendix III.

For the purposes of this study, four age categories are recognised.

(1) Joeys—pouched joeys, from birth to approximately 90 to 100 days. Tooth eruptions: dp4 has emerged and p3 emerges just before the next stage.

(2) Juveniles—between approximately 100 and 200 days old. Tooth eruption: M0.0 to M2.0.

(3) Sub-adults—from approximately 200 days to 10 or 12 months. Tooth eruption: M2.0 to M3.2 before p4 has replaced p3 and dp4.

**Table 3**
SUMMARY OF TRAPPING

| | *Woylie* | *Tammar* | *Quenda* | *Brush-tailed possum* | *Ringtail possum* | *Native cat* | *Numbat* | *Brush wallaby* | *Feral cat* |
|---|---|---|---|---|---|---|---|---|---|
| (*a*) 1975 Burn | | | | | | | | | |
| No. of animals | 206 | 117 | 18 | 10 | 2 | 7 | 1 | 1 | 1 |
| Captures: Cage | 339 | — | 13 | 11 | 2 | 9 | 1 | — | 1 |
| Funnel | 225 | 262 | 9 | — | — | — | — | — | — |
| (*b*) 1976 Burn | | | | | | | | | |
| No. of animals | 82 | 28 | 9 | 44 | — | 2 | — | 1 | — |
| Captures: Cage | 120 | — | 18 | 43 | — | 2 | — | — | — |
| Funnel | 186 | 59 | 8 | 4 | — | — | — | 1 | — |

| | | *1975 Burn* | *1976 Burn* |
|---|---|---|---|
| Total trap nights: | Cage | 4725 | 1808 |
| | Funnel | 1423 | 1053 |
| Per cent capture—Woylie: | Cage | 7·17 | 6·64 |
| | Funnel | 15·81 | 17·66 |
| Per cent capture—Tammar: | Funnel | 18·41 | 5·60 |

Woylie . . . . . *Bettongia penicillata*
Tammar . . . . . *Macropus eugenii*
Quenda . . . . . *Isoodon obesulus*
Brush-tailed Possum . . . . . *Trichosurus vulpecula*
Ringtail Possum . . . . . *Pseudocheirus peregrinus*
Native Cat . . . . . *Dasyurus geoffroii*
Numbat . . . . . *Myrmecobius fasciatus*
Brush Wallaby . . . . . *Macropus irma*
Feral Cat . . . . . *Felis catus*

(4) Adults—from approximately 10 to 12 months and older. Tooth eruption: p4 fully erupted.

Juveniles of up to 166 days old have been recorded still with their mother and sharing her nest, so it is assumed that they stay with their mother until the next joey leaves the pouch. Dispersal is therefore likely to take place towards the end of the juvenile stage and during the sub-adult stage. In view of this a category of non-adults, including juvenile and sub-adult stages, has been used in most of the analyses.

## Population analysis

### *Population structure*

Mean capture percentages by trap types for the entire duration of the study are given in Table 4. Funnel trap percentage captures were consistently higher than those of the cage traps. This is believed to be because the woylies were less reluctant to enter the larger, more spacious funnel traps. However, a chi-square test revealed no selective bias towards trap type either by males or females or by adults or non-adults. Capture data for both cage and funnel traps may therefore be combined for comparison of sex and age categories.

Pre-fire captures and re-captures of males were in nearly all cases higher than those of females (Fig. 22). A chi-square test comparison of pre-fire individual numbers of males and females revealed that this was caused by a higher re-capture rate of males and that there was no significant difference in numbers of individuals.

**Table 4**
THE WOYLIE—COMPARISON OF PRE- AND POST-BURN CAPTURE PERCENTAGES

| *Treatment* | *Trap type* | *1975 burn* | | | | | | *1976 burn* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Pre-burn* | | | *Post-burn* | | | *Pre-burn* | | | *Post-burn* | | |
| | | *C.* | *T.N.* | *Per cent* | *C.* | *T.N.* | *Per cent* | *C.* | *T.N.* | *Per cent* | *C.* | *T.N.* | *Per cent* |
| Control | Cage | 79 | 861 | 9·18 | 61 | 901 | 6·77 | 28 | 378 | 7·41 | 5 | 336 | 1·49 |
| | Funnel | 18 | 130 | 13·85 | 67 | 331 | 20·24 | 58 | 252 | 23·02 | 14 | 168 | 8·33 |
| Burn | Cage | 90 | 1450 | 6·21 | 109 | 1603 | 6·80 | 68 | 610 | 11·15 | 19 | 484 | 3·93 |
| | Funnel | 79 | 551 | 14·34 | 61 | 401 | 15·21 | 73 | 391 | 18·67 | 41 | 242 | 16·94 |

C. = Captures T.N. = Trap nights

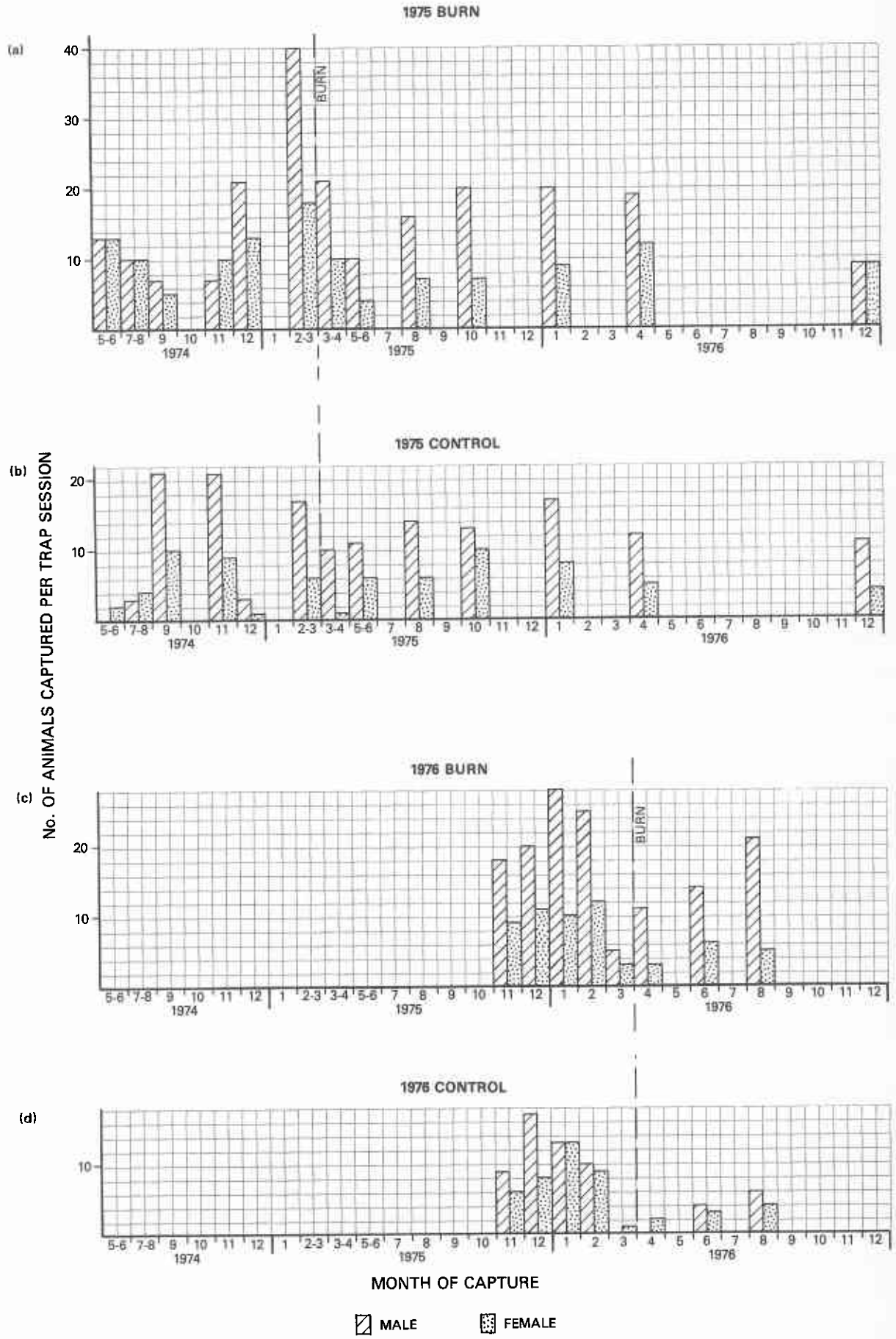



**Figure 22**

The woylie—comparison of total male and female captures and recaptures.

Pre-fire captures and re-captures of adults were consistently higher than those of non-adults in both the 1975 and 1976 burn areas (Fig. 23). Chi-square tests on comparisons of the actual numbers of adults and non-adults revealed this difference to be significant (0·01 level) on the 1975 burn but not on the 1976 burn.

The higher proportion of non-adult males on the 1976 burn area was probably the effect of the adjacent 1975 burn and also the removals. Both treatments resulted in increased numbers of young males (see Section III, Population Analysis).

After the first few trap sessions, when most of the resident woylies had been tagged, new captures tended to be non-adult animals (Figs. 24 and 25). This indicates little immigration of adult animals.

*Survival*

As outlined earlier, it was not possible to use standard methods for estimating survival. By examining known survival in months for all animals caught on the 1975 burn area it was possible to make comparisons of the survival on the control, the burn edge and the burn area (Table 5). Comparison is strictly on a relative basis; the figures mean little in terms of real survival times since animals still alive at the last trap session were included, and the age of animals when first caught was not known. Furthermore, loss may be caused not by death but by emigration. However, the study revealed that very little adult emigration occurred, and loss in most cases could be attributed to death.

Females appeared to survive slightly longer than males on the control and burn area, but the position was reversed on the edge. None of these differences was significant, however. Surprisingly, there was no difference between mean known survival time of adults and of non-adults on the control area. However, on the burn and on the burn edge, adults' survival was significantly higher than that of non-adults. This difference was caused partly by an increase in the mean survival time of the adults and partly by a decrease in the survival time of the non-adults.

Not enough data were available for formal comparisons, but several animals successfully reared young on the burn areas, and there appeared to be no effect of burning on the survival of pouch young. Table 6 shows survival of pouch young over the study as a whole. Joeys that reached the age of eighty-five days, old enough to leave the pouch and hop around, were judged to have survived pouch life. Known survivals are therefore taken to be captured joeys which are over eighty-five days old. Probable survivals include joeys whose mothers were recaptured after the pouch had been abandoned, but were judged to have survived, since the period between successive joeys had not been shortened significantly below the mean of 101·7 days (see below). The unknown category includes joeys on which no definite judgement could be made. Deaths include definite deaths not obviously a result of handling, but including cases where the interval between successive joeys was reduced very significantly below the mean of 101·7 days. On this basis pouch mortality was judged to be 18·5 per cent at the maximum and 8·8 per cent at the minimum. This compared favourably with mortality rates of pouch young in the red kangaroo (*Megaleia rufa*) (Frith and Calaby, 1969).

*Reproduction*

Approximate birth dates of joeys were calculated using curves for pes and head measurements (Appendix III). No differences were detected between years or areas so the data were pooled (Fig. 26). The apparent seasonal difference was owing to uneven

**Table 6**

THE WOYLIE—SURVIVAL OF POUCH YOUNG

| | *Known survivals* | *Probable survivals* | *Unknown fate* | *Mortalities* |
|---|---|---|---|---|
| Number of joeys | 20 | 33 | 71 | 12 |
| Percentage of total | 14·7 | 24·3 | 52·2 | 8·8 |
| Percentage of total minus animals of unknown fate | 30·7 | 50·8 | — | 18·5 |

**Table 5**

THE WOYLIE— KNOWN SURVIVAL

| | *Control* | | | *Burn edge* | | | *Burn* | | |
|---|---|---|---|---|---|---|---|---|---|
| | *Number of animals* | *Total survival (months)* | *Mean survival (months)* | *Number of animals* | *Total survival (months)* | *Mean survival (months)* | *Number of animals* | *Total survival (months)* | *Mean survival (months)* |
| Male | 22 | 128 | 5·81 | 33 | 233 | 7·10 | 17 | 125 | 7·35 |
| Female | 10 | 96 | 9·60 | 21 | 133 | 6·33 | 12 | 109 | 9·10 |
| Non-adult | 18 | 126 | 7·0 | 32 | 145 | 4·53 | 16 | 87 | 5·43 |
| Adult | 14 | 96 | 7·0 | 22 | 221 | 10·04* | 13 | 147 | 11·30† |

* Significant difference at 0·01 level (Students *t* test)

† Significant difference at 0·05 level (Students *t* test)

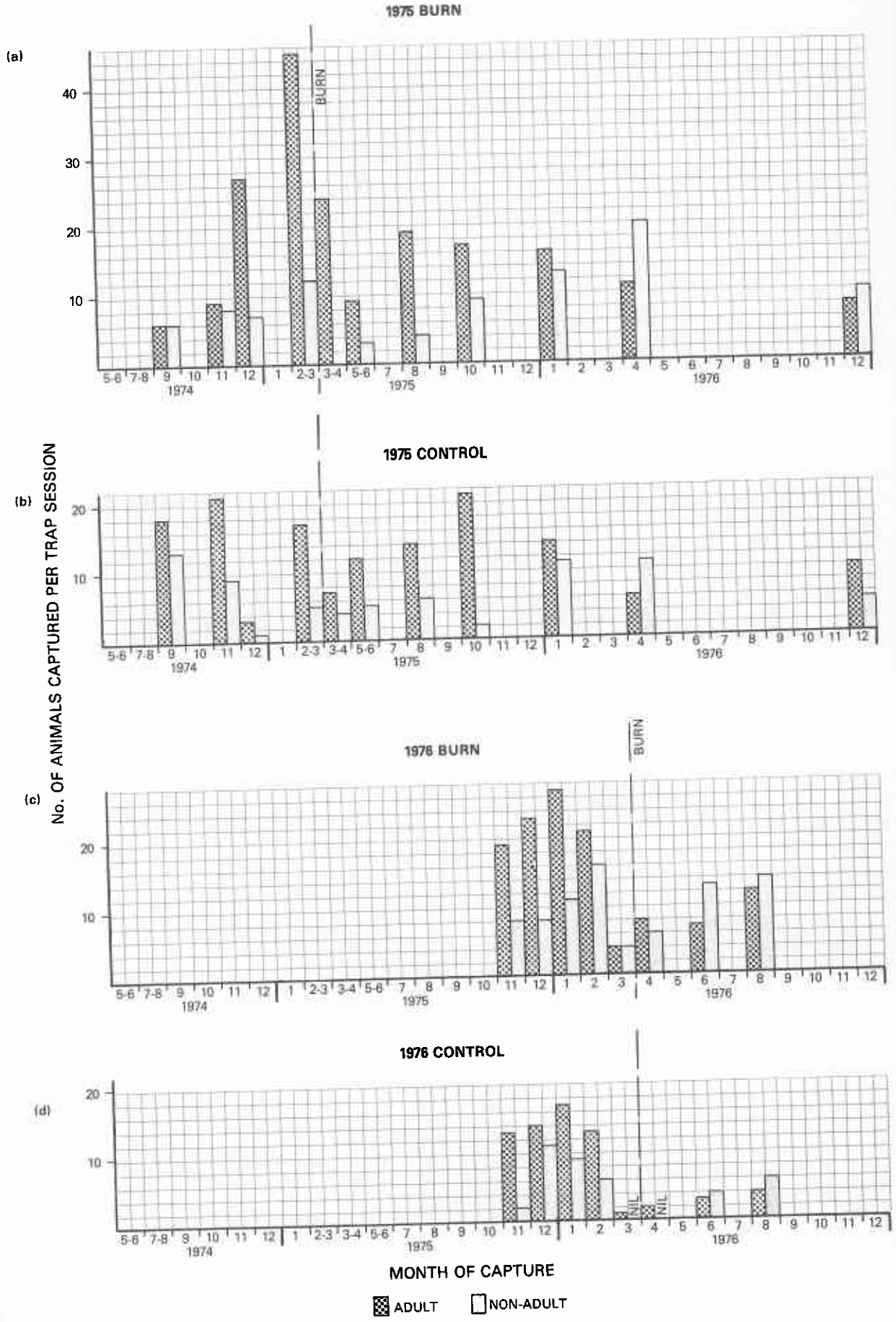



**Figure 23**

The woylie—comparison of adult and non-adult captures and recaptures.

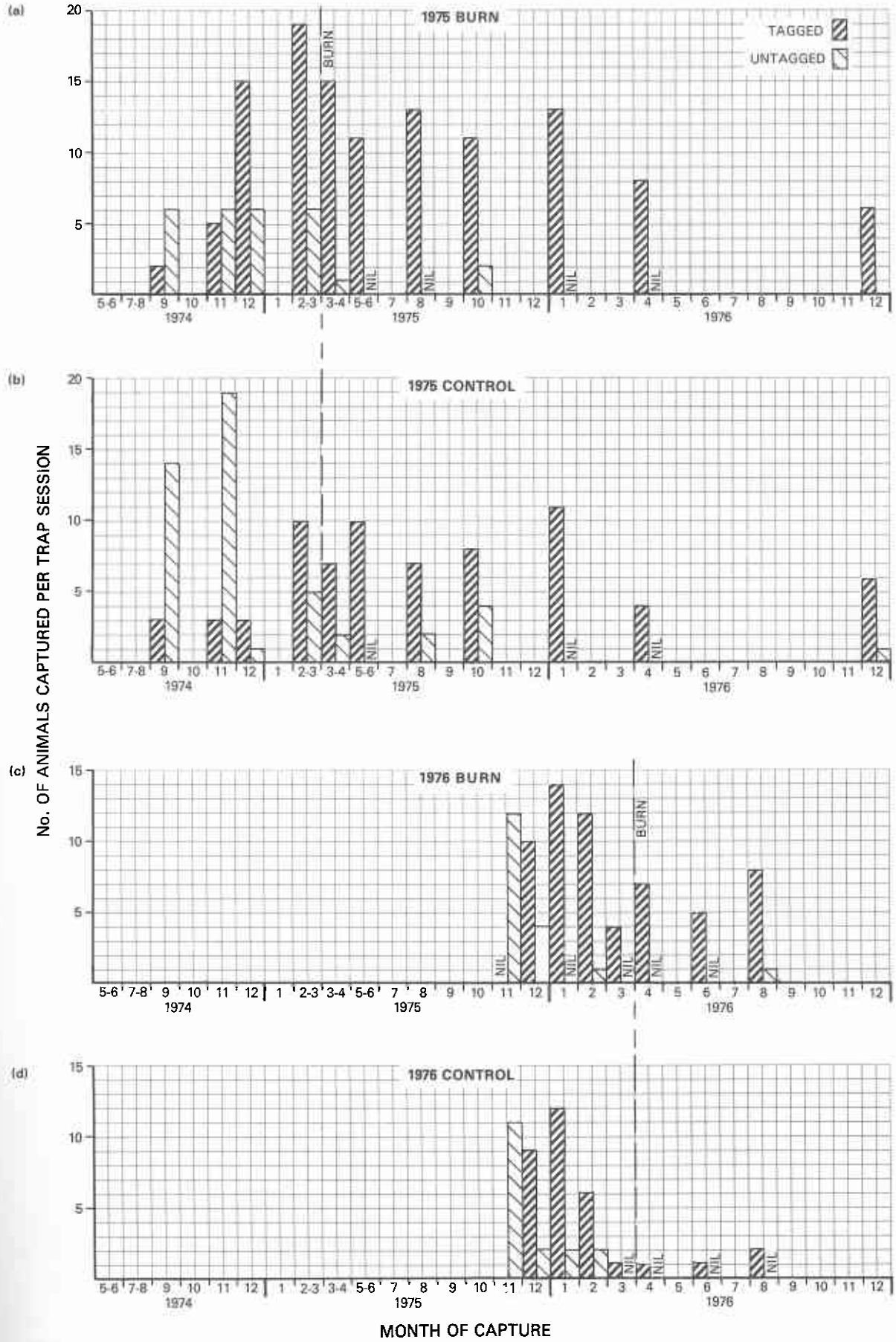



**Figure 24**

The woylie—adults, a comparison of tagged animals and new captures (untagged).

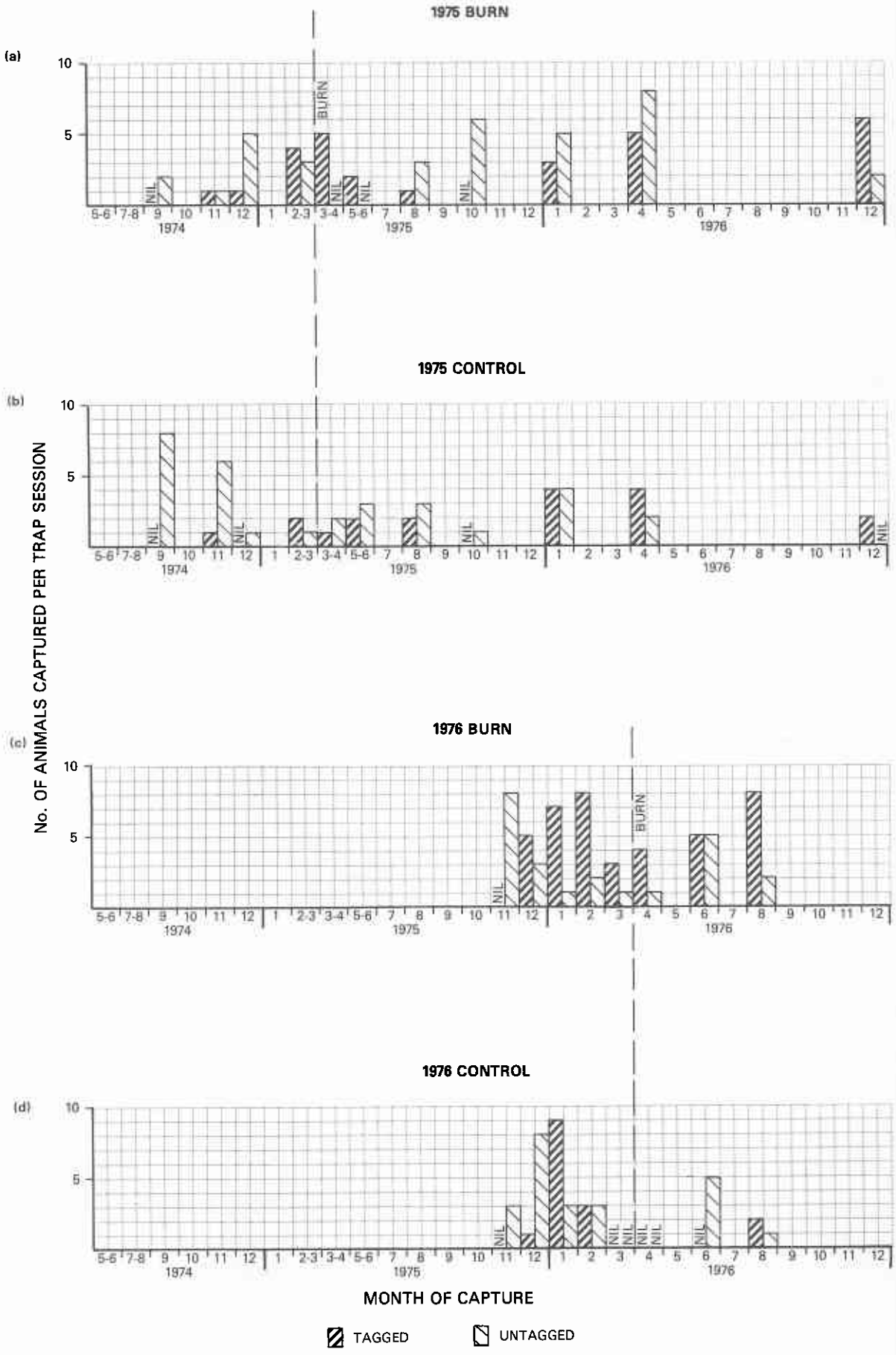



**Figure 25**

The woylie—non-adults, a comparison of tagged animals and new captures (untagged).

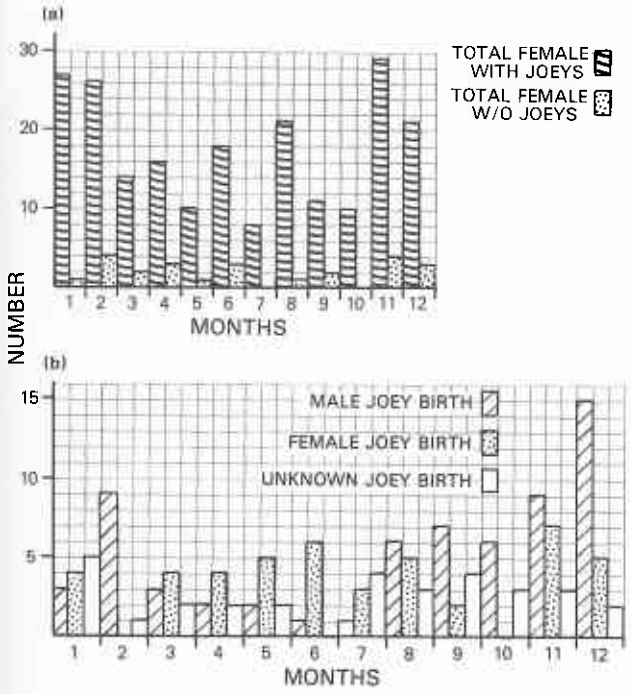



**Figure 26**

The woylie—monthly totals.
(*a*) Females with and without joeys
(*b*) Joey births

trap effort, most trapping being carried out during the summer. As in Tutanning (Sampson, 1971), breeding was continuous. Females had their first joeys at the age of approximately 170 to 180 days (the M2.0 tooth eruption stage). They then continued to give birth at approximately 100-day intervals (101·7 days, SD = 8·66, $n$ = 29). Old females with teeth worn down to the gums, of an estimated age of over four years, still bore young. Females without joeys in the pouch comprised 10·7 per cent of the females on total population. These were mostly females in the "between joeys" stage.

There seemed to be a seasonal change in the sex ratio of births. If the data in Fig. 26 (*b*) are combined by three-month periods, and analysed as a contingency table, the resulting chi-square is 12·58 ($n$ = 3), so that the proportion of male births ranged from a maximum in mid-summer to a minimum in mid-winter.

*Weights*

There were no significant weight differences between males and females caught during this study. Both sexes exhibited significant seasonal fluctuations in body weight (Fig. 27). Weight losses were relatively small; male weights fell from a mean high of 1398·3 g in December to a mean low of 1279·6 g in August, a total weight loss of only 8·5 per cent. However, so consistent were these seasonal changes that they were highly significant for both males and females. They became even more significant when examined in conjunction with Sampson's data (Sampson, 1971) on body fluids, 68 and 81 per cent respectively for summer and winter. The 118·7 g reduction in body weights from the summer peak to the late winter low represents a total reduction in body fluids of 45·7 per cent.

## Movements

The woylies' movements seemed to fall into the typical home range pattern with a territorial nesting area [Fig. 28, see Figs. 29 (*a*) and (*b*), 37 (*a*) and (*b*)]. The methods used for home range estimates are standard methods. They represent a great over-simplification of normal animal movement patterns (Jewell, 1966) but are nevertheless valid for relative comparisons of sizes or of shifts in location before and after fire.

Home range areas from trap data were calculated using the exclusive boundary strip method (Stickel, 1954) (Table 7). As trap-measured home range areas are known to increase with the number of captures (Burt, 1943), some selection of individuals was necessary if comparisons were to be valid. A further restriction was set by the limited number of multiple captures. Accordingly, only animals captured more than four times but less than ten were used for comparison.

**Table 7**

THE WOYLIE—HOME RANGE SIZES CALCULATED FROM TRAPPING AND RADIO-TRACKING DATA

| | *Trapping* | | | | *Radio tracking—pre-burn* | | | | *Radio tracking—post-burn* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Pre-burn* | | *Post-burn* | | *Nest area* | | *Feeding area* | | *Nest area* | | *Feeding area* | |
| | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| Number of animals | 18 | 14 | 5 | — | 12 | 5 | 9 | 4 | 12 | 6 | 9 | 4 |
| Mean area (ha) | 27·31 | 19·64 | 41·88 | — | 2·09 | 2·73 | 8·67 | 7·51 | 2·89 | 2·53 | 8·59 | 11·75 |
| Standard deviation | 8·35 | 9·94 | 3·4 | — | 1·79 | 1·21 | 4·79 | 3·35 | 11·02 | 1·39 | 3·71 | 5·44 |
| Mean per cent overlap | — * — | | — * — | | 19·54 | | 63·85 | | 21·46 | | 60·25 | |

* Animals used not necessarily adjacent, therefore overlap not applicable.

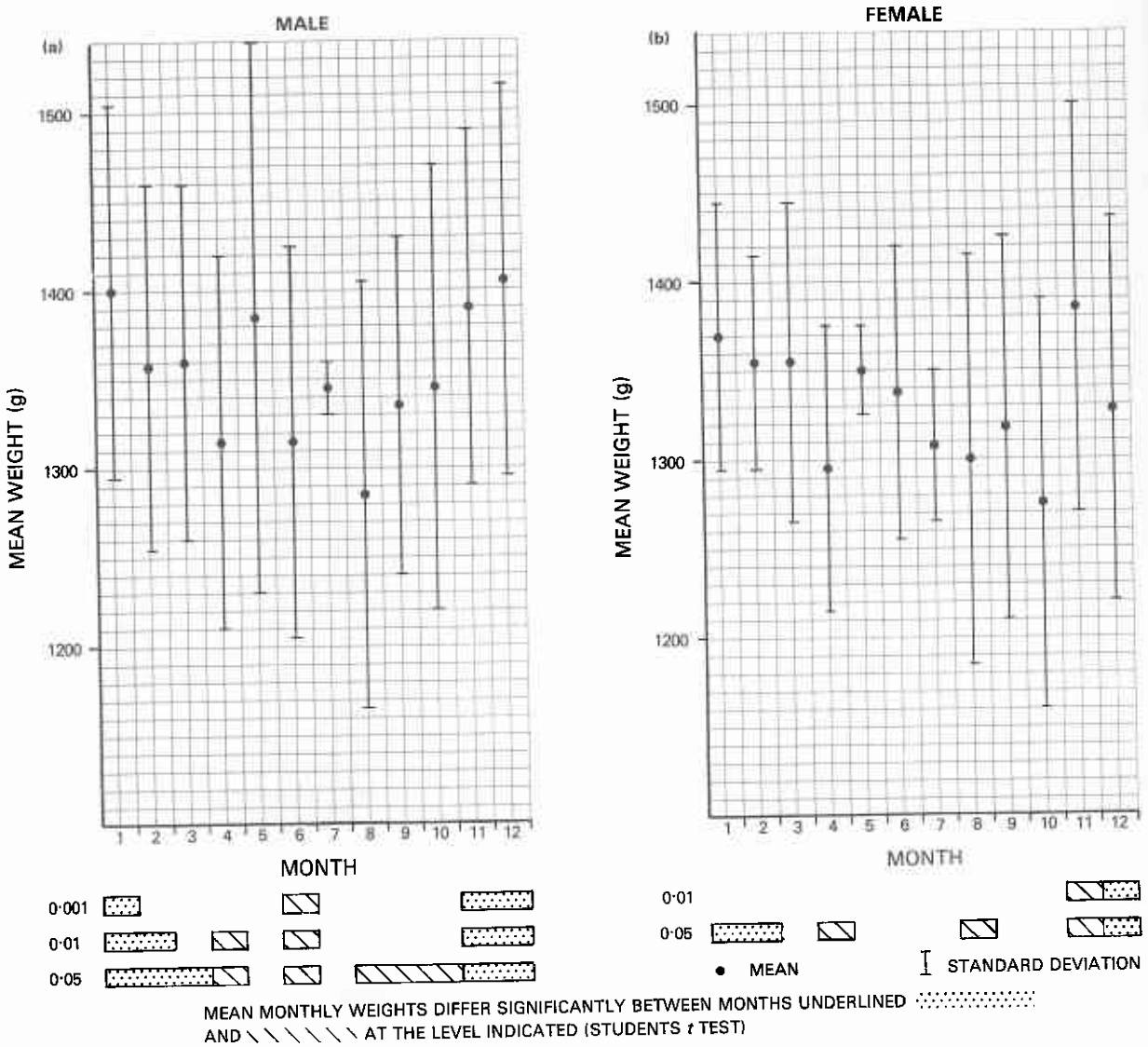



**Figure 27**

The woylie—mean monthly weights.
(*a*) Males (*b*) Females

Home range areas were also calculated using the minimum area method (Stickel, 1954) on the radio location maps for the 1976 burn (see Table 7). The minimum area method was used because it is not possible to use the more accurate exclusive boundary strip method on this type of data. As consequence, comparisons of pre- and post-burn areas should be made separately with trapping data and radio data. It is also considered that radio location data largely reflect the feeding area, whereas the trap data may often indicate agonistic behaviour on the boundaries of the home range, hence tending to give a larger area than that calculated from radio location data.

Home ranges calculated from trapping data (see Table 7) were somewhat smaller than those reported for the Tutanning woylie (Sampson, 1971).

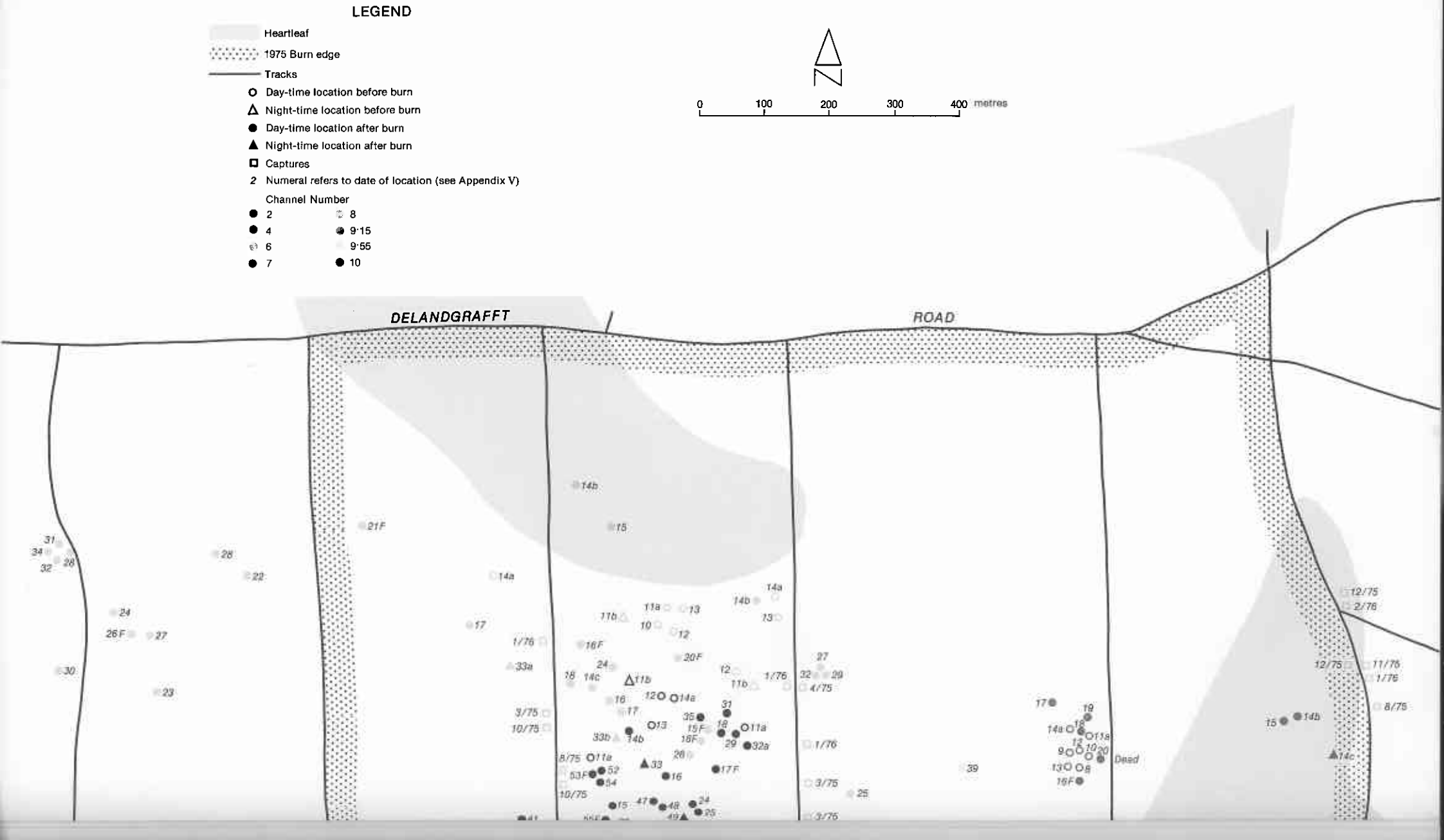
Animals caught three or more times were used to construct a table of movements (Table 8): a move was interpreted as a shift of more than 400 m to an area where the animal was recaptured at least twice. A move was considered successful if the animal remained in the area for a period of four months (the time needed to engage in successful reproduction). No such drifts in home range occurred in the control area.

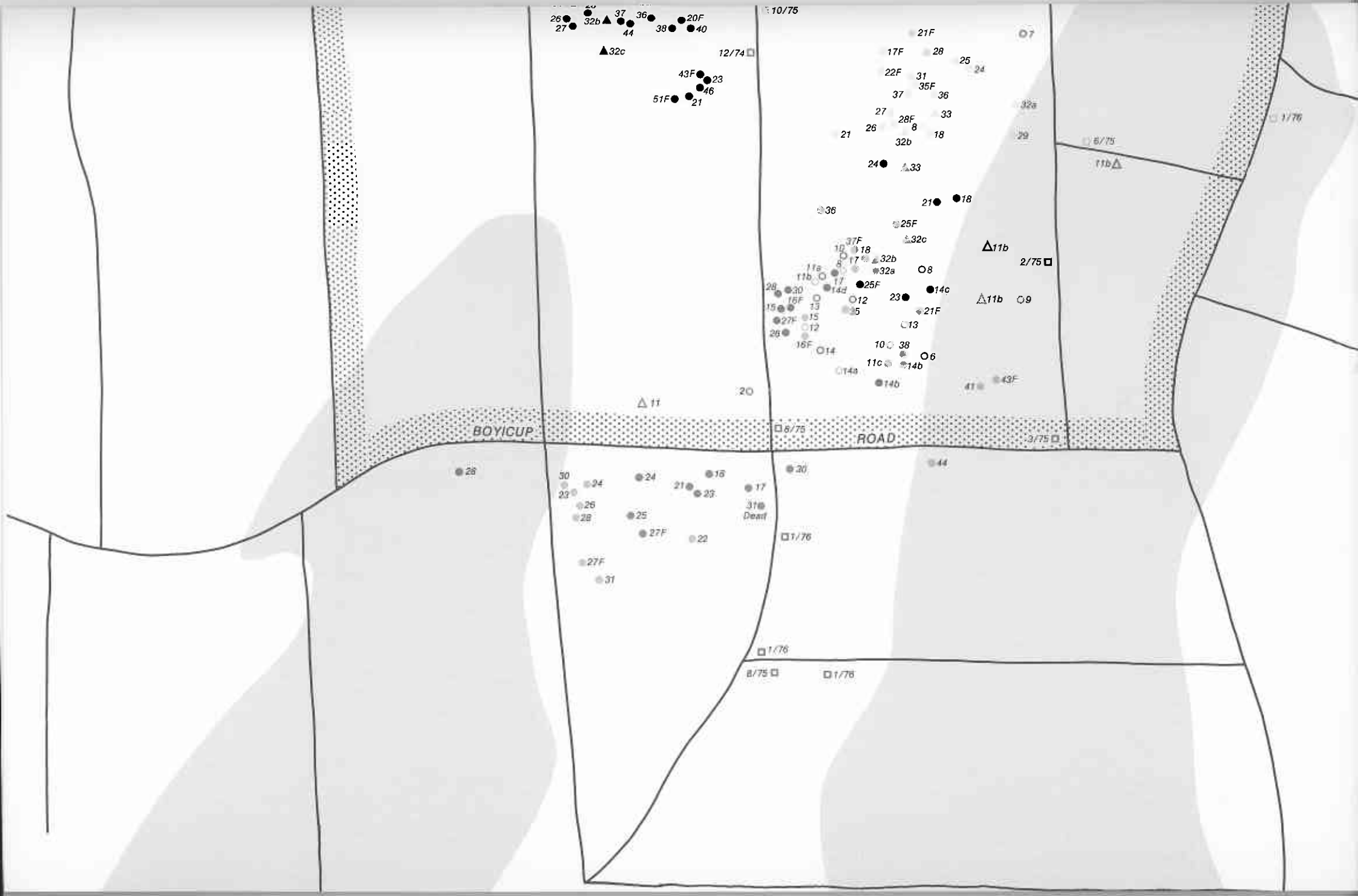
Mapping of the radio location data for the 1976 burn revealed two distinct parts to the home range: a nest area shown by the day time locations and a feeding area shown by nocturnal locations [Figs. 29 (*a*) and (*b*)]. The woylie has several nests in use at any one time: animal transmitter Channel 4.35 illustrated this particularly well (Fig. 29).

A cluster of locations on the map (Fig. 29) represents a nest; each location in a cluster should fall on the same point, but tracking and mapping errors all contribute towards inaccuracies. It can be seen that three or four nests were used alternatively and in a random manner over a period of weeks. Nests (clusters) are less obvious among the radio tracking data for the 1975 burn because aerial interpretation

**Figure 28**

# 1975 BURN—WOYLIE RADIO TRACKING LOCATIONS




BOYICUP
ROAD
10/75
12/74
6/75
1/76
2/75
3/75
8/75
Dead

# 1976 BURN—DAY TI
# BEFO

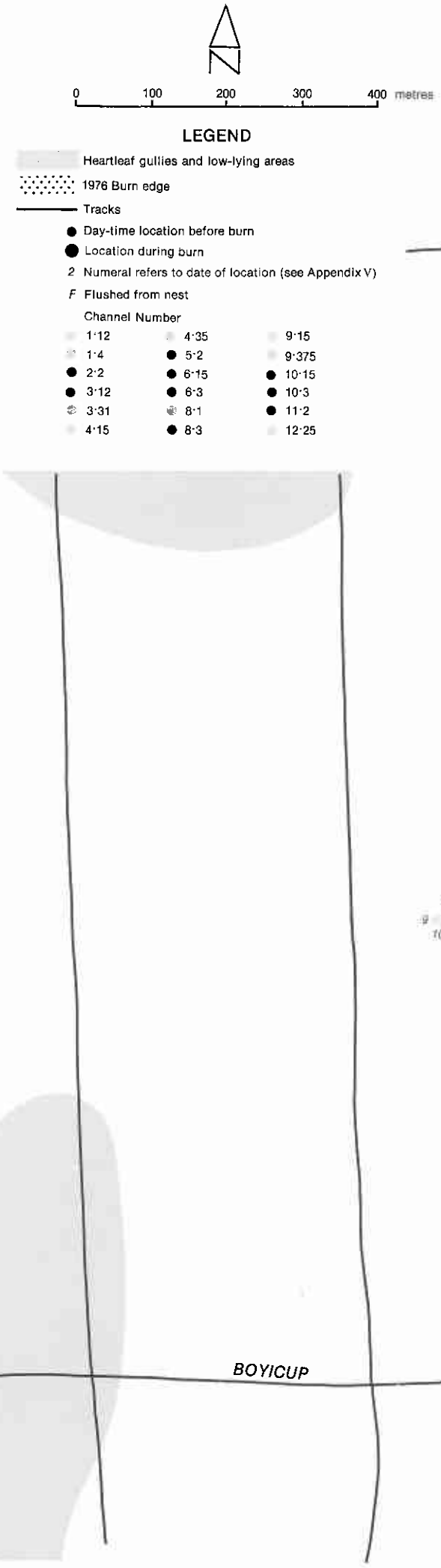
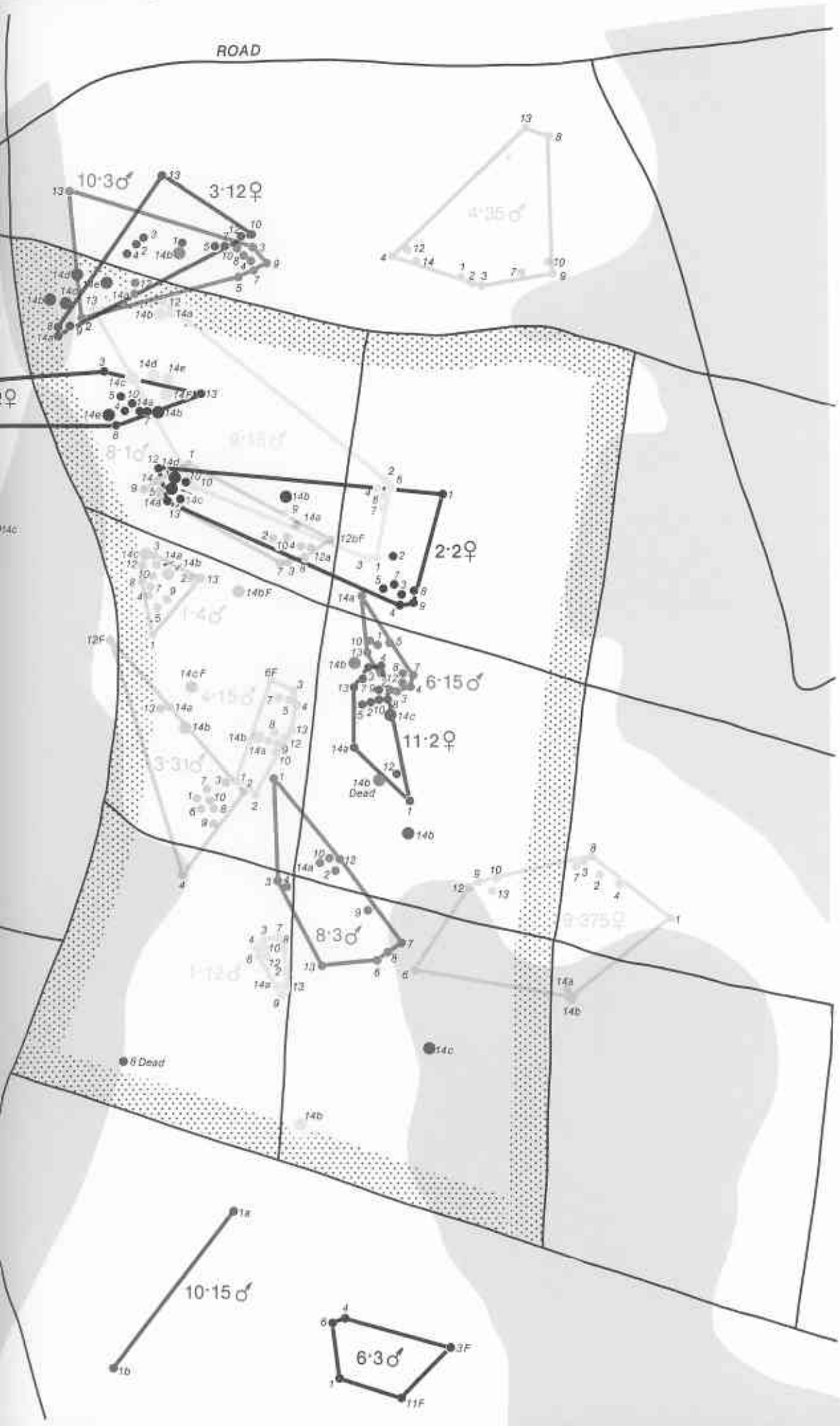
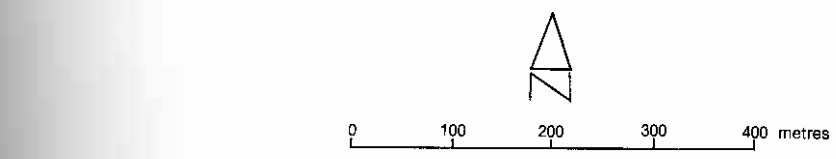


Figure 29 (*a*)

# IE RADIO LOCATIONS OF WOYLIES—
# RE AND DURING BURN



# 1976 BURN—NIGHT
# OF




LEGEND

- Heartleaf gullies and low-lying areas
- 1976 Burn edge
- Tracks
- Night-time location before burn
- Captures
- 2 Numeral refers to date of location (see Appendix V)

Channel Number

| | | |
|---|---|---|
| 1·12 | 4·35 | 9·15 |
| 1.4 | 5·2 | 9·375 |
| 2·2 | 6·15 | 10·15 |
| 3.12 | 6·3 | 10·3 |
| 3·31 | 8·1 | 11·2 |
| 4·15 | 8·3 | 12·25 |

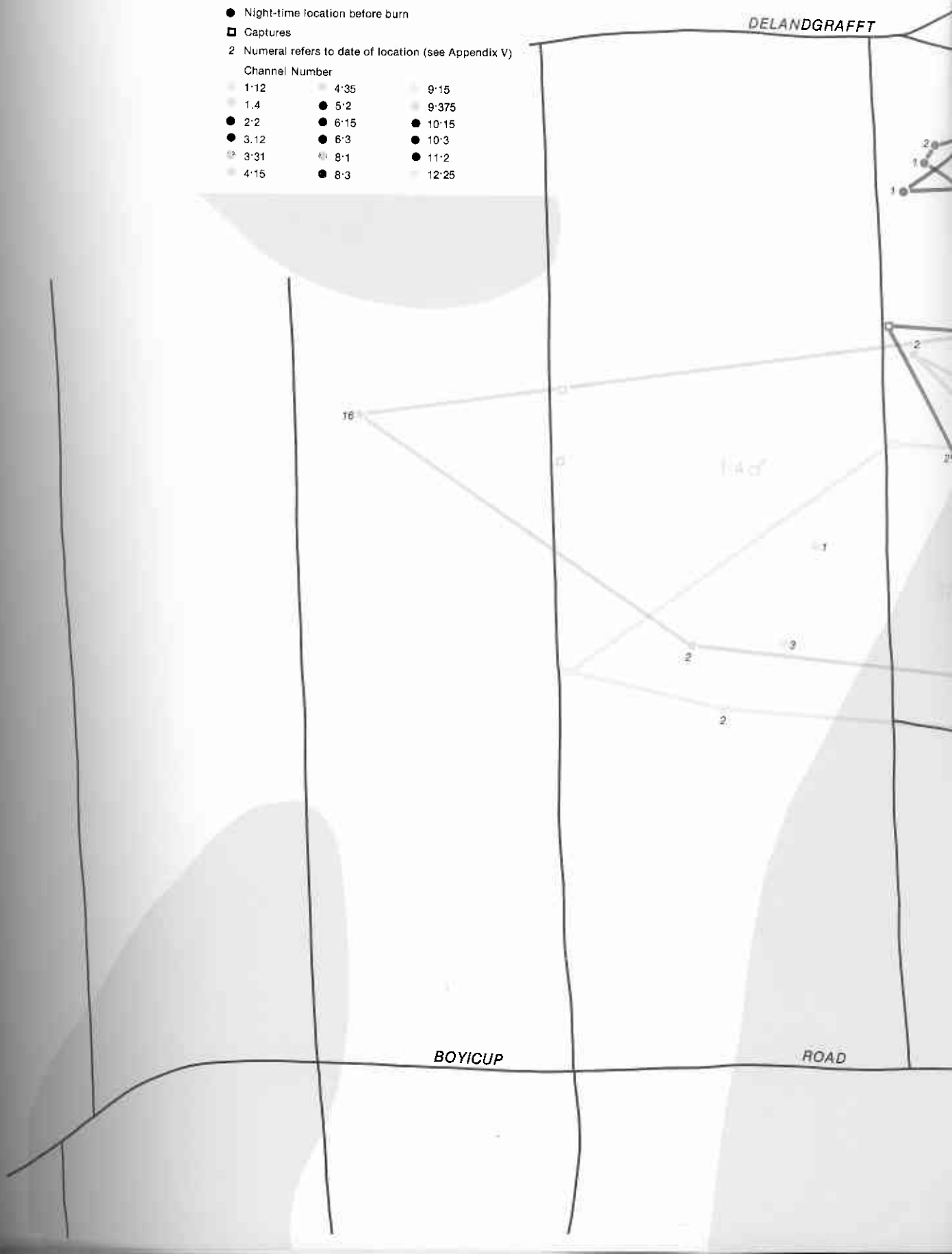


Figure 29 (*b*)

# TIME RADIO LOCATIONS AND CAPTURES WOYLIES—BEFORE BURN

**Table 8**
THE WOYLIE—TABLE OF MOVEMENT

| *Treatment* | *Sex* | *Age class* | *Animals shifting their home range* | | *Animals not shifting their home range* | |
|---|---|---|---|---|---|---|
| | | | *Successful* | *Not successful* | *Successful* | *Not successful* |
| Control | Male | Non-adult | | | 2 | 1 |
| | | Adult | | | 7 | 1 |
| | Female | Non-adult | | | 1 | |
| | | Adult | | | 1 (1) | 2 |
| Edge | Male | Non-adult | 1 | (1) | 2 (2) | 1 |
| | | Adult | | (1) | 7 (3) | 3 (1) |
| | Female | Non-adult | | | 1 (2) | 2 |
| | | Adult | | | 6 (1) | 2 (1) |
| Burn | Male | Non-adult | (2) | | 1 | 3 (1) |
| | | Adult | 3 (2) | (1) | 1 | (1) |
| | Female | Non-adult | | 1 | 1 | 1 |
| | | Adult | 3 | (1) | 1 | (2) |

Figures in parentheses are 1976 burn; other figures are 1975 burn.

maps were used. The map of the 1976 burn was accurately surveyed using compass and chain.

The nest areas (see Fig. 29) appeared to be almost exclusive to individuals. Any overlap that existed (see Table 7) was largely between adjacent males and females; nest areas of males did not overlap one another. Feeding areas of both sexes, however, overlap considerably (see Fig. 29 and Table 7).

These results are partly in agreement with Sampson (1971), who suggested that the males only are totally territorial. However, territoriality seems to be confined to the nesting area. There is evidence that the woylie may possess well developed scent-marking glands (Nick Allen*, personal communication) (Plate 18); the duct from the scent glands ends in a cloacal appendage which may be used in deposition of scent (Plate 19). These glands are morphologically similar to those in the brush-tailed possum (*Trichosurus vulpecula*) (Bolliger and Whitten, 1948) and it has been suggested that they are used for scent-marking of territories by this species (Thompson and Pears, 1962).

**Plate 18**
Male woylie dissected to show paired scent or oil glands.
(Photograph Nick Allan)
(*a*) Prostate gland
(*b*) Scent or oil gland

**Plate 19**
A droplet of fluid exuding from the tip of the cloacal appendage after application of pressure to the scent gland.
(Photograph Nick Allan)

* Zoology Department, University of Western Australia.

Data obtained using the Rustrak continuous recorder, showing the mean number of hours per night spent within its range, suggested that the woylie moved and fed within a fairly restricted area on any one night (Appendix IV). The greater part of most nights was spent within the 200 to 250 m radius range of the recorder.

Further indication of the woylies' limited range of movement is provided by results from the transportation experiment (Table 9). Forty-five woylies were transported and only five returned; four of these were animals transported distances of 3000 m or less from their home range areas.

## THE PRE-BURN POPULATION—THE TAMMAR

A summary of the trapping results over the three-year period is presented in Table 3.

### Ageing the population

Details of the method used are presented in Appendix III. For the purpose of this study four age categories are recognised.

(1) Joeys—pouched joeys from birth to approximately seven to eight months. Tooth eruption: M1.0 is just starting to rise.

(2) Juveniles—approximately between the ages of seven to eight months and fifteen months. Tooth eruption: M1.0 to M2.0.

(3) Sub-adults—from approximately fifteen months to two years. Tooth eruption: M2.0 to M3.0, before p4 replaces p3 and dp4.

(4) Adults—from approximately two years. Tooth eruption: animals with p4 present.

These age classes approximate those of Jones *et al.* (1966).

As with the woylie, a non-adult category including juveniles and sub-adults was used in most of the analyses.

### Population analysis

*Population structure*

Almost all data refer to the 1975 burn. However, where applicable, data from incidental tammar captures made during the 1976 burn for woylie studies were used.

Trapping in the unburnt control block was not properly organised until just before burning. Consequently, capture percentages before burning were largely provided from the burn area (Fig. 30). Pre-burn trapping had not proceeded for long enough, even in the burn block, to enable the numbers of new captures to reach a steady level (Fig. 31).

As with the woylie, male captures were significantly higher (chi-square test) than female captures, but the difference in the actual numbers of males and females caught was not significant. Non-adults comprised 16·67 per cent of the population.

*Survival*

A table of known survival, similar to that constructed for the woylie, was made up for the tammar (Table 10). No significant differences in known survival between sexes of adults and non-adults were observed in the unburnt control.

Reliable figures for the survival of pouched young are not available because too few recaptures of tammars were made during the winter.

*Reproduction*

Birth dates of tammar joeys were estimated using head and pes length (Appendix III). Data from three years of trapping were combined (Table 11).

The breeding season commences in mid-December and finishes in early February, although occasional births may occur during March. The season is almost one month earlier than that of the tammar on Garden Island (Jones *et al.*, 1966). Females have their first joeys at the age of approximately one year (tooth eruption stage M1.8 to M2.0).

*Weights*

The tammar exhibits sexual dimorphism; the mean weight of adult males is 4746·5 g and of adult females is 3657·4 g (significant difference at 0·001 level, Students *t* test). Only the data for males were sufficient for analysis, and these showed considerable seasonal variation. As with the woylie, weights taken

**Table 9**

FATE OF WOYLIES TRANSPORTED FROM THEIR HOME RANGE AREAS

| *Sex* | *Maturity* | *Distance released from home range area (m)* | | | | | |
|---|---|---|---|---|---|---|---|
| | | *2000 to 2500* | *2600 to 3000* | *3100 to 3500* | *3600 to 4000* | *4100 to 4500* | *4600 to 5000* |
| Males | Non-adult | 1 | 5 (2) | 1 | 6 (1) | 1 | 1 |
| | Adult | 1 (1) | 3 (1) | 1 | 3 | 6 | — |
| Females | Non-adult | 1 | 1 | 2 | 1 | 3 | 1 |
| | Adult | 1 | 1 | 1 | 2 | 2 | — |

Figures in parentheses are number of animals that returned to their home range areas.

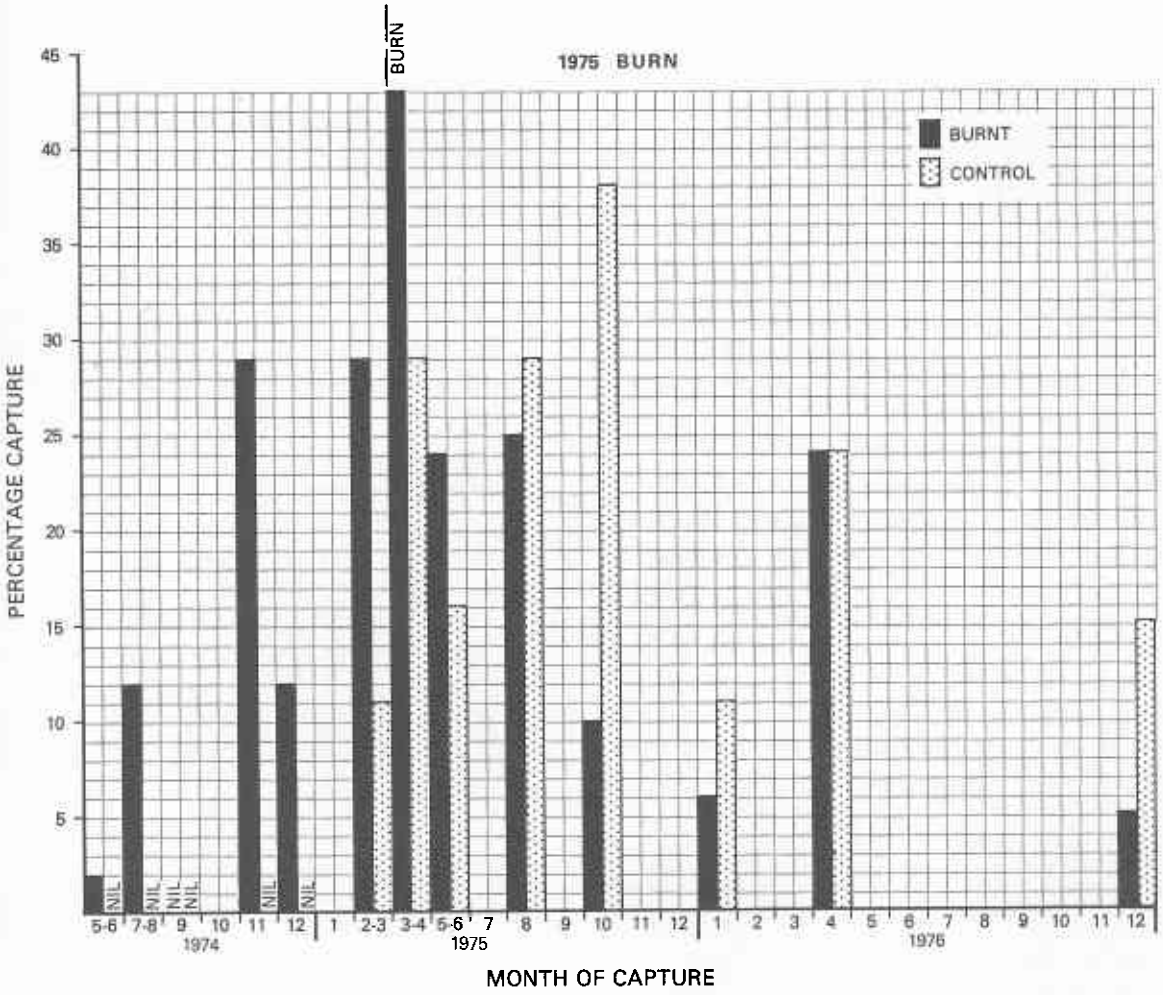



**Figure 30**
The tammar—percentage captures, 1975 burn

from the time when they are heaviest (October to February) differed significantly from weights during the period March to August (Fig. 32). The mean weight of adult males fell from a peak of 5292·4 g during November to a low of 4361·0 g during August, a loss in weight of 17·6 per cent, somewhat higher than that of the woylie.

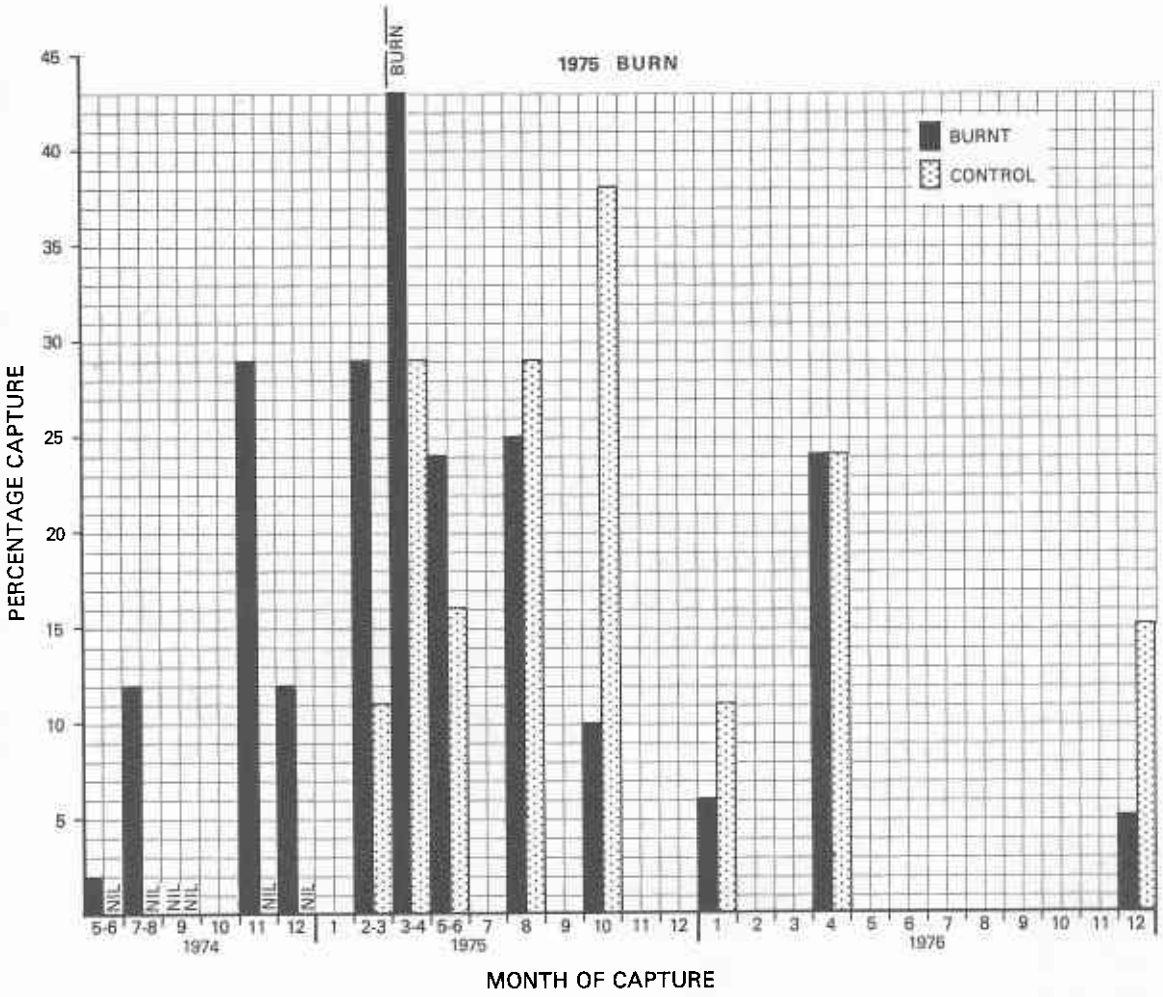
### Movements

Trapping in 1974 indicated that the tammars were confined to the heartleaf thickets and their immediate surrounds. This was confirmed in the 1976 burn, when funnel traps were gridded over the entire area. Tammars were almost always caught in, or very close to, the edge of heartleaf thickets. Only occasionally were individuals caught on the ridges between thickets.

Comparatively small areas of thicket were occupied by surprisingly large numbers of tammar. Trapping data indicated that on a good site approximately thirty to forty tammars may occupy a thicket area of only forty hectares. How many separate groups these animals comprised is not known.

**Table 10**
THE TAMMAR—KNOWN SURVIVAL

| | *Control* | | | *Burn edge* | | | *Burn* | | |
|---|---|---|---|---|---|---|---|---|---|
| | *Number of animals* | *Total survival (months)* | *Mean survival (months)* | *Number of animals* | *Total survival (months)* | *Mean survival (months)* | *Number of animals* | *Total survival (months)* | *Mean survival (months)* |
| Male | 13 | 58 | 4·46 | 27 | 161 | 5·59 | 11 | 53 | 4·82 |
| Female | 11 | 32 | 2·91 | 23 | 81 | 3·52 | 11 | 20 | 1·82 |
| Non-adult | 12 | 52 | 4·33 | 14 | 57 | 4·07 | 4 | 1 | 0·25 |
| Adult | 12 | 38 | 3·17 | 36 | 175 | 4·86 | 18 | 72 | 4·00 |

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| Female | 11 | 32 | 2·91 | 23 | 81 | 3·52 | 11 | 20 | 1·82 |
| Non-adult | 12 | 52 | 4·33 | 14 | 57 | 4·07 | 4 | 1 | 0·25 |
| Adult | 12 | 38 | 3·17 | 36 | 175 | 4·86 | 18 | 72 | 4·00 |

**Table 11**

THE TAMMAR—JOEY BIRTHS 1974 TO 1976 COMBINED DATA

| | *December* | | | | *January* | | | | *February* | | | | *March* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Weekly births | — | — | 4 | 7 | 8 | 5 | 6 | 4 | 7 | 9 | — | 1 | — | 1 | — | — | 1 |

A table of movements, similar to that constructed for the woylie, was made up for the tammar (Table 12). Unlike the woylie, there was considerable movement of tammars in the control area. Most of the animals that emigrated were mature males.

Radio-tracking data on the tammar were limited to those obtained from five individuals and hence are not as comprehensive as the woylie data (Fig. 33).

Tammars live in groups, individuals having no defined home range or territory. They appear to be group-territorial (Jones *et al.*, 1966). No reliable information was obtained on the size of groups. However, it appears that they may comprise a dozen or more individuals. Family units comprising a male, a female and a sub-adult joey were occasionally caught together in the traps. Observations of tammars at a feeding station suggested that there is a strict social hierarchy. Agonistic behaviour was frequently observed, although physical encounters were rare.

Animals with transmitters which moved to neighbouring thickets after the 1975 burn occupied "fringe areas" in what appeared to be sub-optimum habitat, close to other groups. This may indicate a degree of hostility between members of different groups. Certain individuals, usually males, appeared to be able to move freely between adjacent groups in neighbouring thickets. One of these animals with a transmitter, Channel 7, appeared to be equally at home in two adjacent groups occupying thickets 1 km apart.

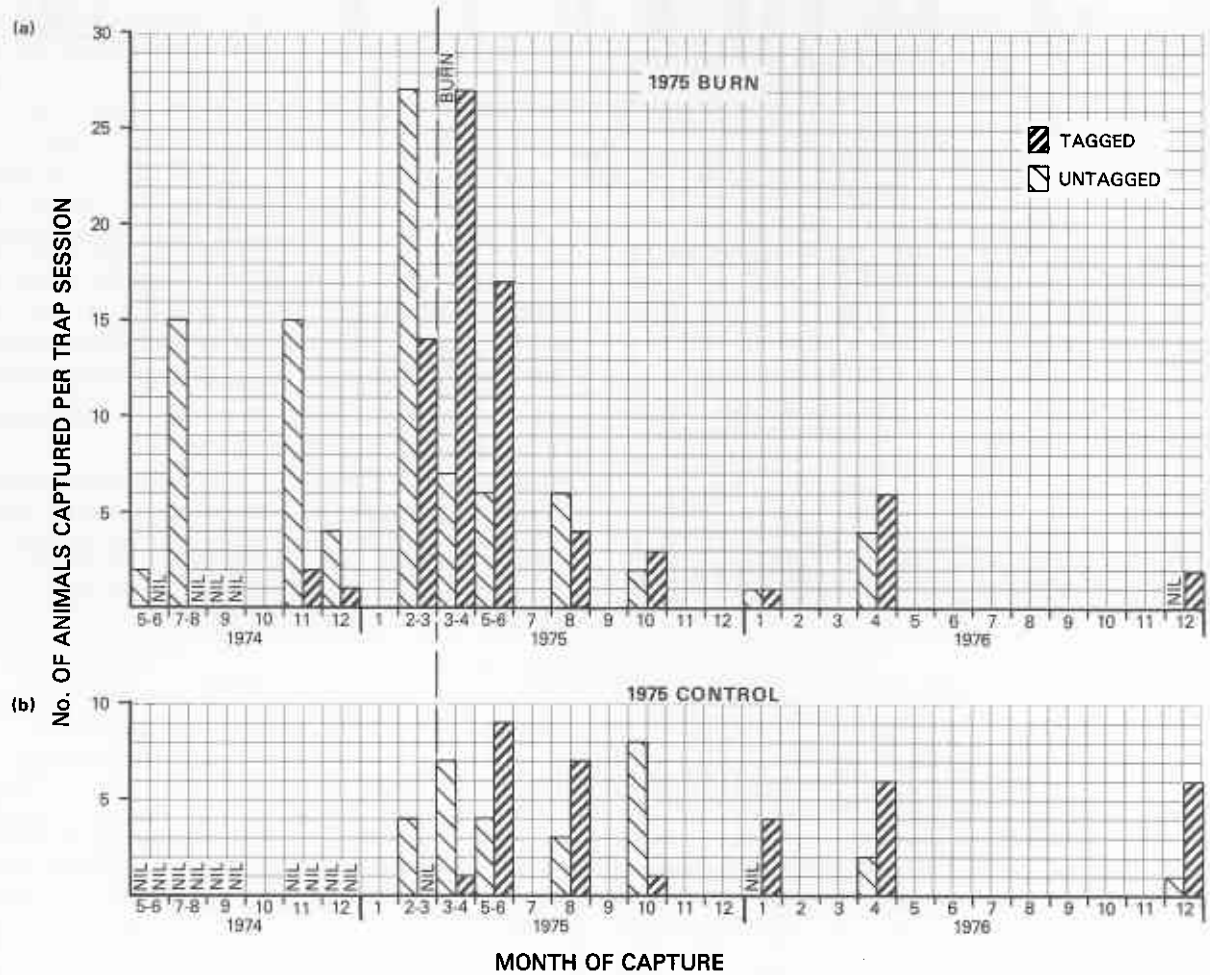



**Figure 31**

The tammar—comparison of tagged animals and new captures (untagged).

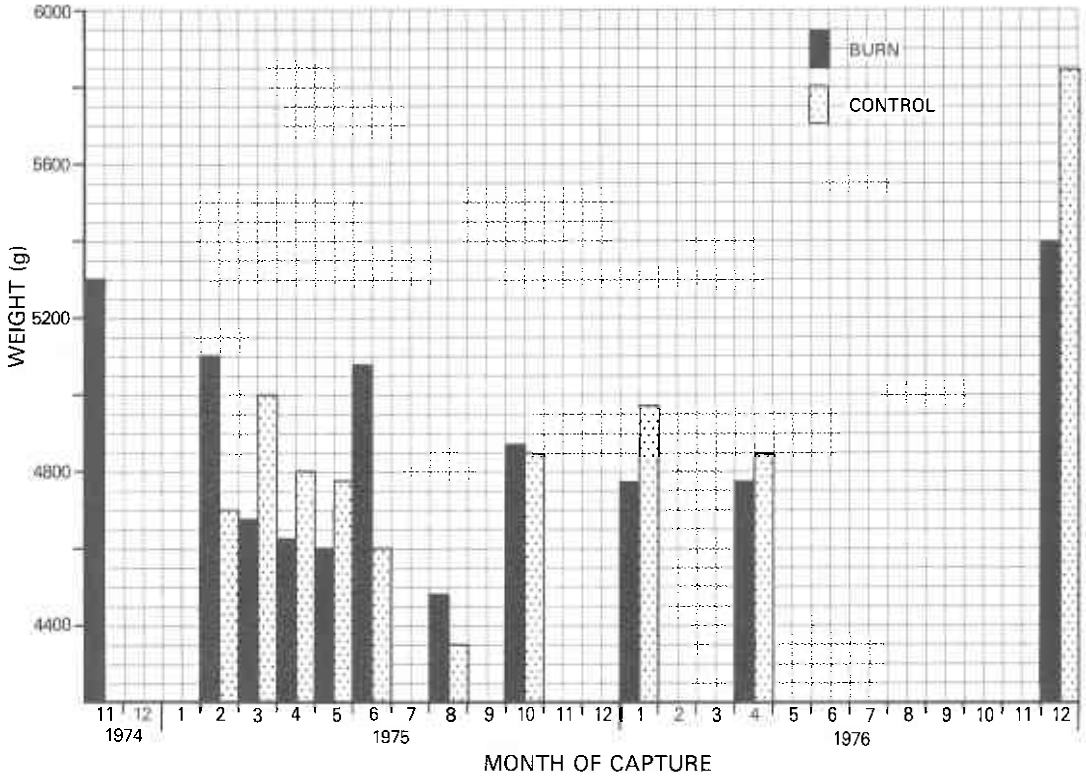



**Figure 32**

The tammar—mean weight per trap session.

## FIRE EFFECTS—THE WOYLIE

### Description of fires

Both fires were autumn burns, lit soon after the opening of the burning season on 15 March. Hot dry weather was chosen for both burns so that the fires were relatively hot and a more thorough burn was achieved than under the normal control burning conditions. The 1975 burn in particular had to be a hot fire to ensure that the heartleaf thickets were burnt. Fire intensity was not uniform over the area and various intensities of fire could be recognised (Fig. 34 and Plates 20, 21 and 22).

**Table 12**

THE TAMMAR—TABLE OF MOVEMENT

| *Treatment* | *Tammar* | | *Shifts in home range* | | *No shift in home range* | |
|---|---|---|---|---|---|---|
| | | | *Successful* | *Unsuccessful* | *Successful* | *Unsuccessful* |
| Control | Male | Non-adult | 1 | 1 | | 1 |
| | | Adult | 4 | 1 | | |
| | Female | Non-adult | | 1 | 1 | |
| | | Adult | | | | 3 |
| Edge | Male | Non-adult | | | | |
| | | Adult | 2 | | | 5 |
| | Female | Non-adult | | | 1 | |
| | | Adult | | | 1 | 3 |
| Burn | Male | Non-adult | 2 | 1 | | 1 |
| | | Adult | 4 | 3 | | 3 |
| | Female | Non-adult | 1 | | | 1 |
| | | Adult | 3 | 2 | | 6 |

**Plate 20**

Tree canopy scorch. Note the blackened trunks and dead leaves of the overstorey trees. The ground vegetation has been completely removed by the fire.

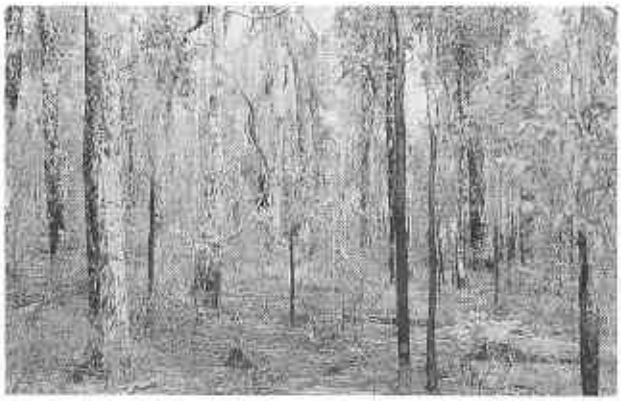


**Plate 21**

Understorey burnt. Note green leaves on the overstorey trees. Clumps of dead understorey remain.

**Plate 22**

Understorey burnt. Areas of ground vegetation remain unburnt in some places.

**Plate 23**

Regeneration of forest in area of canopy scorch eight months after the fire.

## Animal behaviour during the fires—woylie and tammar

Animals with radio transmitters, both woylies and tammars, were monitored during the fires. Results are given in Table 13. In no instance did any of the animals leave their known home range areas during the burn [see Figs. 28, 29 (*a*) and (*b*) and 33]. Only one animal, radio transmitter Channel 8·3, died as a direct result of fire. This individual sought refuge in a hollow log which subsequently caught fire, and the animal was choked to death.

One animal's movements during the fire, a woylie (animal transmitter Channel 6·15), were recorded in detail (Fig. 35). This animal's behaviour was fairly typical of that exhibited by other individuals of both species. Woylies remained in their nests, and tammars in their resting places, until the very last minute when they vacated them to move in front of the flames until an unburnt patch became evident. Such unburnt patches are common in most fires (see Fig. 34) and even a small one will provide sufficient refuge.

The tammar with transmitter Channel 7 sheltered underneath a log in an unburnt patch of no more than 20 m² while the fire raged all about it, scorching the leaves on trees 40 m high.

In cases where no suitable unburnt patches remained before the fire had pushed the animal to the limits of

**Table 13**
BEHAVIOUR OF ANIMALS WITH TRANSMITTERS DURING FIRE

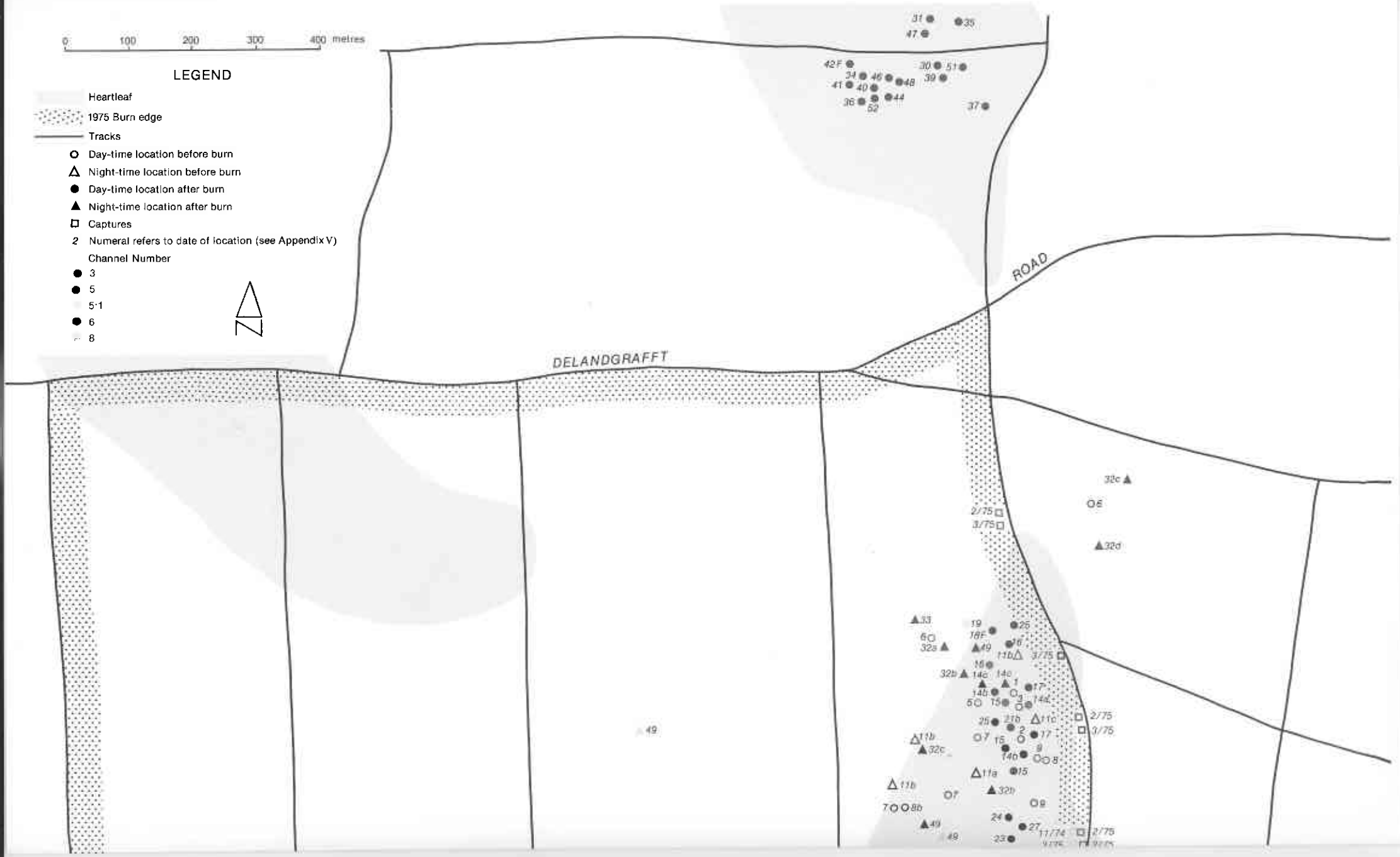
| *Species* | *Number of individuals* | | | |
|---|---|---|---|---|
| | *Unburnt* control* | *Doubled back through flames* | *Found in unburnt patch* | *Hid in log* |
| Woylie | 6 | 9 | 6 | 4† |
| Tammar | — | — | 4 | — |

* Control animals in unburnt habitats remained in their nests.

† One individual died from suffocation.

Figure 33

# 1975 BURN—TAMMAR RADIO TRACKING LOCATIONS



BOYICUP ROAD
Dead

**Figure 34**

Boyicup trapping area—map showing fire intensity on the 1975 and 1976 burn areas.

its home range area, an animal would double back through the flames to the safety of the burnt ground beyond. Directly after the 1976 burn most of the woylies with transmitters were found to be sitting on the burnt, still-smoking ground, in the vicinity of their former nest sites. Some individuals were observed in a dazed state, allowing close human approach after the fire. They are thought to have been suffering from a form of shock (see Section III, Mortality Factors).

## Population analysis

### *Population structure*

Immediately after the 1975 fire, in March-June, there was a decrease in total captures on the burn area (see Figs. 22 and 23). This appears to be owing to a complete absence of captures of new non-adults during this period (see Figs. 24 and 25). No such decrease was evident after the 1976 burn.

There was no significant decrease in the overall percentage capture after the 1975 burn (see Table 4). But there was a general decrease in overall percentage captures after the 1976 burn (see Table 4). This decrease was greatest in the control block, but the burn area also showed a considerable decline. Since this decline had its origins in February, following the removals, and was particularly pronounced in the unburnt control area, it is reasonable to assume that it was a result of these removals rather than an effect of the fire.

Although the overall percentage capture remained relatively unaffected by the burns, a considerable change in the population structure followed the fires.

After the 1975 burn there was a marginal increase in the number of male captures relative to female captures [see Fig. 22 (*a*)]. This represents a real difference; significantly more of the animals caught per session were males and a significantly higher proportion of the new untagged animals was male (Table 14). A slightly increased proportion of the post-fire capture in the control plot was also male (see Table 14); inspection of the data showed this to be an edge effect.

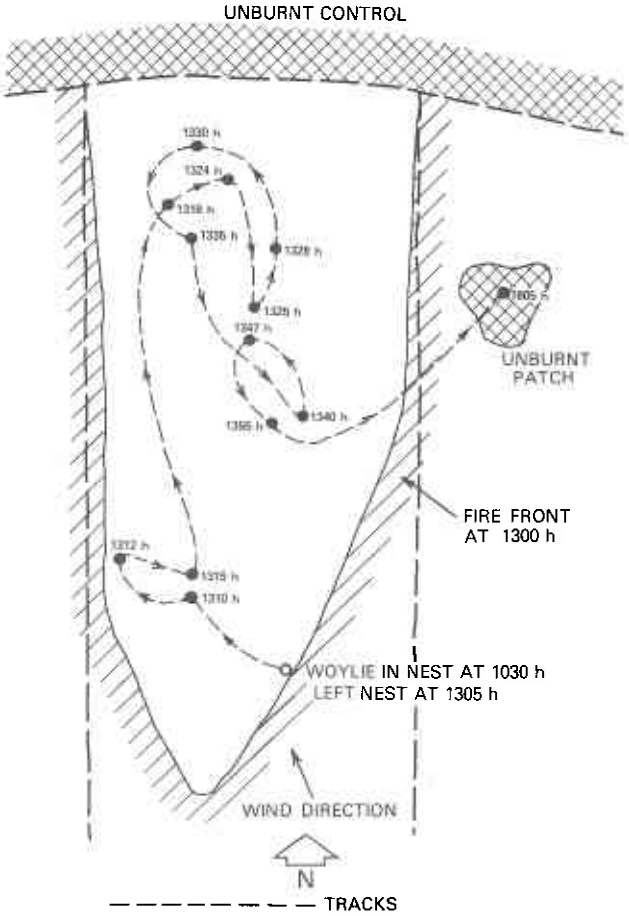



**Figure 35**

Woylie, transmitter animal Channel 6.15, movements during the 1975 burn.

No changes in the relative proportion of males to females were observed in the 1976 burn. However, the last trap session appeared to have a relatively higher proportion of male captures, so it may be too soon yet to make an assessment on this burn.

The most obvious change after the 1975 fire was the increasing proportion of non-adult captures relative to adult captures (see Fig. 23). Again, this difference was a real one in terms of the number of animals caught per session. Before the fire the numbers of adults caught per session were very significantly higher than non-adult numbers, whereas after the fire this difference was only just significant. Among the new untagged animals the ratio changed from significantly more adults before the burn to significantly more non-adults after the burn (Table 15). Some of this difference was undoubtedly owing to the fact that at the start of the study all animals, including adults, were new and untagged. However, since the difference in the control was much smaller it seems that there was a significant increase in the proportion of non-adults on the burn.

Exactly the same pattern may be observed after the 1976 burn [see Fig. 23 (*c*) and (*d*), and Table 15]. Note that the pattern in the control, where re-population was taking place after removals, was similar to that of the burnt area.

Not enough animals were captured for detailed analysis, but a broad comparison of the total number of non-adults compared with the numbers of adult females caught each year provides further evidence of an increase in non-adults on the burn (Table 16). The population of non-adults increased three times as much as the adult female population over the three years of the study. No increase was evident in the control area.

Re-population of both burns and the 1976 removal (control) area was effected almost exclusively by new untagged non-adults. This was similar to the "normal" pattern of replacement in the unburnt control (see Fig. 24). After all trappable animals in the area had been captured, any new untagged woylies must all have been non-adult (see Fig. 24).

The pattern of re-population in the 1976 burn removal area was similar to that on the burnt areas.

**Table 14**

TOTALS OF ANIMALS CAUGHT PER SESSION, COMPARISON OF SEXES

| | | | *Total number of animals* | | | *New captures* | | |
|---|---|---|---|---|---|---|---|---|
| | | | ♂ | | ♀ | ♂ | | ♀ |
| 1975 Burn | Pre-burn | C | 65 | * | 31 | 40 | NS | 26 |
| | | B | 98 | NS | 69 | 37 | NS | 33 |
| | Post-burn | C | 88 | ** | 40 | 15 | NS | 9 |
| | | B | 114 | ** | 56 | 20 | * | 7 |
| 1976 Burn | Pre-burn | C | 49 | NS | 37 | 19 | NS | 15 |
| | | B | 96 | ** | 45 | 22 | NS | 11 |
| | Post-burn | C | 10 | NS | 9 | 4 | NS | 2 |
| | | B | 46 | ** | 14 | 7 | NS | 2 |

C = Control B = Burn

**Table 15**
THE WOYLIE—TOTALS OF ANIMALS CAUGHT PER SESSION, COMPARISON OF ADULTS AND NON-ADULTS

| | | | *Total number of animals* | | *New captures* | |
|---|---|---|---|---|---|---|
| | | | *Adults* | *Non-adults* | *Adults* | *Non-adults* |
| 1975 Burn | Pre-burn | C | 59* | 28 | 50** | 16 |
| | | B | 88*** | 33 | 59*** | 11 |
| | Post-burn | C | 84* | 44 | 9 NS | 15 |
| | | B | 104* | 66 | 3** | 24 |
| 1976 Burn | Pre-burn | C | 58* | 28 | 17 NS | 17 |
| | | B | 94** | 47 | 17 NS | 16 |
| | Post-burn | C | 9 NS | 10 | 0 NS | 6 |
| | | B | 27 NS | 33 | 1 NS | 8 |

C = Control B = Burn

Re-population was effected entirely by young animals from the immediate surrounds with little or no contribution by immigrants from further afield; after the first removals in the unburnt control in January, six non-adults appeared in February. When these were removed no further non-adults appeared until the June trapping session [see Fig. 25 (*d*)].

This slow re-population suggests occupation by young animals from the immediate surrounds, with few or no immigrants from further afield.

*Survival*

Some indications of immediate post-burn survival were provided by animals fitted with transmitters. These data indicate that many animals on the burnt area may have been victims of predators soon after the fire (Table 17). Animals on the edge of the burn may have survived by moving on to the unburnt edge and a few may have survived on the burn itself. Survivals of adults and non-adults in the unburnt control area did not differ significantly during the period of the study (see Table 5). However, on the burn and the edge of the burn, survival of non-adults was significantly lower than adult survival (Students *t* test 0·05 and 0·01 levels respectively). Survival of the remaining adults had increased while the survival of non-adults had decreased.

The capture data confirm that there was a higher mortality among these new non-adult immigrants to the burn. In the burn area the number of single captures increased after the fire; in the control block the number of single captures decreased over the same period (Table 18).

These survival data suggest either a high mortality or a high immigration rate amongst non-adults which colonised the early post-burn.

**Table 17**
THE WOYLIE—FATE OF ANIMALS WITH TRANSMITTERS

| *Fate of woylie* | *Weeks after fire* | | | |
|---|---|---|---|---|
| | *5-6* | *7-14* | *15-28* | *28+* |
| Killed by native cat | 4 | | | |
| Killed by fox | 3* | 2* | 2* | |
| Died from stress (shock) | 2 | | | |
| Survived on burn | | | | 2 |
| Survived—moved to edge of burn | | | | 6 |
| Controls—in unburnt habitat | | | | 3 |

1975 and 1976 burn data combined.
* One of each of these deaths is a control animal.

**Table 16**
THE WOYLIE—NON-ADULTS AS A PERCENTAGE OF THE TOTAL FEMALE POPULATION, 1975 BURN

| *Number of animals captured* | 1974 | | 1975 | | 1976 | |
|---|---|---|---|---|---|---|
| | *Burn edge* | *Control* | *Burn edge* | *Control* | *Burn edge* | *Control* |
| Non-adults | 9 | 10 | 20 | 14 | 25 | 10 |
| Adult females | 22 | 18 | 24 | 25 | 18 | 24 |
| Non-adults as percentage of females | 40·9 | 55·6 | 83·3 | 56·0 | 138·8* | 41·7 |

*Significantly (0·01 level) higher than control (chi-square test).

**Table 18**

THE WOYLIE—PERCENTAGE OF ANIMALS PER CAPTURE CLASS DURING THREE PERIODS OF FOUR TRAP SESSIONS EACH, 1975 BURN

| *Trap period* | *CONTROL* *Percentage of animals per capture class* | | | | *BURN* *Percentage of animals per capture class* | | | |
|---|---|---|---|---|---|---|---|---|
| | *1 capture* | *2 captures* | *3 captures* | *4 captures* | *1 capture* | *2 captures* | *3 captures* | *4 captures* |
| *Pre-burn* Sept. 1974 to March 1975 | 75·0 (24) | 18·7 (6) | 6·3 (2) | — | 40·7 (24) | 35·6 (21) | 16·9 (10) | 6·8 (4) |
| *Post-burn* March 1975 to August 1975 | 71·0 (22) | 25·0 (8) | 4·0 (1) | — | 66·7 (24) | 19·4 (7) | 11·1 (4) | 2·8 (1) |
| *Post-burn* Oct. 1975 to Dec. 1976 | 41·7 (15) | 41·7 (15) | 13·9 (5) | 2·7 (1) | 60·0 (30) | 20·0 (10) | 14·0 (7) | 6·0 (3) |

Figures in parentheses are actual numbers of animals.

*Reproduction*

No effects of fire on reproduction were observed.

*Weights*

There was an increase in the weights of adult animals on the 1975 burn relative to those on the unburnt control following the first spring after the fire. Weights of animals on the burn were significantly higher (0·001 level, Students *t* test) than those on the control area between October and April [Fig. 36 (*a*)]. The difference was still apparent in December 1976, but the figures were not significant.

Woylies on the 1976 unburnt control area did not show the same seasonal loss in weight as those on the 1975 burn area [Fig. 36 (*b*)].

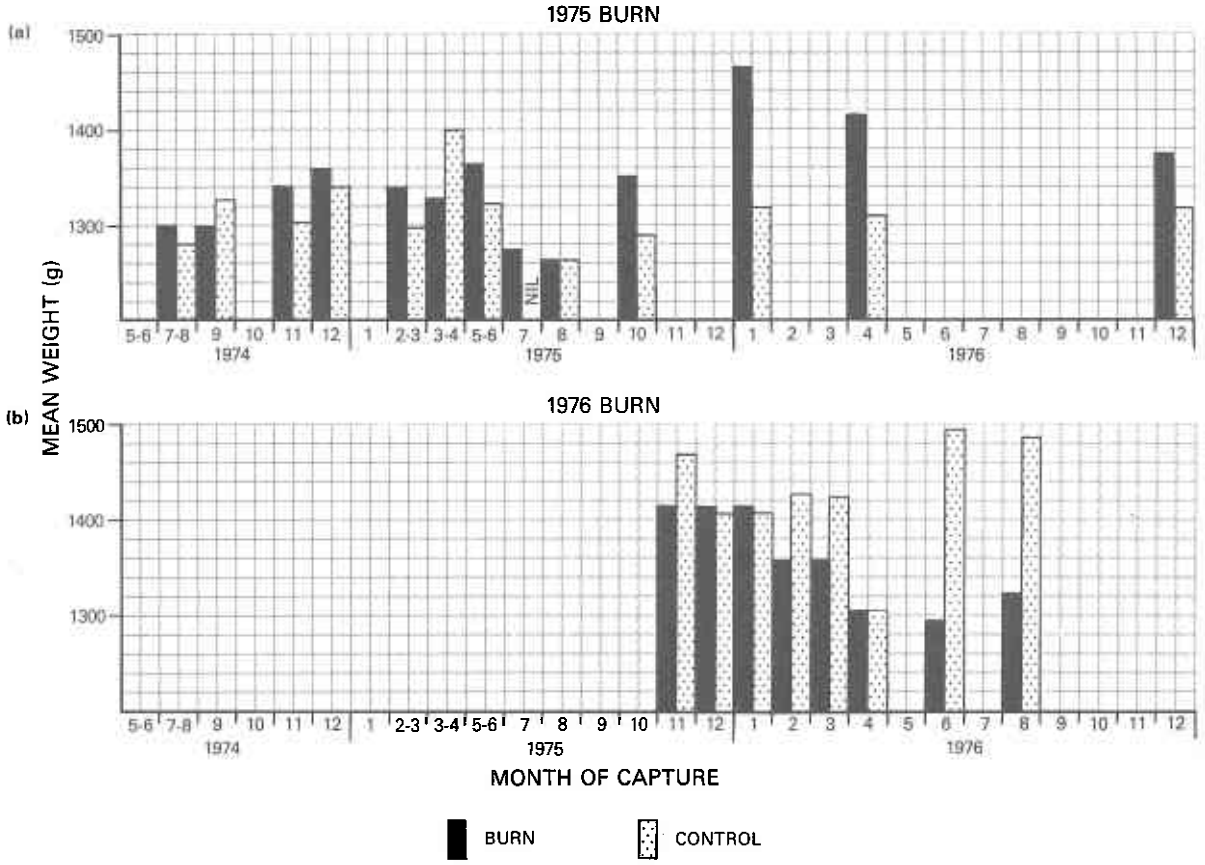



**Figure 36**

The woylie—mean weight per trap session.

Weights of animals on the control area appeared to increase relative to those on the burn area following removals in February. They were significantly higher over the February, March, June and August trapping sessions. Although significant, the figures were based on the weights of a few individuals, and these results should be treated with caution. It is possible, however, that they indicate a real weight increase reflecting reduced competition for food or less intra-specific interactions following the removals. The animals in question were well away from the burnt area.

**Movements**

The detailed movements, after the burn, of animals with radio transmitters are plotted in Figs. 28, 29 and 37.

A variety of reactions to the burn was observed and no particular behaviour may be said to be typical. The most commonly observed behaviour consisted of shifting nesting areas to the edge of the burn while returning to feed in their burnt-out home range areas during the night. Such behaviour frequently resulted in permanent shifts in territory or home range area. The animal with radio transmitter Channel 8 attached moved to the eastern edge of the burn after the 1975 fire. In 1976, after a new transmitter was fitted (Channel 1.4), it was found that it still nested on the eastern edge of the 1975 burn and returned to feed in its old home range in the 1975 burn, a distance of over 1000 m from its nest site [see Figs. 37 (*a*) and (*b*)].

After the 1976 burn this behaviour manifested itself in a reversal of nesting and feeding areas. Animals which had formerly nested on the edge of the 1975 burn shifted their nesting areas into the one-year-old burn after the 1976 fire. They returned at night to feed on the new burn. Such reversals of nesting and feeding areas ordinarily did not involve animals extending their normal range. The changes were carried out within the limits of their former ranges (see Fig. 37).

Two animals remained within the area of the 1975 burn. A female, radio transmitter animal Channel 10, had almost its entire range burnt out and yet survived till the following summer, rearing one joey and carrying another in its pouch (see Fig. 29). Radio transmitter animal Channel 9.55, a male, survived with its nesting area centred on an unburnt patch of approximately three hectares. The range of this animal was further documented in 1976, when it was given another radio transmitter, Channel 12.25 (see Figs. 29 and 37). This animal was still alive at the end of the study in December 1976.

One individual, radio transmitter animal Channel 3.3, a young male, shifted its range to a completely new location after the 1976 fire. Shortly after the fire this animal was lost (see Fig. 37) and it was not re-located until September, three months later, when it was located some 2000 m to the east. It was found to be nesting and feeding in this new area away from the burn and on the other side of the 1976 burn removal area. It was one of only three complete breaks with an established home range area recorded during the entire study.

The control animals with ranges largely outside the burn, such as radio transmitter animals Channels 4.35, 6.3 and 12.25, made no shifts in their home range areas during the period of study (see Figs. 29 and 37). Results are summarised in Table 8.

Trapping results generally confirm the results obtained using radio telemetry. Table 8 shows that of the 25 animals recorded on the burns, 13 shifted their home ranges after the fire. On the edge only 3 out of the 37 animals recorded shifted and there were no movements in the unburnt control blocks.

Of the 13 that moved from the burn area, 10 were successful, whereas only 1 of the 3 moves on the edge was successful. Of the animals which made no moves only 4 out of 12 were successful on the burn, whereas 24 out of 34 and 12 out of 16 were successful on the edge and in the control blocks respectively. Most of these moves were only to the edge of the burn, and the animals still fed in the burn at night.

Shifts in home ranges after fire were therefore most successful but a good proportion of the animals that remained also survived.

There were no significant differences between pre- and post-burn home range sizes calculated using either radio points or trapping data (see Table 7). Some error may have been introduced by the different numbers of radio points for each animal, but in most cases many points were available and the error is considered minimal. Areas of male post-burn home ranges calculated from trapping data appeared to be larger than pre-burn areas, but the difference was not significant as individual variation was very high.

There is some indication from well documented individual cases that the home range area may be increased after burning (Fig. 38). This increase in range appears to take place over the summer after the burn.

**Movements—the 1976 burn**

Post-fire radio tracking results (see Fig. 37) show that woylies in the 1976 burn took no advantage of the adjacent unburnt area from which resident woylies had been previously removed. Behaviour was essentially the same as that of woylies fitted with transmitters on the 1975 burn, where no removal had taken place in areas adjacent to the burn. Only two animals, radio transmitter Channels 1.12 and 9.375, moved into the empty area. The latter's nest area was already largely within the empty area before the burn. One animal, radio transmitter Channel 3.3, already mentioned, moved right through the area to occupy a new home range 500 m to the east of the empty area.

The behaviour of transmitter animal Channel 1.12, however, was interesting. The position of groups of

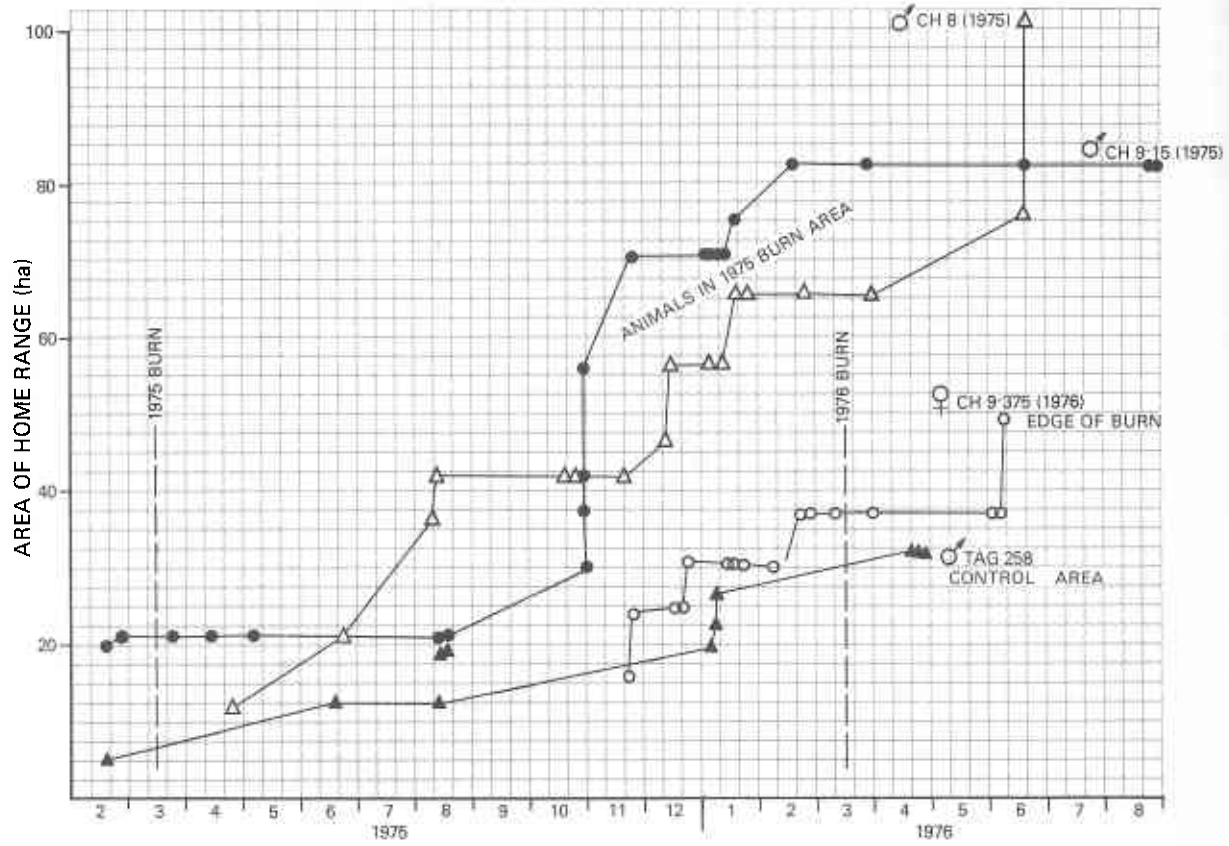



**Figure 38**

The woylie—home range areas calculated for successive captures.

locations (nests) gradually shifted further eastwards into the empty area through time [see Fig. 37 (*a*)]. This behaviour typifies the general pattern of movement observed after the burn, viz. there was no immediate exodus from the burn but rather a gradual change brought about by "probing" moves into new and unfamiliar areas.

## FIRE EFFECTS—THE TAMMAR

### Population analysis

*Population structure*

Despite considerable trap interference by brush-tailed possums (*Trichosurus vulpecula*) and a bird, the squeaker (*Strepera versicolor*), large numbers of which were trapped after the fire, the capture rate of tammars increased dramatically (see Fig. 30). The highest capture rate recorded during the study (42 per cent) was recorded immediately after the 1975 fire. A general weight loss at this time (see Weights, below) although not significant, suggests that the high capture percentage might have been the result of shortages of food in the new burn.

Capture numbers decreased after this, and after June they were consistently and significantly lower than before the fire and lower than those on the control. There was an increase in captures on the burn during the April 1976 session and this was attributed to the animals' attraction to the new green grass on the burn after autumn rain.

The structure of the population caught in the burnt area also changed. During the four trapping sessions between October 1975 and December 1976, nineteen adults and no non-adults were captured on the burn (difference significant at 0.01 level). During the same period twenty-one adults and seven non-adults were captured on the control area (difference N.S.). Eleven of nineteen animals on the burn were tagged animals coming in from the unburnt surrounds, three having previously lived in the burnt area. The remaining eight were all new untagged adults.

Unlike the woylie, there was no increase after the fire in the number of tammars trapped only once (Table 19). This suggests that there was no increase in mortality on the burn area after the fire. This is because there had been no re-colonisation by young tammars on the burn. The animals caught there were adult animals from the surrounding unburnt areas.

*Survival*

Survival of female compared with male, and non-adult compared with adult tammars appeared to be considerably lower on the burn area than on the edge and control areas (see Table 10). The differences were, however, not significant.

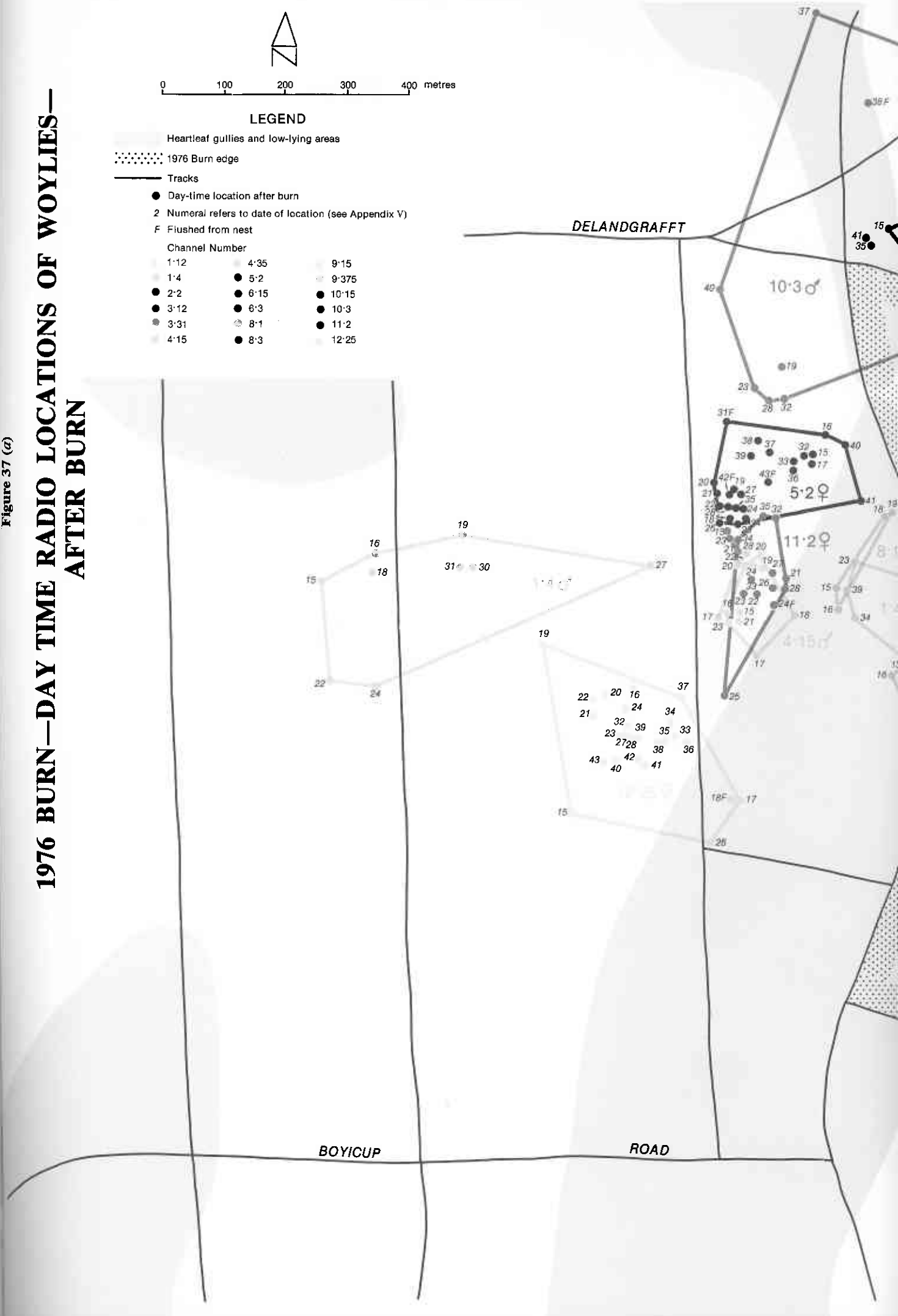
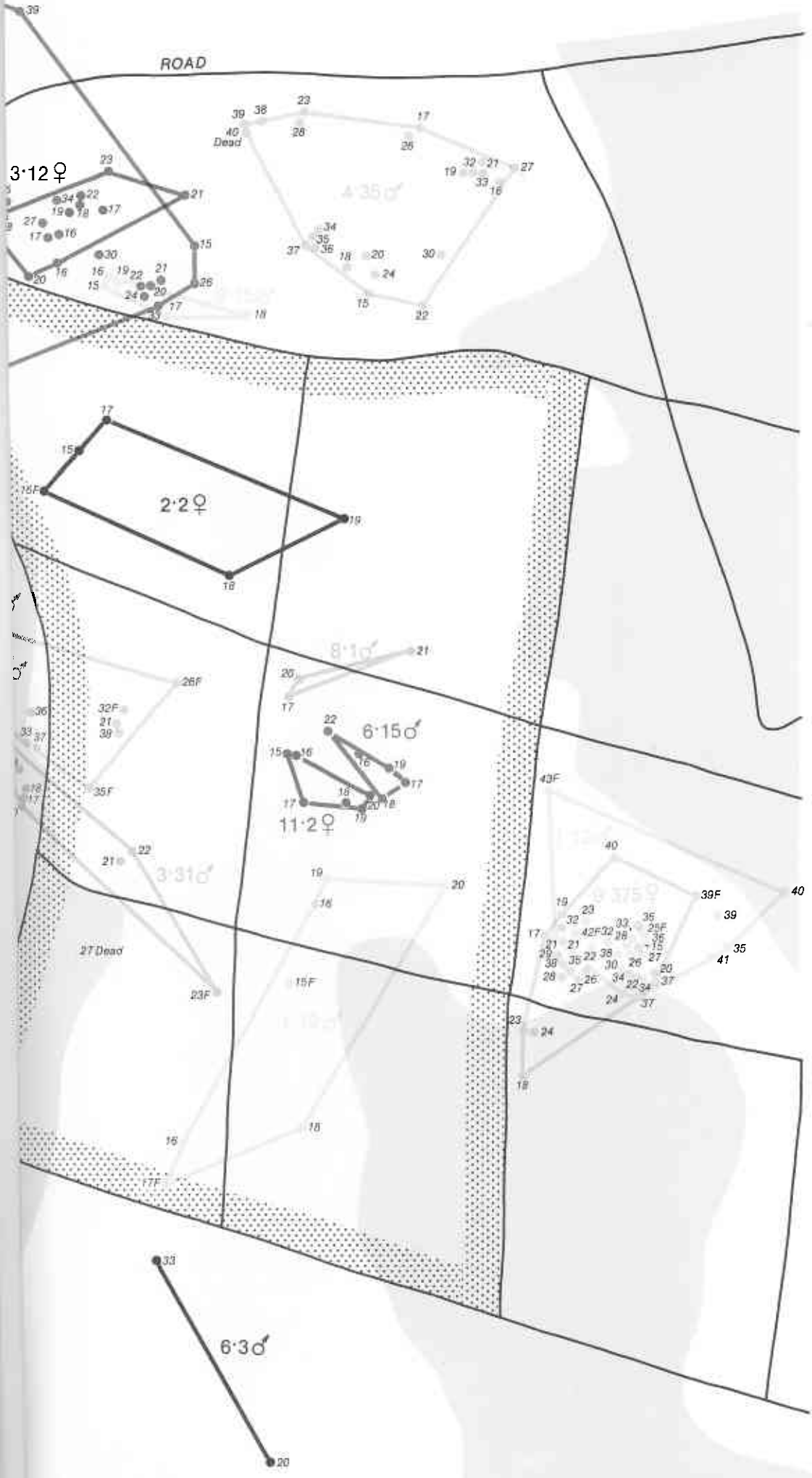

1976 BURN—DAY TIME RADIO LOCATIONS OF WOYLIES—AFTER BURN
0 100 200 300 400 metres
LEGEND
Heartleaf gullies and low-lying areas
1976 Burn edge
Tracks
Day-time location after burn
2 Numeral refers to date of location (see Appendix V)
F Flushed from nest
Channel Number
1·12
1·4
2·2
3·12
3·31
4·15
4·35
5·2
6·15
6·3
8·1
8·3
9·15
9·375
10·15
10·3
11·2
12·25
DELANDGRAFFT
BOYICUP
ROAD
10·3♂
5·2♀
11·2♀

Figure 37 (a)


ROAD
3·12♀
2·2♀
8·1♂
6·15♂
11·2♀
3·31♂
4·35♂
6·3♂
27 Dead
40 Dead

# 1976 BURN—NIGHT

Figure 37 (*b*)

# TIME RADIO LOCATIONS OF WOYLIES—AFTER BURN

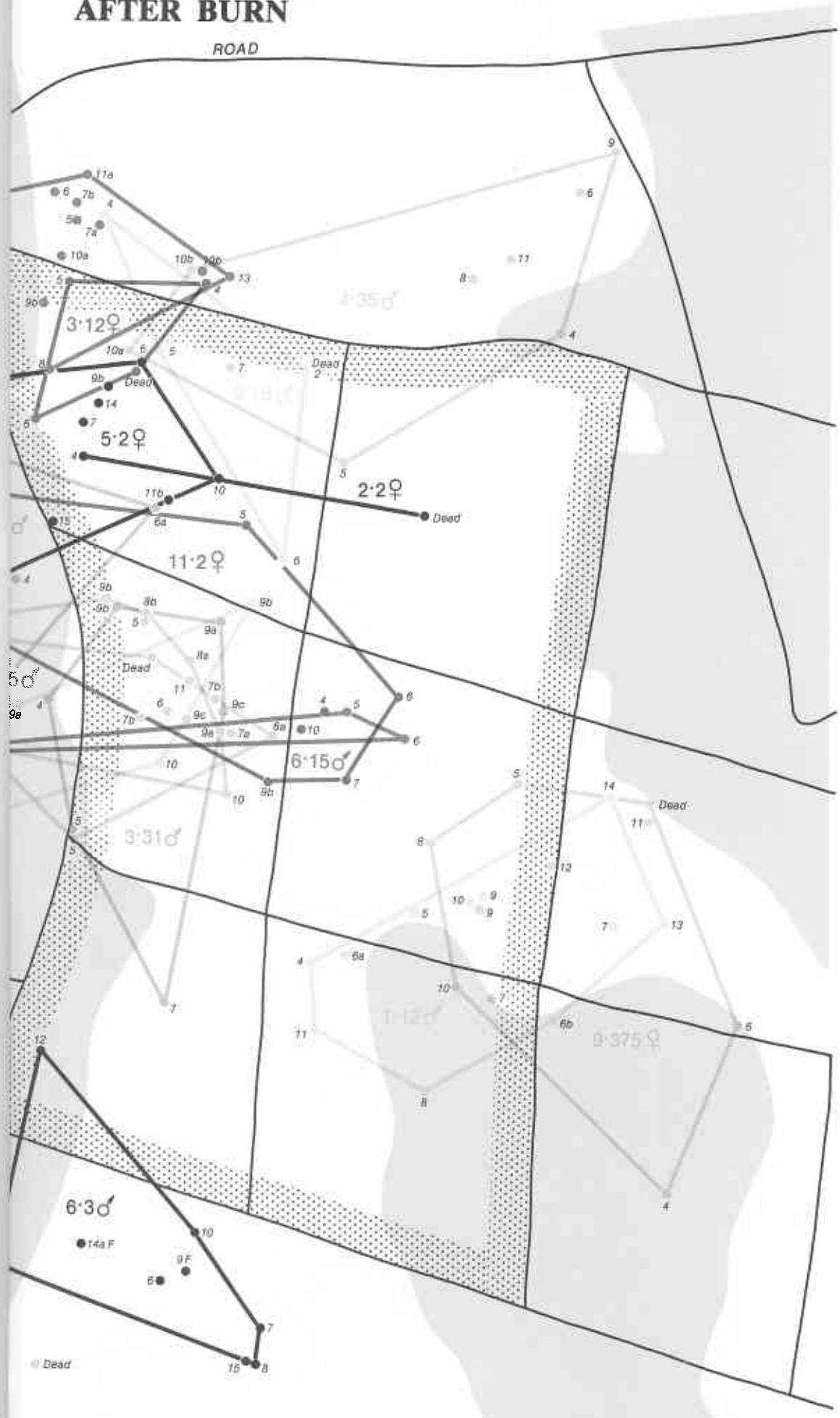


**Table 19**

THE TAMMAR—PERCENTAGE OF ANIMALS PER CAPTURE CLASS DURING TWO PERIODS OF SIX TRAPPING SESSIONS EACH

| *Trap period* | *CONTROL* *Percentage of animals per capture class* | | | | *BURN* *Percentage of animals per capture class* | | | |
|---|---|---|---|---|---|---|---|---|
| | *1 capture* | *2 captures* | *3 captures* | *More than 3 captures* | *1 capture* | *2 captures* | *3 captures* | *More than 3 captures* |
| *Pre-burn* May 1974 to March 1975 | 100·0 (3) | — | — | — | 68·4 (39) | 17·5 (10) | 12·3 (7) | 1·8 (1) |
| *Post-burn* April 1975 to December 1976 | 61·3 (19) | 9·7 (3) | 19·4 (6) | 9·6 (3) | 69·4 (43) | 17·7 (11) | 6·5 (4) | 6·4 (4) |

Figures in parentheses are actual numbers of animals.

Changes in numbers of non-adults, expressed as a percentage of the total female population, were also inconclusive owing to the low number of captures.

*Reproduction*

No effects due to fire were observed.

*Weights*

Sufficient data for analysis were available only for male tammars. Weights of animals caught on the burn during the first three months following the fire, March, April and May, were lower than those of control animals (see Fig. 32). The differences were not significant. During June and August the weights of tammars caught on the burn were significantly higher (0.05 level) than those on the control. This may be a reflection of the abundant feed available on the new grassy areas of the burn.

**Movements**

(1) All four tammars fitted with radio transmitters behaved in a similar manner following the burn (see Fig. 33). For the first few days they stayed on the burn using small unburnt patches of heartleaf thicket for cover. Later, two animals shifted to an unburnt patch on the edge of the thickets, where they remained for some days. During this period, one animal, radio transmitter Channel 5, died in a funnel trap as a result of self-inflicted injury. Its collar was then attached to another animal known to live in the same area.

A tammar with radio transmitter Channel 3 disappeared, presumed the victim of a predator. The remaining three animals moved to neighbouring thickets. One large male, radio transmitter Channel 7, appeared to settle in well, seemingly mixing with the resident tammars in the new area. This may be because it was an animal which roamed between adjacent groups and was thus already familiar with tammars in the new area. The remaining two animals, radio transmitter Channels 5 and 6, appeared not to settle in with the residents in the new area. Captures were in traps along the fringes of heartleaf thickets in sub-optimum habitat.

Hand-monitoring and records using the Rustrak recorder indicated that animals with transmitters returned to feed on the burn at night (Appendix IV). The remains of the tammar with radio transmitter Channel 5, almost certainly killed and eaten by a fox, were discovered in September. They were found at a point between the new daytime refuge and the feeding area on the burn.

(2) Table 12 shows that all eleven animals that remained on the burn disappeared, presumed the victims of predators. Ten of the sixteen animals that moved from the burn survived. Numbers on the edge and control areas are too low for valid comparisons, but they nevertheless show that at least three animals that stayed were successful.

## MORTALITY FACTORS

**The woylie**

During the course of the study some information on the cause of mortality in both species was obtained (Table 20). The main predator in the study area appeared to be the European fox. Surprisingly, for it is not a large animal, the native cat is also a major predator of the woylie. Apart from deaths directly attributed to this animal, two woylies were savaged, their tails ripped by native cats attempting to get at them inside cage traps. Tracks indicated that the culprits were native cats. One woylie was also taken from a funnel trap by this animal, and another was killed by a wedge-tailed eagle (*Aquila audax*).

Fire "shock" deaths appeared to be caused by some form of psychological shock brought on by the effects of the fire. After fire, some animals appeared dazed and in a state of shock and allowed close human approach before they hopped away slowly. They may also have been affected by smoke, but some never recovered; they appeared to lose the will to live and made little attempt to survive. A number

**Table 20**
MORTALITIES RECORDED DURING THE STUDY
**(a) The woylie**

| | *Probable cause of death* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *European fox* | *Native cat* | *Wedgetailed eagle* | *Fire "shock"* | *Starvation* | *Fire* | *Paralysis* | *Others* |
| Animals with transmitters | 9 | 4 | — | 2 | — | 1 | — | — |
| Recorded on recent burn | 4 | 2 | — | — | — | — | 1 | — |
| Recorded elsewhere | 2 | 1 | — | — | — | — | 1 | — |
| Trap deaths | — | — | 1 | — | — | — | — | 5 |
| TOTALS | 15 | 7 | 1 | 2 | — | 1 | 2 | 5 |

**(b) The tammar**

| | *Probable cause of death* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *European fox* | *Native cat* | *Wedgetailed eagle* | *Fire "shock"* | *Starvation* | *Fire* | *Paralysis* | *Others* |
| Animals with transmitters | 1 | — | — | — | — | — | — | — |
| Recorded on recent burn | 2 | — | — | — | 1 | — | — | — |
| Recorded elsewhere | 4 | — | 5 | — | — | — | — | — |
| Trap deaths | — | — | — | — | — | — | 24 | 4 |
| TOTALS | 7 | — | 5 | — | 1 | — | 24 | 4 |

of such animals were found dead with no marks on them. A proportion of the deaths attributed to the fox and the native cat after fire were undoubtedly shocked animals which would fall easy prey to these predators.

### The tammar

The European fox again appeared to be the main predator in the study area. The deaths attributed to the wedge-tailed eagle are known from skulls collected from underneath a nest in Dryandra forest. Most studies on eagles suggest a large scavenging component, so their role as a predator is difficult to determine precisely. One very thin emaciated animal was found dying, apparently from starvation, shortly after the 1976 burn.

The largest single cause of death during the study was owing to trap mortality, usually attributable to shock. When caught in the funnel traps, animals would normally leap about wildly on human approach.

On occasions an animal would collapse, paralysed in the hind- or the fore-quarters, pupils dilated as in shock. There were no cases of recovery from this "shock syndrome" and injections with corticosteroids were of no avail. A post mortem carried out on two animals by the Veterinary Pathologist, Department of Agriculture, Perth, revealed nothing specific which could be related to the animals' condition.

The condition might be a form of the so-called "over-straining disease" (Harthoorn and Van Der Walt, 1974) or "fear shock" (Guthrie *et al.*, 1967).

Recent research (Oliver *et al.*, 1977) indicates that many species of animals in the south-west have a very high resistance to the poison sodium fluoroacetate, a compound occurring in certain species of native legume. Heartleaf has a high sodium fluoroacetate content, and it is possible that the animals eat the seeds or vegetative parts. Animals with high poison loadings subjected to excessive strain could suffer some form of breakdown leading to the symptoms observed.

## DISCUSSION

### The woylie

The pre-fire population is composed largely of adults, seemingly with a higher proportion of males than females. Mortality in the juvenile stage is very high indeed; only 11·4 to 15·4 per cent may be expected to survive to the non-adult stage. No evidence was found for widespread dispersive movements; areas are vacated through death of the resident and appear

to be filled by young animals from within the population or from the immediate vicinity. This was particularly evident in the pattern of recolonisation observed when trapped animals were removed from the 1976 burn site.

Both sexes occupy stable home ranges. These ranges overlap in part but include well defined nesting areas where no overlap occurs. These are likely to be defended areas. There are few or no losses during fire, but after fire there is a drop in the capture rate. This is owing largely to the loss of non-adult animals within the area. This loss appears to be a result of increased predation, and on the whole adult animals fare better than non-adults. Capture numbers soon increase, the population being replenished by non-adults from the immediate surrounds and from the burn itself.

The composition of the population changes; there are significantly more males in the post-burn population, and most of them are non-adults. Survival rate of juveniles increased on the burn and immediate surrounds so that 23 per cent ($n$ = 20) in 1975 and 38·6 per cent ($n$ = 25) in 1976 reached the non-adult stage (see Table 16).

Thus the burnt areas appear to be re-populated mainly by surplus non-adult animals, a high proportion of which are males. During the first twelve to eighteen months these suffer a high rate of mortality. This mortality may be expected to decrease as the vegetation on the burn returns to pre-fire density. The importance of cover density in relation to predation is discussed in a later section (see Section V, Testing the Hypothesis). Recovery of the understorey may be expected to take three to five years in dry sclerophyll forest (Christensen and Kimber, 1975).

Results from the 1976 removal experiment support the idea of a very high home range fidelity. It seems that fidelity to home range, rather than the existence of neighbouring animals or any agonistic behaviour from such animals, is the reason for the reluctance to move from burnt-out home range areas.

Any moves are, typically, made very slowly with a gradual extension of home range areas by limited exploration.

The increase in weight of animals on the burn may indicate an increased food availability. Certainly, there was a short-lived increase in digging activity immediately after the burn, which may indicate that fungi were easier to find. However, since a similar weight increase was observed amongst re-colonisers on the 1976 removal area, the increase in food availability is attributed to a lower density of animals rather than to any beneficial effects of the fire. This suggests that there may be considerable competition for food resources in the pre-fire environment. This is speculative, however, since the weight increase could also be the result of an increase in food density: the animals' diet may comprise a higher proportion of dry fungi.

**The tammar**

The tammar in the study area appears to be group territorial, groups being centred on different areas of heartleaf thickets. The size and composition of groups is unknown, since only a few individuals were radio-tracked. A certain proportion of the population, largely adult males, appears to move freely between two or perhaps more adjacent groups, occupying different thickets. Disparity in numbers between the sexes appears to reflect a higher male capture rate rather than any real differences. Juvenile mortality and/or emigration rate is low compared with that of the woylie. Over a three-year period thirty-four late juveniles and non-adults were recorded in a total population of fifty-one adult females. This represents a survival rate of 66·7 per cent compared with the 11·4 to 15 per cent of the woylie.

Like the woylie, the tammar remains within its home range area, sheltering in unburnt patches during the fire. In contrast to the woylie, there was a sharp increase in captures immediately after the burn. A loss of weight at this time suggests that they may be easier to trap because of food shortages.

The population then declines; some individuals are victims of predators while others move to new areas. A few individuals appear to settle in with other colonies, others occupy what seems to be sub-optimum habitat on the fringes of other colonies. Many of the animals that move return to feed on the burn at night; a number of these ex-residents were still being caught on the burn at the end of 1976. During the first winter after the burn, when tammars on the control area were at their lowest weights, those caught on the burn were significantly heavier. This may indicate an improvement in feed after burning.

No re-colonisation had occurred at the conclusion of the study, probably because the heartleaf seedlings had not yet formed suitable cover. At the end of the study animals caught on the burn were still adult animals from neighbouring colonies.

# Food Studies

## INTRODUCTION

Detailed work on food seemed beyond the scope of this study in the time available. Sampson (1971) was unable to recognise anything substantial in the gut contents of woylies obtained from the Western Australian Museum. From the results of some cursory scat analyses he postulated that roots and tubers formed a substantial portion of their diet.

Examination of the gut contents of a road casualty indicated that a food study might be feasible, and that it might be of considerable interest. No green matter was recognisable in the gut; the contents appeared to be an unrecognisable amorphous mass as reported by Sampson (1971). However, detailed microscopic examination revealed vast numbers of fungus spores. Six distinct spore types were recognised, and much of the "amorphous mass" appeared to be fungal in origin.

On the strength of this observation soil in the vicinity of diggings, presumed to have been made by woylies, was carefully sifted and some small white hypogean fungi discovered. Further sifting of soil in the area yielded a collection of twenty-six specimens. The spores of some of these matched those found amongst the gut contents of the woylie road casualty.

The collection was examined by R. Hilton (Botany Department, University of Western Australia) and was found to comprise four species of gasteromycetes and one specimen of a species of *Tuberales*. One of the gasteromycetes was a species of *Mesophellia* (Plate 24). Pieces of the outer peridium of specimens of this genus have since been found frequently in association with fresh diggings in burnt areas (Plate 25).

**Plate 24**

Sporocarps of *Mesophellia* sp. The transverse section shows:
(*a*) Outer peridium
(*b*) Spore-bearing layer (hymenium)
(*c*) Central edible sterile columella

**Plate 25**

Digging on recently burnt ground. Pieces of outer peridium can be seen discarded on the freshly dug soil.

A more extensive collection of hypogean fungi is currently being examined by Dr. J. M. Trappe (U.S. Department of Agriculture). It seems that a wide range of species is involved, many of which are as yet undescribed.

Although small mammal mycophagy is well known (Fogel, 1976; Trappe and Maser, 1976), there are few records amongst the larger mammals. One study of the potoroo (*Potorous tridactylus*), an animal similar to the woylie in many ways, indicated that its diet contained a high proportion of fungi (Guiler, 1971). Guiler considered that the potoroo's diet of hypogean fungi was a major factor in enabling the animal to survive when most other species perished after bush fires at Mount Nelson in Tasmania in 1967.

Cleland (1934) records husks of *Mesophellia* species near scratchings made by animals in burnt country near Kuitpo, South Australia, and suggests that these and other species are associated with bush fires.

In view of this it seemed likely that:

(1) hypogean fungi might form a substantial part of the woylies' diet;

(2) fire might be implicated in the germination and growth of these fungi.

Fungus spores passed through the gut of the woylie unharmed, losing none of their identifiable characteristics (Plate 26), so that it was comparatively simple to obtain data on this diet by means of scat analysis.

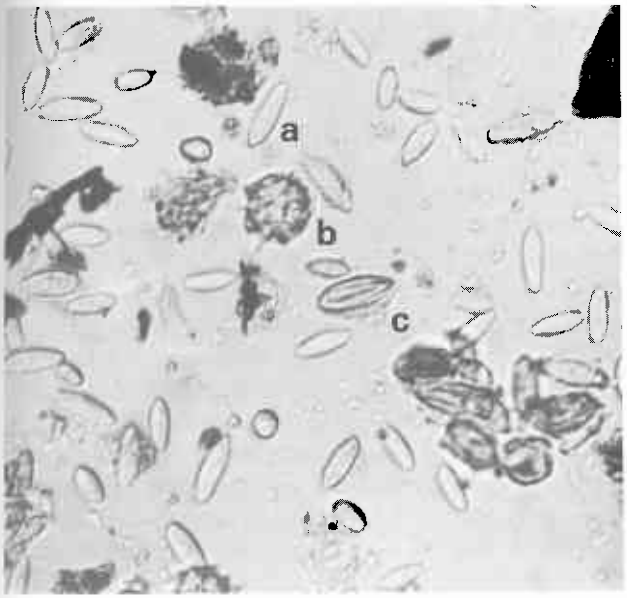



**Plate 26**

Spores in prepared scat sample as seen under light microscope 600 magnification.

(*a*) *Mesophellia* sp.
(*b*) *Martellia* sp.
(*c*) *Australasia chlorospora*

These data may be correlated with digging activity on burnt and unburnt areas.

The short-nosed bandicoot (*Isoodon obesulus*) is a potential competitor for this food source, so scats of this species were collected for analysis wherever possible. A study of tammar diet was also included, although in far less detail than for the woylie.

## SCAT AND STOMACH CONTENT ANALYSIS—THE WOYLIE

### Method

Scat samples were collected from traps during normal routine trapping in Boyicup; a total of 163 samples, representing ten months of the year, were collected. For analysis these were divided into those from burnt areas, the edge of burn and unburnt control areas for each of the ten months available. From these subdivisions, three samples were selected at random, where available, for processing. A total of sixty-seven samples was used. Samples from Tutanning (Coll. J. Sampson) were obtained from the Zoology Department, University of Western Australia, and eleven of these, representing six months of the year, were used for comparison with samples from the Boyicup woylies. Nine short-nosed bandicoot scat samples representing six months were also collected from Boyicup.

Scat samples were prepared for examination under the light microscope as follows: 0·3 g of oven-dried scat was thoroughly macerated in 10 ml of distilled water with 0·5 ml of formalin. A pipette was used to place a drop of the mixture on to a Hawksley haemocytometer. Twenty fields, 1 mm apart, on two transects across the slide, were examined. Each field represented twenty-five squares of a gridded optical eye piece under 15 × 40 magnification. This is equivalent to 0·00156 $m^3$ of solution per field.

The following categories were recognised in the sampling:

(1) Spore types—spores were classified into types according to morphological characteristics (Appendix VI). A reference collection of line drawings and photographs was kept to aid identification (Plates 27, 28 and 29). The total number of spores of each type per field was recorded.

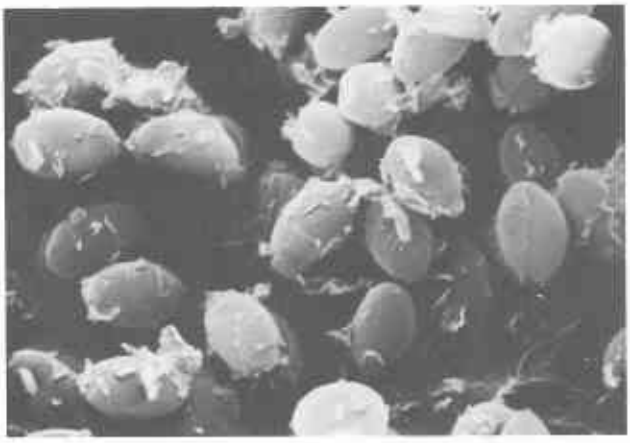


**Plate 27**

Spores of *Mesophellia* sp. (Electron micrograph, 2 500 magnification). (Photograph Nick Malajczuk)

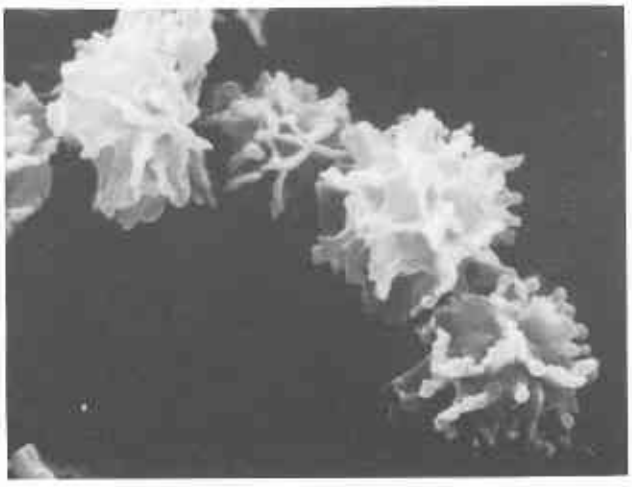


**Plate 28**

Spores of *Martellia* sp. nov. (Electron micrograph, 2 500 magnification). (Photograph Nick Malajczuk)

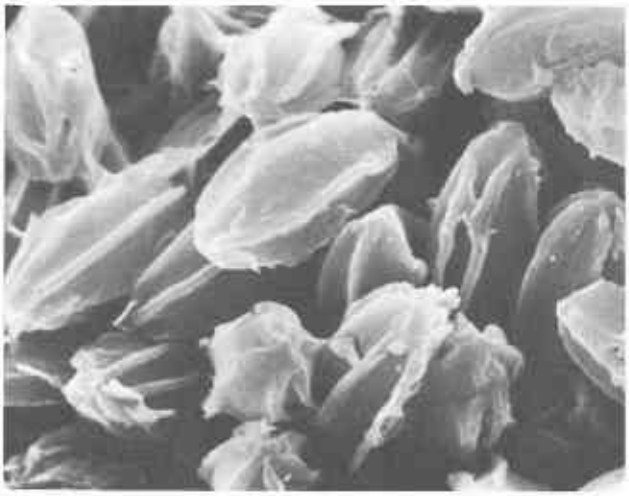


**Plate 29**

Spores of *Australasia chlorospora* (Electron micrograph, 5000 magnification). (Photograph Nick Malajczuk)

(2) Fungal matter—hyphal tissues and sterile columella

(3) Cellular matter—cellular plant tissues, non wheat

(4) Wheat—wheat grain tissue

(5) Sand grain

Categories (2) to (5) were recorded in terms of the total number of squares occupied by each per field. The separation of wheat grain tissue was found necessary because the grain used for baiting traps frequently occurred in scats collected from the traps. Sand grains, although recorded, were ignored in the analysis because faeces were generally contaminated by having been in contact with the ground.

Sampling errors per slide, at 95 per cent confidence limit expressed as percentage variation of the mean, were: 18·24 per cent (range 11·4 to 28) for fungus spores (based on the most frequent type, *Mesophellia* species); and 51·7 per cent (range 31·1 to 106) for fungal and cellular matter. It would have been possible, but very time-consuming, to reduce the error on the fungal and vegetative matter by taking a much larger sample. This was not warranted because of the comparative rarity of cellular material in the diet (Table 21).

The stomachs of eleven individuals that died during the study were available for analysis. The results were used to confirm scat analysis data. The method employed was to take a sample, wash it through cheesecloth under a running tap until clean, float it in a petri dish of water and examine it under the microscope at 12 × 4 or 12 × 8 magnification. Twenty fields were examined in each of two separate samples using

**Table 21**

STOMACH CONTENT ANALYSIS—THE WOYLIE

| *History of animal* | *Non-spore material (per cent of total)* | | | | | *Fungus sport types* | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Fungal* | *Cellular* | *Wheat* | *Insect* | *Meso-phellia* | *4* | *1* | *16* | *15* | *40* | *45* | *28* | *14* | *44* | *33* | *12* | *41* | *32* |
| Killed by eagle in trap. B2/6. 11 Feb. '75 | 60 | 1·9 | 37·3 | 0·7 | 2 | | | | | | | | | | | | | |
| W284 died heat exhaustion. G4/14. 5 Mar. '75 | 5 | — | 95 | — | 1 | | | | | | | | | | | | | |
| W51 killed by tammar in trap. G/6.5. 6 Mar. '75 | 37 | 2·4 | 55·7 | 4·8 | 5 | 2 | | | | | | | | | | | | |
| Ch 9.15 died after fire. 9 Apr. '76 | 89 | — | 11 | — | 4 | 3 | | | | | | | | | | | | |
| W123 killed by tammar in trap. 18 June '75 | 70 | — | 19·1 | 10·8 | 4 | 3 | | | | | | | | | | | | |
| W327 paralysis sample. B2/4. 19 June '75 | 75·5 | — | 24·5 | — | 4 | 2 | | | | | | | | | | | 4 | 1 |
| W133 died paralysis. 18 June '75 | 5 | — | 95 | — | 2 | 1 | | | | | | | | | | | | |
| Killed by native cat in trap. G/22. 1 July '74 | 60 | — | 40 | — | 5 | | 3 | | 1 | | | | | | 1 | 2 | | |
| Road casualty, Landgraft Rd. 13 Sept. '74 | 99·2 | 0·4 | 0·4 | — | 4 | 1 | 1 | | 2 | | | | 3 | 1 | | | | |
| W6026 ex Tutanning coll. J. Sampson | 98·8 | 1·2 | — | — | — | | | 4 | 1 | 1 | 1 | | | | | | | |
| Ch 8.3 asphyxiated during fire. 19 Mar. '76 | 96·7 | 3·3 | — | — | 5 | 1 | | | | | | | | | | | | |

Fungal spores are estimated on a five-point scale (see Scat and stomach content analysis—the woylie, method).

the optical grid: relative amounts of fungal and cellular matter, wheat and insect cuticular remains were recorded. Spore types were recorded from two smears of stomach content on microscope slides. Spore type frequency was estimated on a five-point scale (Havel, 1975*a*) since the samples were non-quantitative.

**Results**

The Boyicup woylies' diet appeared to be composed largely of fungi throughout the year (Fig. 39). Dependence on fungi was most marked over the dry summer-autumn period, with a drop in fungal matter and a corresponding, though marginal, increase in cellular material over the wet winter-spring period: the incidence of starch grains showed a definite increase during this period (Fig. 40). Some of the starch grain appeared to be from wheat. However, since the graph shows little correlation with the occurrence of wheat tissue, it seems certain that a substantial portion must originate from some other source, perhaps seeds or tubers.

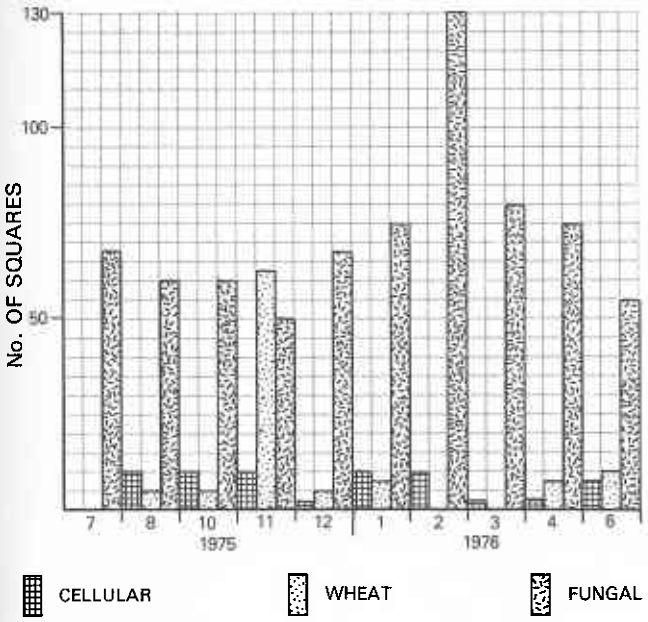



**Figure 39**
Boyicup—seasonal variation in the quantity of cellular, wheat and fungal matter from woylie scats.

The Tutanning woylie and the Boyicup bandicoot both have a much higher cellular component in their diet than the Boyicup woylie (Figs. 41 and 42): there is a more pronounced increase in the proportion of cellular matter over the spring in the case of the Tutanning woylie and Boyicup bandicoot.

Results of stomach content analysis (see Table 21) support the scat sampling results. With the exception of those stomachs contaminated with wheat, the major item in all stomachs was fungal matter. The lack of cellular material in the one stomach from Tutanning was interesting. Unfortunately it was undated and little is known about it.

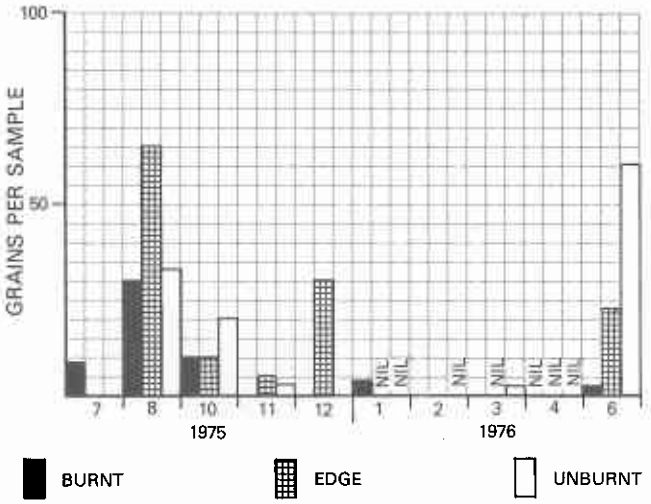



**Figure 40**
Boyicup—seasonal variation in the number of starch grains in samples from woylie scats.

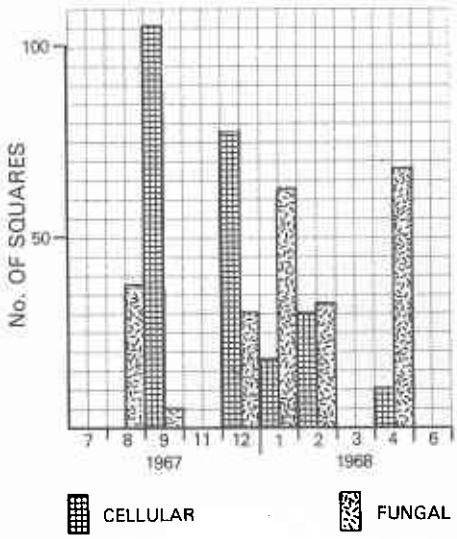



**Figure 41**
Tutanning—seasonal variation in the quantity of cellular and fungal matter in samples from woylie scats.

There was a seasonal variation in the number of spore types (species?) recorded in scat samples (Fig. 43).

The number of spore types reached a peak during spring with a smaller peak in autumn. Least variety existed over the summer. If spore types are graphed individually it can be seen that this is because most spore types appear in spring and autumn [for example *Australasia chlorospora* (Fig. 44)] or more rarely in spring alone [for example, spore type 15 (Fig. 45)]. A bimodal fruiting pattern is common in fungi where sporocarp production is controlled by environmental factors (Fogel, 1976).

The outstanding exception to this pattern of occurrence is the most frequently encountered spore type *Mesophellia* (Fig. 46). This spore type occurs

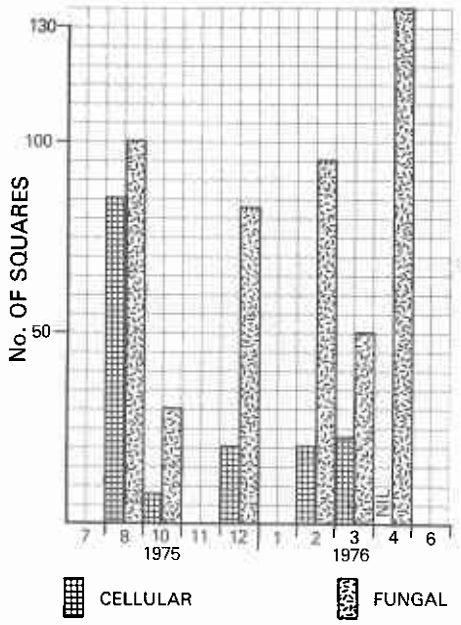



**Figure 42**

Boyicup—seasonal variation in the quantity of cellular and fungal matter in samples from bandicoot scats.

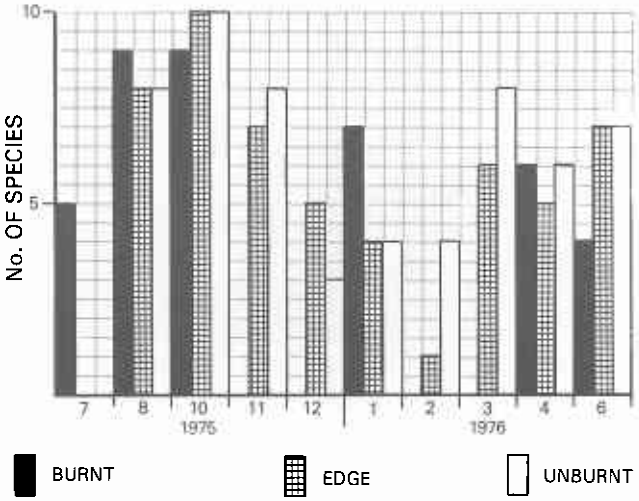



**Figure 43**

Boyicup—seasonal variation in the number of fungus species recorded in samples from woylie scats.

more frequently during the summer: it was hardly ever eaten during the winter, except in areas within and on the edge of the burn.

Some caution should be exercised when making comparisons of spore types, since spore production may differ between species. The proportion of spores swallowed by the woylie may also vary according to fungal structure.

## DIGGING ACTIVITY

### Method

The woylie makes characteristic small diggings when searching for fungi and other foods (see Plate 25). Some confusion may arise since other animals, notably

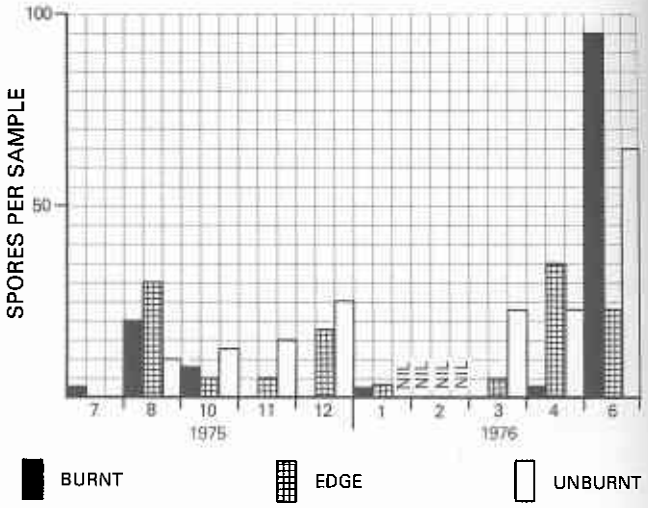



**Figure 44**

Boyicup—seasonal variation in the number of *Australasia chlorospora* type spores in samples from woylie scats.

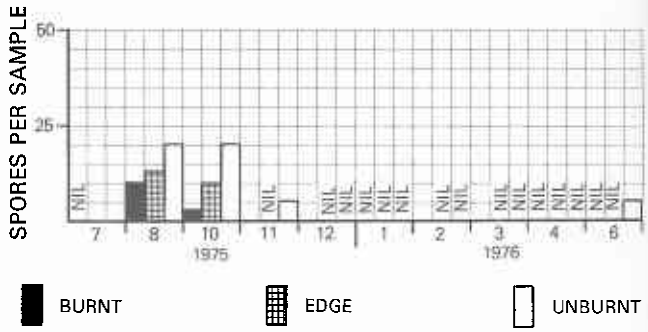



**Figure 45**

Boyicup—seasonal variation in the number of "Spore Type 15" spores in samples from woylie scats.

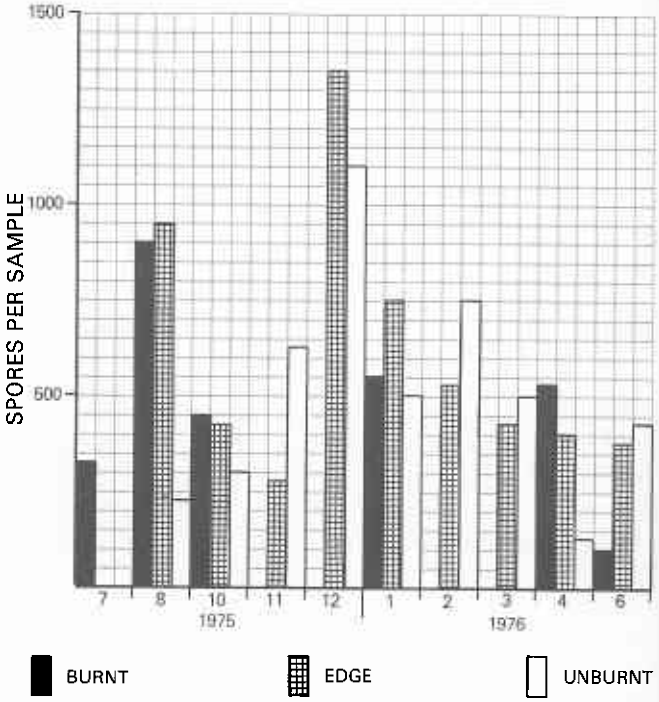



**Figure 46**

Boyicup—seasonal variation in the number of *Mesophellia* spores recorded in samples from woylie scats.

bandicoots, also dig holes. However, this species is not very common in the study area (see Table 3) and furthermore, it is often possible to recognise its diggings by the characteristic "V notch" shape and steep sides.

To record digging activity on a seasonal basis, thirty-six plots each 15 × 15 m square were established in September 1975. Three paired plots were established on each of three sites, a *B. ornata* ridge and a heartleaf gully within the 1975 burn area and a *B. ornata* ridge in the 1976 burn area. The plots were replicated in the burnt and unburnt treatments on each site. To assess any possible edge effects, the paired plots, 100 m apart, were located one pair on the edge of a treatment block, the next pair 150 m from the edge, and the third pair 300 m from the edge.

Diggings were recorded on a monthly basis and each one was filled in as it was recorded.

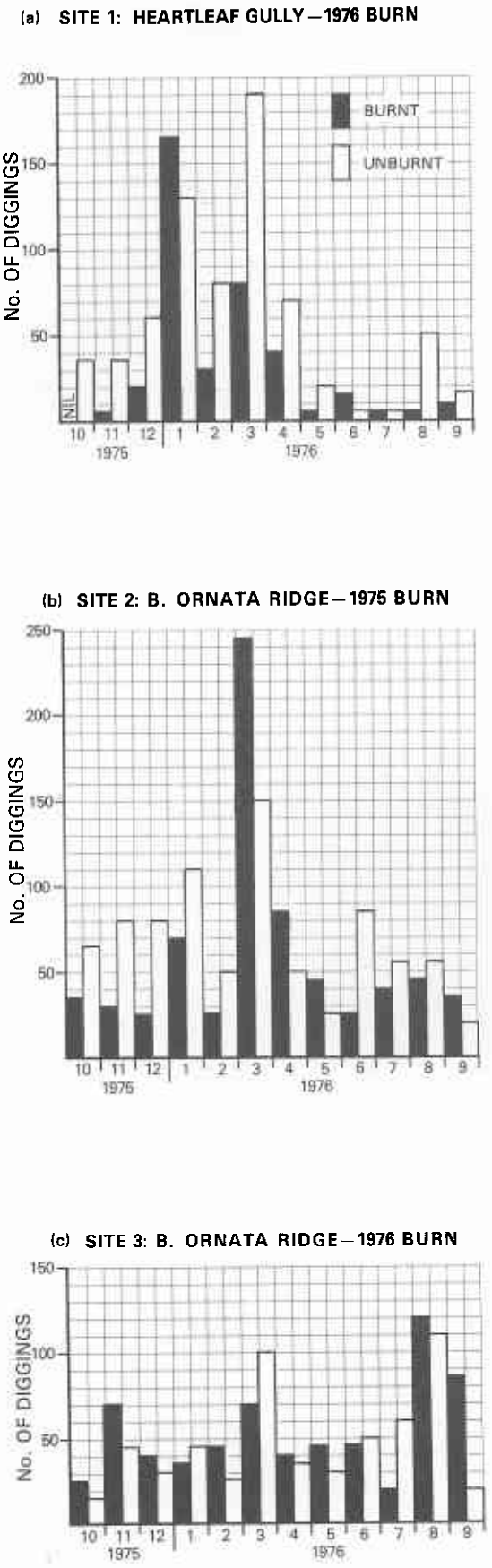
## Results

Over a period of twelve months a total of 1944 and 1761 diggings were recorded on the unburnt and the burnt plots respectively. This represents some 4574 diggings per hectare per year. The seasonal consistency of fungal spores in the scats, coupled with the common occurrence of peridial remains at each digging site, suggest that it is reasonable to assume that diggings are made to acquire fungi. Assuming a mean of one sporocarp with a dry weight of 1·0 to 1·5 g (range 0·68 to 9·84) per digging this gives some 4·6 to 6·9 kg of sporocarp per hectare per year.

This compares favourably with a figure of 2·3 to 5·4 kg.ha$^{-1}$ per year obtained by more accurate methods in a Douglas fir stand in western Oregon (Fogel, 1976).

No significant differences were recorded between sites or between months of recording; there was digging activity on all sites throughout the year (Fig. 47). Significant seasonal differences (0·01 level Students *t* test) were, however, recorded on the heartleaf site, where there was more digging activity during the summer-autumn period, December to April, than during the winter-spring period, May to November [Fig. 47 (*a*)]. Significant differences were also recorded between individual unburnt plots on the same site (Figs. 48 and 49). Both of the plots with higher digging activity were on the edge of heartleaf thickets.

It was at the head of the drainage lines, often close to or on the edge of heartleaf thickets, that most of the digging took place. Diggings were recorded on 280 plots each 10 × 8 m along eight 1-km transects located through the 1975 burn three weeks after the fire. The results were stratified according to topographical position (Table 23).




MEAN NUMBER OF DIGGINGS PER MONTH IN SIX, 225 m² PLOTS IN BURNT AND UNBURNT AREAS ON THREE SITES.

**Figure 47**

Woylie digging plots.

MONTHLY DIGGING ACTIVITY ON PAIRS OF UNBURNT PLOTS FROM EACH OF RIDGE SITES 2 and 3. THE PLOTS SHOW A SIGNIFICANT DIFFERENCE IN THE NUMBER OF DIGGINGS OVER A ONE YEAR PERIOD. SIGNIFICANT AT 0·01 LEVEL.

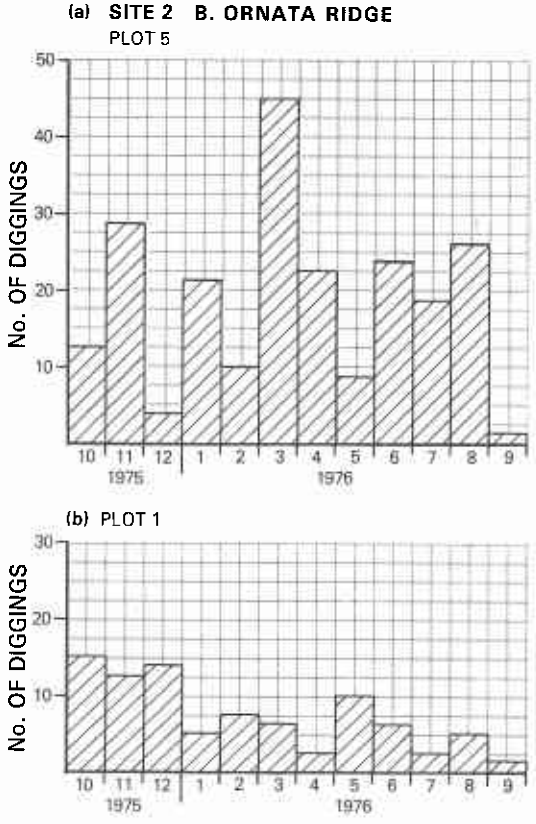



**Figure 48**
Woylie digging plots

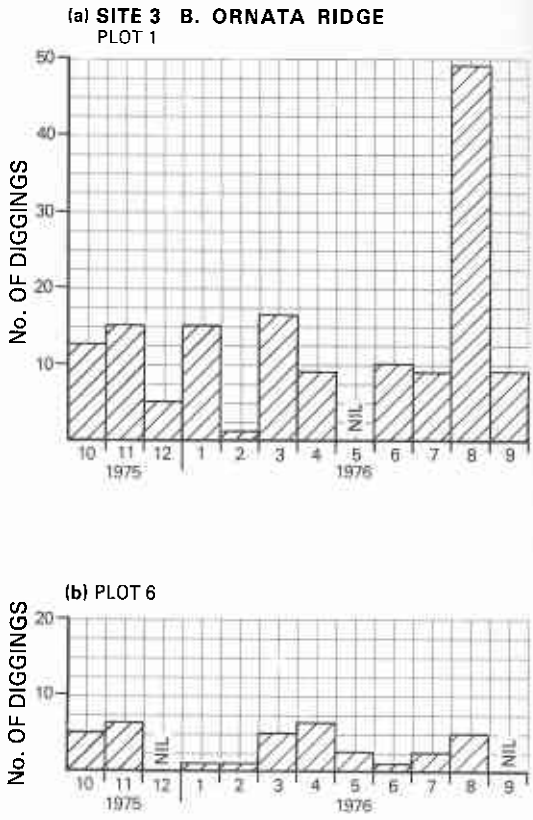



**Figure 49**
Woylie digging plots

The most intense digging activity was recorded on the sandy loams associated with the heartleaf areas. On the lower slopes on the edge of the heartleaf thickets the number of diggings recorded was significantly higher than on either of the ridge sites.

## SEED-BURYING HABITS

The woylie has a peculiar habit of burying small quantities of seed, seemingly at random, in places close to the source of origin. The habit has been commented on by a number of observers (Sampson, 1971). During this study it was first noticed after the 1975 fire when small clumps of green wheat plants appeared on the blackened soil in the vicinity of the funnel traps. Most of the clumps were within 20 to 30 m of a trap (Table 22). Approximately 40 to 50 grains were buried in any one hole.

Heartleaf seed was observed germinating in similar small clumps after the fire (Plate 30). It is not clear whether the woylies ever return to these "caches"; clumps of wheat were occasionally found uprooted, the seeds eaten. With regard to seed eating, it is of interest that the woylie has an exceptionally high tolerance to fluoroacetate, a toxin in heartleaf and other species of *Gastrolobium* (T. Oliver*, personal communication).

## STOMACH CONTENT ANALYSIS—THE TAMMAR

From a study of the tammar in three localities, viz. Garden Island, East Wallabi Island and Tutanning Reserve, Kelsall (1965) concluded that it is a very adaptive feeder. Tammars browse predominantly on

**Table 22**
DISTANCE FROM FUNNEL TRAPS TO CLUMPS OF WHEAT GERMINATED FROM SEED BURIED BY WOYLIES

| | *Distance from funnel trap (m)* | | | | | |
|---|---|---|---|---|---|---|
| | *0 to 10* | *11 to 20* | *21 to 30* | *31 to 40* | *41 to 50* | *>50* |
| Number of clumps observed | 37 | 32 | 18 | 10 | 6 | 7 |

* Agriculture Protection Board, Perth.

**Table 23**

MEAN NUMBER OF DIGGINGS PER PLOT ON DIFFERENT SITES THREE WEEKS AFTER THE 1975 BURN

| *Transect No.* | *Lower slope, edge of heartleaf* | *Valley bottom, heartleaf* | *Ridge, 4 years since burn* | *Ridge, 9 years since burn* |
|---|---|---|---|---|
| 1 | 3·4 | 1·8 | 0·43 | 0·44 |
| 2 | 3·6 | 2·8 | 0·39 | 0 |
| 3 | 0·5 | 0 | 0·43 | 0 |
| 4 | 2·0 | 0 | 2·06 | 1·25 |
| 5 | — | — | 0·74 | — |
| 6 | — | — | 1·93 | 0·08 |
| 7 | 2·0 | 2·0 | 1·80 | 0·13 |
| 8 | 2·0 | 3·75 | 1·50 | 0 |
| Mean | 2·25 (44) | 1·72 (43) | 1·16 (127) | 0·27 (63) |

Figures in parentheses are total number of 10 × 8 m plots sampled within each site type.

scrub species, particularly species of *Acacia*. They are also attracted in large numbers to grassy areas such as those which have been established on Garden Island and on farmland at Tutanning.

Contents of four tammar stomachs were examined; the technique used was similar to that used for the woylie. The Boyicup tammar's food consists almost entirely of green vegetative material: grasses and other monocotyledons are a major constituent (Table 24). The one stomach which contained monocotyledonous material came from an individual displaced by the fire, living on the fringe of an established colony.

Radio-tracking data indicated that the tammar rarely left the heartleaf areas, spending the nights feeding within or close to these thickets. The major understorey was composed almost entirely of grasses and annual herbs. Five species of grass have been identified in the area, viz. *Danthonia pilosa, Stipa semibarbata, Airia caryophylla, Bromus hordaceus* and *Vulpia bromoides*. The last three species are introduced. Observations before the fire indicated that there was very heavy grazing pressure on these grasses.

**Table 24**

TAMMAR STOMACH CONTENTS

| *History of animal* | *Percentage monocot. material (grass)* | *Percentage dicot. material* | *Comments* |
|---|---|---|---|
| Died in trap. 27 Nov. '74 | 95 | — | A little fungal matter present |
| Fox killed 21 Apr. '75 | — | 95 | No monocot. material, a little fungal matter |
| Died in trap. 10 July '75 | 50 | 50 | |
| Died in trap. 26 Nov. '75 | 90 | 10 | |

## FIRE EFFECTS ON FOOD RESOURCES

### The woylie

Division of the woylie scat data into burn, burn edge and unburnt control revealed no significant differences in the relative proportion of fungal and cellular matter. One spore type, *Mesophellia,* showed a reversal of the general seasonal trend by appearing in increased numbers in scats collected from the burn and burn edge during April 1976, directly after the burn. Similarly, during the late winter-spring months (July, August and October) in the 1975 burn, *Mesophellia* species increased in the scats (see Fig. 46).

Fire had remarkably little effect on digging activity as evidenced from the permanent plots, and there was no significant difference in the number of diggings recorded on the edge and 300 m inside the burn.

**Plate 30**

Clump of heartleaf seedlings germinated after a hot fire from seed buried by a woylie.

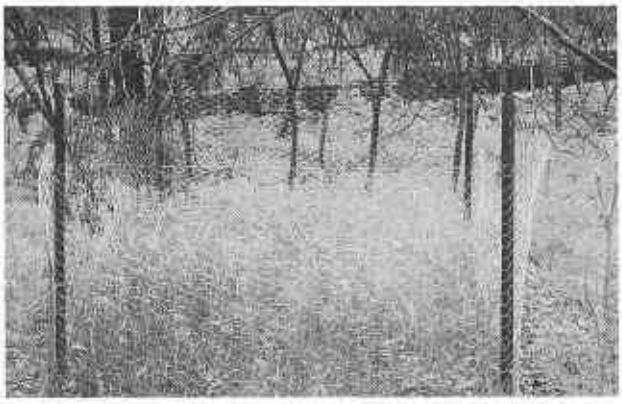


**Plate 31**

Exclusion plot in burnt heartleaf eight months after burning. Note growth of grasses within enclosure compared with that outside.

There was, however, a significant (0·01 level, Students *t* test) decrease in digging activity on the burnt heartleaf plots compared with that on the unburnt plots [see Fig. 47 (*a*)]. There was also significantly less digging (0·001 level, Students *t* test) on the burnt plots on site 2, the *B. ornata* ridge, compared with the unburnt plots during spring, October to December, after the 1975 fire [see Fig. 47 (*b*)].

A definite fire effect seems to be indicated by the fact that there were significantly (0·05 level, Students *t* test) more diggings after the 1975 burn on the ridge sites that had been burnt four years previously compared with those that had been burnt nine years previously (see Table 23).

The decrease in digging activity during spring after the fire coincided with the increase in *Mesophellia* spores in scats from burnt areas and occurred at a time when consumption of *Mesophellia* was at its lowest on the unburnt areas (see Fig. 46). There was also a marked increase in peridial remains, mainly *Mesophellia* species, associated with diggings after the fire [Table 25 (*a*) and (*b*)].

It seems that in the study area, there may be a number of species or forms of *Mesophellia,* one of which is eaten after fire. In the beginning several different *Mesophellia* spore types were recognised in the scats and these were separated as types 2, 3, 5, 7 and 13. However, the differences were small and it was difficult to distinguish with certainty between the spore types, so the distinction was abandoned.

Limited data from those samples where this distinction was attempted indicate that the *Mesophellia* spores recorded from scats from within the burn may be a shorter form than the others. The fact that peridial remains are found associated with diggings only after fire also suggests a different species or type.

The question arises, is *Mesophellia* sporocarp formation stimulated immediately following a fire? There was an increase in *Mesophellia*-type spores in scats from burnt areas after fire. In addition there was a steady increase in the numbers of diggings with *Mesophellia* peridial remains during winter and spring after the 1976 fire; this decreased again during the second year (Table 26).

On the other hand, *Mesophellia*-type sporocarps formed the vast majority of the fungus collection during May 1975 on an unburnt area. Also, the fact that peridial remains were found next to diggings so soon after fire [see Table 25 (*a*)] suggests that they were already present before the fire and that the fire merely made them more accessible to the woylie.

It may be that sporocarp production in some forms or species of *Mesophellia* is stimulated by fire. However, the problem must, to some extent, remain unresolved until more definite identification of the *Mesophellia* group is possible from scat samples.

One food source which is most certainly stimulated to higher production by fire, and which appears to be greatly relished by all the macropods in the area, is the epigean fungi.

The production of sporocarps by many species appears to be a direct result of fire, some species appearing even before substantial rains have fallen. This observation is in agreement with that of Petersen (1971), who records species of "fire-place" fungi appearing after fire in Denmark. About ten days after fire a large white mushroom appears, which is followed three to four weeks later by a species of *Amanita*. A few are nibbled by animals but they do not appear to be palatable. About a week later *Boletus* species and a species of *Rozites* start to appear. The latter appears in huge numbers and is greatly relished by the grey kangaroo in particular so that the woylie may not always get to them before they are eaten to ground level. Counts along transects gave an overall mean of eighty-one *Rozites* per hectare. On sandy loams they averaged 240 per hectare. The rate of production appears high, so that these figures would be multiplied many times over a period of weeks. By the end of June, fourteen weeks after the fire, few fungi were to be found.

**Table 25**

(*a*) NUMBER OF DIGGINGS WITH HYPOGEAN FUNGAL REMAINS—1975 BURN, SIX DAYS AFTER FIRE

| *Transect* | *Burnt* | | | *Unburnt control* | | |
|---|---|---|---|---|---|---|
| | *Mesophellia* | *Other* | *Nil* | *Mesophellia* | *Other* | *Nil* |
| 1 | 44 | 4 | 15 | 0 | 0 | 40 |
| 2 | 52 | 6 | 13 | 0 | 0 | 51 |
| 3 | 57 | 4 | 27 | 8 | 0 | 59 |
| 4 | 12 | 4 | 2 | 0 | 1 | 52 |
| 5 | 98 | 1 | 21 | 0 | 0 | 83 |
| TOTALS | 263 | 19 | 78 | 8 | 1 | 285 |

(*b*) NUMBER OF DIGGINGS WITH HYPOGEAN FUNGAL REMAINS—1976 BURN, THREE WEEKS AFTER FIRE

| *Transect* | *Burnt* | | *Unburnt control* | |
|---|---|---|---|---|
| | *Mesophellia* | *Nil* | *Mesophellia* | *Nil* |
| 1 | 28 | 41 | 2 | 5 |
| 2 | 20 | 24 | 0 | 15 |
| 3 | 4 | 7 | — | — |
| 4 | 20 | 23 | — | — |
| 5 | 15 | 10 | — | — |
| 6 | 10 | 20 | — | — |
| 7 | 13 | 30 | — | — |
| 8 | 32 | 18 | — | — |
| TOTALS | 142 | 173 | 2 | 20 |

Table 26

THE DISTRIBUTION OF *MESOPHELLIA* SPECIES PERIDIAL REMAINS ON THE DIGGING PLOTS

| | *Burnt plots* | | | *Unburnt plots* | | |
|---|---|---|---|---|---|---|
| | *Ridge plots* | | *Heartleaf gully, 18 March '75* | *Ridge plots* | | *Heartleaf gully* |
| | *18 March '75* | *18 March '75* | | *Control 1* | *Control 2* | |
| Oct. 1975 | — | — | — | — | — | — |
| Nov. 1975 | 1 | 0 | 0 | 0 | 1 | 0 |
| Dec. 1975 | 0 | 0 | 0 | 0 | 0 | 0 |
| Jan. 1976 | 0 | 0 | 0 | 0 | 0 | 0 |
| Feb. 1976 | 2 | 0 | 0 | 0 | 0 | 0 |
| Mar. 1976 | 0 | 6 | 0 | 1 | 1 | 0 |
| Apr. 1976 | 9 | 10 | 0 | 0 | 2 | 0 |
| May 1976 | 13 | 10 | 0 | 2 | 4 | 0 |
| June 1976 | 5 | 13 | 0 | 4 | 1 | 0 |
| July 1976 | 1 | 5 | 0 | 1 | 1 | 0 |
| Aug. 1976 | 0 | 79 | 0 | 0 | 0 | 0 |
| Sept. 1976 | 4 | 47 | 0 | 0 | 0 | 0 |

Figures represent the number of diggings with *Mesophellia* remains on six 15 × 15 m plots. Burns were carried out on 18 March 1975 and 18 March 1976.

**The tammar**

There is direct evidence that fire intensity can influence the grasses that are the tammars' main food source in the Boyicup area (see Table 2). In those places where fire is hot enough to cause canopy scorch, heartleaf germinates and grows prolifically and little or no grass appears. Where fire is less intense (areas with no canopy scorch), grasses proliferate and germination and development of legumes is poor.

No quantitative data on grazing were collected but a small exclusion plot set up directly after the fire clearly demonstrated the grazing pressure on the grasses (Plate 31). Some of the grazing is by kangaroos but radio-tracking and trapping data clearly indicate that many tammars feed in this area.

The delicate balance between grasses, heartleaf and fire has already been discussed (see Section II).

## DISCUSSION

**The woylie**

Clearly, more work needs to be done to identify and evaluate the proportion of cellular material in the diet, particularly in areas such as Tutanning, where it appears to form an important component. However, this may only be possible by adequate sampling of stomach contents. The faecal analysis from Boyicup suggests that cellular material does not form a major component of the diet at any time of the year. There appears to be some competition for this food resource from the bandicoot.

The food value of the hypogean fungi is difficult to assess. Values of trace element requirements for animals expressed simply as concentrations of the element in the diet may be open to challenge because of variation in availability (Egan, 1975). Nevertheless, a comparison of the concentrations of elements in the central core of *Mesophellia* species with those in selected green and senescent leaves is instructive (Appendix VII).

The brush-tailed possum (*Trichosurus vulpecula*) eats mainly leaves (Sampson, 1971). In Boyicup it concentrates almost entirely on jarrah (*Eucalyptus marginata*) and marri (*E. calophylla*) leaves (personal observation). The element concentrations in *Mesophellia* cores compare favourably with those in green jarrah leaves, being somewhat lower in potassium, calcium, magnesium and manganese, but higher in nitrogen and phosphorus. It would appear that the fungi have the necessary elements to sustain the woylie. In addition, they have a very high fat content, lipid = 41·6 per cent ($MEOH/CH_3Cl$ extraction) and 37·5 per cent (petroleum ether extraction) (J. Kinnear*, personal communication).

Hypogean fungi may depend entirely on animals to be spore vectors (Trappe, 1976). The most common sporocarp, that of *Mesophellia* species, seems well adapted for this type of dispersal; it is virtually impossible for any animal to gain access to the nutritious central core without at the same time ingesting numerous spores (see Plate 24). Most of the spores in woylie scats appear to be morphologically mature and pass through the gut apparently unharmed (see Plate 26). Trappe (1976) was able to germinate spores of a hypogean fungus (*Glomus macrocarpus*) obtained from vole (*Microtus oregoni*) faecal samples.

An interesting aspect, and one which may be important with regard to fire effects, is that many

* Zoology Department, University of Western Australia.

woylie scats are buried and eaten by scarab beetles. Three species, *Onthophagus ferox, O. rupicra* and a *Thyregis* species have all been observed burying woylie scats at approximately the depth at which the sporocarps are located in the ground. All three species, when fed woylie scats, passed the spores through the gut apparently unharmed.

A feature of *Mesophellia* species is that the sporocarp can remain stored in the soil in a dried-out state over summer. This is an unusual characteristic in a fungus and almost certainly accounts for the concentration of *Mesophellia*-type spores observed in the woylie scats during the dry summer period.

Most species of hypogean fungi are mycorrhizal (Trappe, 1962), so that sporocarp production may be expected to relate directly to the health and vigour of the plant community. Jarrah forest soils are very infertile (McArthur and Clifton, 1975) and most of the understorey plants have low nitrogen contents (Hatch, 1977). Moreover, in the absence of fires, plant communities on infertile soils may "degenerate", nutrients becoming "locked up" in woody tissues (Specht *et al.*, 1958). The role of understorey legumes in nitrogen fixation has been demonstrated (Shea and Kitt, 1976; Malajczuk and Grove, 1977) and Shea and Kitt stress the role of legumes in an environment in which nitrogen must be continually lost as a consequence of fire.

Hot fires at moderately frequent intervals promote legume germination and growth; cool fires or infrequent fires result in a reduction of legume numbers or in their disappearance (Christensen and Kimber, 1975).

The high nitrogen content of hypogean fungi, together with the fact that digging activity on sites nine years old was significantly less than on sites four years old, supports the hypothesis that fire may influence sporocarp production. The vigour of the understorey vegetation is at a peak during the first few years after a fire.

The concept of nitrogen as a limiting factor is not new; Main (1968) proposed that the carrying capacity of the land with respect to kangaroos and wallabies may be defined by the amount of nitrogen fixed in the system.

There is thus considerable evidence to suggest that fire may play an important role in hypogean fungus sporocarp production and thereby influence the woylie population.

**The tammar**

The available data suggest that the main food of the Boyicup tammar is grass. There are indications that tammars may feed more on dicotyledon plants in fringe habitats when displaced by fire from their usual home range areas. Small amounts of heartleaf seed or leaves may also be eaten at times. Like the woylie, the tammar has a very high tolerance to fluoroacetate.

There is a simple relationship between the germination and growth of grasses, and fire. However, the cover requirements of the tammar in terms of heartleaf thickets, and the effect of heavy grazing on the flammability of the habitat, complicate the situation (see Section II). The rarity of grasses in south-western ecosystems has already been mentioned (see Section II), and it is considered that the role of heartleaf in nitrogen fixation may be an essential factor in the growth of grasses on the site.

The productivity of grasses in the Boyicup area is therefore in a very delicate balance. Not only does fire directly influence the grasses, but it may have a considerable and perhaps greater indirect influence through the legume, heartleaf.

SECTION V

# General Discussion

## TESTING THE HYPOTHESES

With the exception of the section on food, this study was planned to test the three basic hypotheses stated in the introduction.

### Hypothesis 1

Both woylie and tammar populations are centred around certain site types which may be defined by distinctive plant associations. These plant associations are indicative of site characteristics, some or all of which are identifiable through the use of ordination techniques.

The first part of this hypothesis is considered proven. Both species have been shown to be associated with distinctive site-vegetation types. The second part of the hypothesis was proven only in general terms. The attempt to identify each of the principal component axes, reflecting the major factors influencing the distribution of vegetation species, with specific environmental factors proved unsuccessful. These findings are in general agreement with those of Havel (1975*a*), who found indications that vegetation responds to the sum total of environmental factors rather than to the precise levels of individual factors.

The pattern of distribution of the woylie and the tammar within the component space forms a kind of "epicentre", surrounded by areas of progressively lower-order population extending outwards in an uneven spread. Such a pattern of distribution indicates a definite preference for a specific sector in the continuum of site-vegetation types. It is further suggested that the site-vegetation complex in the respective sectors of the continuum where the woylie and the tammar occur may also reflect the optimum requirements for growth and development of the woylie and tammar food species.

Thus, well drained, fairly deep sandy soils of the type associated with woylie sites may be a requirement of the hypogean fungi which form a major part of the woylie diet. The major genus, *Mesophellia,* also occurs in sandy soils in South Australia (Cleland, 1934). Other records of hypogean fungi from scat samples of *Rattus fuscipes* and *Setonix brachyurus* are all from sandy soils (P. Christensen, unpublished data).

Grasses, a major item in the tammar's diet, are rare in south-west ecosystems (Diels, 1906; Gardner, 1957). The moist low-lying sites in which the tammar occurs appear to be optimum sites for grasses and other small monocotyledons.

The necessity for food plants of each species to occur in conjunction with the narrow range of scrub densities and percentage bare ground preferred by each species is considered the main reason for their limited distribution. Situations where optimum site types occur in conjunction with the preferred scrub density and bare ground, in the right proportions and large enough in extent, are relatively rare.

Fire, included in the analysis as "years since burn", did not feature as a parameter with influence in the distribution of either species within the study area. Predation, particularly by the introduced European fox, *Vulpes vulpes,* is often quoted as being a limiting factor in the present distribution of native species. Wood-Jones (1924) assumed that it was the fox which was mainly responsible for the decline of the woylie. The conclusions reached above do not appear to support this. It was further demonstrated during this study that both the woylie and the tammar continue to inhabit the Perup despite continued heavy predation by foxes.

However, despite the overwhelming evidence, it is unwise to dismiss predation as a limiting factor. Predation is the most likely reason why cover density is such a critical limiting factor for both species in the Perup.

The options of cover may be different now, since the fox has replaced the dingo (*Canis familiaris*) as a major predator of both the study species. This is supported by evidence of the disappearance of the woylie from certain areas of State forest some time after 1930 (D. H. Perry, personal communication), soon after the introduction of the fox to Western Australia. The fox first appeared near the south coast in 1915 (Agriculture Protection Board records, see Sampson, 1971).

The assumption by Wood-Jones that the fox was mainly responsible for the decline of the woylie thus becomes plausible. Further evidence is provided by the offshore islands, where, in the absence of the fox, the tammar, the quokka (*Setonix brachyurus*) and other medium-sized marsupials exist under conditions of comparatively sparse cover. Thus the fox through the medium of cover density, rather than cover density *per se,* may be a secondary limiting factor.

### Hypothesis 2

Woylies and tammars will survive within the burn but they will fall prey to predators during the first weeks after fire. Re-population of the area will be effected by young animals from the unburnt surrounds and large unburnt patches.

Results generally agreed with the first part of the hypothesis, but there were important deviations from the general trend. Thus, although all woylies except those along the perimeter remained on the burn, not all were victims of predators during the weeks after the fires. More than one animal survived to breed on the burn itself and others survived by moving from the burnt area. Most movement occurred amongst animals on the burn perimeter and involved a re-organisation of the nesting and feeding sectors of their home range. Complete re-location or major shifts in home range were made by a few individuals.

The tammar fits the first part of the hypothesis more closely than the woylie. None of the tammars which stayed on the burn survived. However, a fairly high proportion made successful moves to new areas.

It appears that the second part of the hypothesis will hold good for the tammar. Re-colonisation of the burn by the woylie was more or less according to the hypothesis but a proportion of the juveniles came from within the burn itself.

These deviations from the hypothesis are important for two reasons. Firstly, the range of responses, viz. staying and dying, partial re-organisation of home range, total re-location of home range, or surviving to reproduce on the burn itself, indicate the lack of stereotyped behaviour. This is undoubtedly of value to any population, particularly one living in a fire environment where the situation in each fire is different and the results vary enormously (Kozlowski and Ahlgren, 1974; Christensen and Kimber, 1975). Secondly, survival to the breeding stage of both woylies and tammars that moved and woylies that stayed demonstrates the survival value of both forms of behaviour.

**Hypothesis 3**

Woylies remain within their home range areas after fire, not because they are excluded from the unburnt surrounds by other home range owners, but because of an innate fidelity to their home range.

All results support the hypothesis. A high order of fidelity to home range was observed in all animals except one, animal transmitter Channel 3.3. This animal, a young male, moved its home range to an entirely different locality soon after the burn. It moved through the "empty area", from which woylies had been removed, to establish itself on the eastern edge of this area. All other movements involved a re-organisation of home range area, usually taking the form of a reversal of nesting and feeding area. The "empty area" was not taken advantage of by the animals on the burn. Their behaviour was in all respects similar to that of woylies radio-tracked on the earlier burn where the surrounds contained resident woylies.

Two main conclusions may be reached as a result of this study:

(1) The woylie has a very strong "attachment to site" or site fidelity.

(2) Since some animals survived to breed, fidelity to site after burning is not disadvantageous to the survival of the species.

In considering the advantages of "attachment to site", if the home range concept of Jewell (1966) is accepted, many of the suggested advantages for territorial behaviour may be applicable to the woylie. These include: regulation of breeding by affecting courtship and nesting; influencing dispersion; regulation of food resources; and serving as a buffer against disease (Hinde, 1956; Tinbergen, 1957; Brown, 1969; Carrick, 1963).

Many of the suggested advantages would still apply if the animals had moved into the "empty area" after the fire and established new home ranges. What then keeps the animals on the burnt area? A possible explanation is the advantage gained by an intimate knowledge of an area in terms of escape from predators (Tinbergen, 1957). In view of the almost total destruction of ground cover, this explanation does not appear sufficient in itself.

A less tangible concept, that of "territorial confidence" advanced by Mykytowycz *et al.* (1976) working with marking-odours of rabbits, may be the explanation. While marking-odours are not necessarily still detectable after a fire, it is suggested that the woylie may still "feel more confident" in an area it knows intimately. It is significant that most woylies spent the first few days after the fire entirely within their nesting areas. There is obviously a considerable psychological factor involved in early post-fire survival and "confidence" may be very important. The early "shock deaths" are evidence of a failure to regain full "confidence" after the fire, and an absence of the will to live. The woylies' attachment to home range may be considered a manifestation of the "territorial confidence" factor. Furthermore, fidelity under such extreme conditions suggests that this factor may be a major function of "territoriality".

In this study many edge animals moved out of the burnt area. The size of the fire is obviously important and in a large fire there may well be less movement out of the burnt area.

## MAJOR CHARACTERISTICS OF WOYLIE AND TAMMAR POPULATION

Before any attempt is made to determine whether specific traits are those of fire adaptation or not, examination of certain major characteristics of each species in relation to its general biology may be useful. The characteristics considered to be important are:

(1) The woylie—continuous breeding, high male-female ratio, social repression of juveniles, occupation of discrete home range areas, limited dispersal, absence of panic during fire, fidelity to home range.
(2) The tammar—seasonal breeding, lack of repression of juveniles, group territoriality, wide dispersal, absence of panic during fire, some fidelity to home range.

Why do these characteristics adapt the woylie and tammar to their habitat?

The well defined home range area with the apparent territorial nesting area enables the woylie to make maximum use of a widely distributed, patchy and continuous food source. Similarly, limited dispersal is suited to an animal whose habitat occurs as a continuous or semi-continuous patchwork or mosaic of suitable sites. Continuous breeding may be related to conditions which do not favour young at any specific season of the year. Social repression of juveniles follows as a natural consequence of this. There is a latent potential for expansion at any time if social pressures on juveniles are released. The various advantages of attachment to site or fidelity were discussed earlier.

The group territorial system of the tammar is well suited to its grazing habits and cover requirements. Its food source is concentrated in small isolated pockets adjacent to suitable cover. This forces many animals into confined space and the group territorial system may be an adaptation of a herbivore to living within a confined space. Wide dispersal is suited to the patchy discontinuous nature of its habitat. Seasonal breeding may be a response to food availability; juveniles start feeding independently in spring, when there is maximum food available. There is no need for social repression of juveniles in a species with seasonal breeding and wide dispersal.

How has fire influenced these traits?

## SELECTIVE ADAPTATION AND FIRE

A high proportion of plants in a fire-prone environment is exposed to fire at some stage. Long-lived tree species may experience several fires, while short-lived scrub and herbs, which may not actually experience fire themselves, may have their dormant seed exposed to fire. Unlike plants, animals can move and so avoid the direct effects of fire. Also, several consecutive generations of mammals may occur in periods between fires so that a high proportion of individuals may never be exposed to its selective influence. For this reason the direct effects of fire on selective adaptation are likely to be less obvious among mammals than plants.

It is difficult to identify direct adaptations to fire with confidence. Kites and eagles coursing over the fire front on an African prairie, capturing insects, birds, lizards and rodents flushed by the advancing fire, is considered by Handley (1969) to be an adaptation to fire, as also is the nesting of the Kirtlands warbler in only the early stages of succession in jack pine forest. The first of these examples may be a general adaptation to disturbance, and the second is not a direct adaptation to fire.

A trait which could be an adaptation to fire, and which is certainly an advantage in a fire situation, is the tendency not to panic. Both the woylie and the tammar displayed this behaviour and it has been recorded amongst birds and other mammals during fire in Alaska (Hakala *et al.*, 1971) and during a fire in Florida (Vogl, 1973).

Most adaptations of mammals relate to their biotic environment rather than to the abiotic factors which influence it. Hence, Kozlowski and Ahlgren (1974), in discussing the evolution of birds and animals in a burnable habitat, refer to adaptations of birds and mammals to flammable habitat.

Features that are probably adaptations to flammable open grassland are recorded by Handley (1969) and Komarek (1962) and include the ability to run quickly, burrowing and storing food, pressing flat to avoid detection, and migration. Geist (1971) records the population properties of a fire-follower, the moose, as: a high, variable birth rate; high dispersal; and fluctuating abundance.

Some of the characteristics of woylies and tammars may be interpreted this way. Hence the woylie's fidelity to home range allows a percentage of the population to survive to breed on the burn. The repression of juveniles, released after fire, ensures an immediate supply of colonisers for the burn. Similarly, the tammar is well adapted to re-colonise areas of new habitat as they become available after fire.

However, this concept only permits the interpretation of adaptation related to fire in a very general manner. There is a need for more specific interpretation of some of the obvious and very close relationships that exist between some animals and fire.

Gill (1975) points out that plants are not adapted to fire *per se* but may be adapted to a fire regime. Although not directly applicable in the context of mammal adaptation and fire it does assist the clarification of certain fire-related characteristics of animals living in flammable habitats. For example, the Kirtlands warbler nesting only in the early growth stages of jack pine (Mayfield, 1960) is viewed as a fire adaptation by Handley (1969). But this bird is not adapted to fire *per se,* or even to a fire regime; it is adapted to the early seral stages of jack pine. It is the jack pine that is adapted to a specific fire regime. Similarly, the tammar is not adapted to fire, nor indeed to a particular fire regime, but to a certain seral stage of heartleaf. It is the heartleaf that is adapted to a certain fire regime.

It is suggested that such associations between animals and seral stages after fire should be regarded as "fire dependence", not fire adaptation. Such a

concept, although it does not eliminate the problems associated with the interpretation of selective adaptation and fire, may nevertheless lead to a better understanding of the significance of relationships between fire and animal populations.

## THE SIGNIFICANCE OF FIRE DEPENDENCE IN RELATION TO THE WOYLIE AND THE TAMMAR

Fire dependence may be expected to manifest itself to varying degrees in different species, depending on the importance of fire in the habitat in which they live. In most cases the degree of dependence may be difficult to determine, since many factors will invariably be involved and a full knowledge of the species' biology is seldom available.

### The structural component of the habitat

*The woylie*

Plant associations in the jarrah forest habitat of the woylie and the tammar are adapted to frequent fire (Christensen and Kimber, 1975). As we have seen, the woylie is well adapted to cope with this situation but it may nevertheless be vulnerable to fire under certain circumstances. In Dryandra forest much of the woylies' nesting cover comprises "fire-weed" species such as *Acacia pulchella, Gastrolobium oxylobioides* and *G. calycinum*. These species, together with another cover plant, *Dryandra nobilis,* all require periodic hot fires for their regeneration. Too-frequent cool fires will result in a reduction in cover and the eventual disappearance of such species (Christensen and Kimber, 1975). This process of habitat degradation accompanied by a decline in the woylie population may already be in progress in this area (P. Christensen, personal observation). The whole process is aided by the spread of introduced grasses. Fertiliser drift from adjoining farmlands helps to establish the grasses, which in turn encourage more frequent cool fires.

The effect of fire exclusion on the woylie is more difficult to observe. Once again, Dryandra forest provides an example. Large areas of what appear to have been the woylies' best feeding areas were planted to mallet (*Eucalyptus astringens*) in the 1920s. These plantations have been protected from fire since then and consequently are virtually devoid of understorey, with very little sign of digging activity by woylies or bandicoots (*Isoodon obesulus*).

The woylie in Tutanning reserve near Pingelly may also be vulnerable to fire in a manner similar to that described above.

On present knowledge the problem should not arise in the Perup, at least in the short term. In this higher rainfall area regeneration of the understorey is more rapid than that in the lower rainfall Tutanning area and is largely from rootstock species.

*The tammar*

Like the woylie, the tammar may be vulnerable to too-frequent mild fires. The growth of grasses during the first few years after fire in the heartleaf thickets is such that there is sufficient fuel to support a mild fire during the dry summer months. Such a fire would kill the developing heartleaf seedlings and encourage the spread of grasses without germinating sufficient new heartleaf seed to replace the thickets. A series of very frequent cool fires could thus eliminate the heartleaf thickets entirely. Once again the situation is aggravated by the presence of introduced species of grasses and weeds and would be most serious adjacent to farmland areas.

The group structure of the tammar population helps maintain grazing pressure, which keeps the flammability of the grasses at a minimal level.

Similarly, if fires occurred less frequently than every twenty-five to thirty years in the Perup area, tammar thickets of both heartleaf and *Melaleuca viminea* would degenerate and die, resulting in the eventual disappearance of the tammar.

The tammar appears to be able to exist on offshore islands in the prolonged absence of fire. This may be because the thicket-forming species are not fire-dependent species. It may also be that the absence of the fox and the dingo makes the cover density factor less critical, so that fairly dense thickets are not necessary.

### Nitrogen fixation by legumes in the habitat

A more fundamental factor which may increase the fire dependence of both the study species is nitrogen. Many of the soils of the south-west are very infertile and have low nitrogen contents. As was shown earlier, this element may be important in the growth and production of both hypogean fungus sporocarps and the grasses that constitute the food of the tammar.

There is increasing evidence that native legumes play an important role in the nitrogen turnover of the jarrah forest environment (Shea and Kitt, 1976). Good germination and growth of native legume species is promoted by hot fires (Christensen and Kimber, 1975; Shea and Kitt, 1976). The present fuel reduction or control burning programme (Peet, 1967) involves "cool fires" at regular and frequent intervals. Such fires favour regeneration of rootstock species and reduce the numbers and species of legumes.

Although no experimental evidence is available, there are indications that legume nitrogen-fixation may be one of the factors limiting the size and distribution of woylie and tammar populations. The decline of the woylie population in Dryandra forest was examined in relation to cover reduction. But the reduction of legumes resulting from fire exclusion in certain key feeding areas may be a contributing factor.

It may not be coincidence that the legume, heartleaf, is dominant in the low-lying areas and that *Bossiaea ornata,* another legume, dominates the ridges

on all the best woylie areas within the Perup. Furthermore, most diggings occurred on sites adjacent to the heartleaf, an area where *Macrozamia riedlei,* another species associated with nitrogen fixation (Halliday and Pate, 1976), is common.

The prolific growth of grasses associated with the heartleaf thickets is almost certainly dependent to some degree on the nitrogen fixation in these thickets. Tammars occur in *Melaleuca viminea* thickets also but are nowhere as densely populated as in the heartleaf.

Detrimental effects of regular frequent and widespread cool control burning on the nitrogen budget of the system may take some time to become apparent. It is likely to be a slow insidious process. However, it could have far-reaching consequences, as the nitrogen budget of some species of native fauna may be finely balanced (Main, 1968). Brown (1968) showed that nitrogen was a limiting factor in macropods living in an arid environment. The jarrah forest is an arid environment for at least six months of the year.

In conclusion, it may be said that although neither the woylie nor the tammar shows any direct adaptation to fire, both seem to be influenced by it, both in distribution and numbers.

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APPENDIX I

# Sites Sampled in Vegetation Studies

| *Site and location* | *Plots sampled* | *Woylies* | *General description* |
|---|---|---|---|
| A Cup Rd. | 10 | * | Ridge-top site, low quality jarrah forest, canopy height 16 to 18 m, low open understorey, typical sp. *Leucopogon pulchellus*; others *Hakea lissocarpha, Astroloma pallidum* and *Pimelea suaveolens.* Light-coloured stony soil. |
| B Camelar | 10 | † | Ridge site, jarrah-wandoo forest, canopy height 17 to 21 m. Low open understorey, typical spp. *Hypocalymma angustifolium, L. pulchellus, Dryandra nivea, Acacia pulchella.* Clayey soil. |
| C Dudijup | 10 | ‡ | Ridge-top site, jarrah forest, canopy height 25 to 30 m. Low fairly dense understorey, typical spp. *Bossiaea ornata, Xanthorrhoea gracilis, L. capitellatus, Persoonia longifolia.* Gravelly sandy loam. |
| D Eastern Rd. | 15 | § | Lower slopes, jarrah-wandoo forest, canopy height 19 to 24 m. Low to medium understorey, typical spp. *Hakea lissocarpha, L. capitellatus, Trymalium ledifolium, A. pulchella.* Grey sandy loam. |
| E Fordson Rd. | 15 | † | Largely ridge-top sites, poor to medium jarrah forest, canopy height 20 to 30 m. Low understorey, typical spp. *B. ornata, H. lissocarpha, Thomasia grandiflora, A. pallidum.* Light-coloured clayey soil. |
| F Boyicup | 32 | § | Ridge sites, jarrah forest, canopy height 18 to 25 m. Low fairly dense understorey, typical spp. *B. ornata, H. lissocarpha, L. capitellatus, Macrozamia riedlei.* Gravelly sandy loam. |
| G Mordalup Rd. | 10 | * | Ridge site. High quality jarrah forest, canopy height 25 to 30 m. Low dense understorey, typical spp. *B. ornata, H. lissocarpha, L. capitellatus, P. longifolia.* Gravelly clayey loam. |
| H Moopinup | 15 | † | Largely ridge sites. Dry eastern jarrah forest, canopy height 16 to 25 m. Low open understorey, typical spp. *Conostylis setigera, L. pulchellus, H. lissocarpha, B. ornata.* |
| I Northern Rd. West | 15 | † | Jarrah forest, seasonally flooded flats, low ground cover under open thickets, typical spp. *Acacia cyanophylla, Hakea prostrata, Hypocalymma angustifolium, Drosera bulbosa.* Very shallow clayey soils. |
| J Nyamup | 15 | * | Ridge-top site, high quality western jarrah-marri forest, canopy height 35 to 40 m. Medium height dense understorey, typical spp. *Hovea elliptica, B. linophylla, Pteridium esculentum, Clematis pubescens.* Clayey soils. |
| K Granite outcrop | 10 | † | Ridge-top granite outcrop, few trees, dense low understorey. Typical spp. *Dryandra armata, Hakea undulata, Gastrolobium bilobum, Baeckea camphorosmae.* Shallow coarse sandy soil. |
| L Northern Rd. South | 15 | † | Low lying marri-jarrah forest, canopy height 25 to 30 m. Low open understorey largely composed of monocot. spp., also present are *B. linophylla, Hibbertia glabberrima, L. australis.* Grey sand. |
| M Northern Rd. Wandoo | 12 | † | Low ridges, wandoo forest, canopy height 18 to 20 m. Very open understorey, typical spp. *H. angustifolium, A. pulchella, L. pulchellus, D. nivea.* Clayey soil. |
| N Warrup | 15 | † | Ridge, high quality jarrah forest, canopy height 26 to 32 m. Low open understorey, typical spp. *L. propinquus, C. aristata, Macrozamia riedlei, Banksia grandis.* Sandy loam. |

| *Site and location* | *Plots sampled* | *Woylies* | *General description* |
|---|---|---|---|
| O Melaleuca thicket | 7 | † | Eastern jarrah-wandoo forest. Dense medium height thickets of *Melaleuca viminea* on grey sandy soil along drainage lines. Generally bordered by wandoo forest, seasonally wet. Understorey of monocots. with occasional *E. rudis* tree present. |
| P Melaleuca flat | 7 | * | Eastern jarrah-wandoo forest. Dense medium height thicket of *M. viminea* and *Casuarina humilis* on wide open shallow seasonally wet flats. Soils very shallow underlain by impermeable layer. |
| Q Agonis thicket | 6 | * | High quality jarrah forest, valley bottom thickets very dense, high *Agonis parviceps* thickets on deep grey sand. |
| R Boyicup heartleaf | 12 | ‡ | Jarrah-marri forest, medium dense tall thickets of *Gastrolobium bilobum,* very open underneath with a ground cover of grasses and annuals. Sandy loam. |
| S Dudijup thicket | 5 | * | Jarrah forest, dense medium height *M. viminea* thicket on grey sandy soil along drainage lines, seasonally wet, understorey of small monocots. |

NOTE. These sites are not equivalent to the site-vegetation types of Havel (1975). Site-vegetation mapping in the northern jarrah forest (Darling Range). 1—Definition of site-vegetation types. *Bulletin 86,* Forests Department of Western Australia.

**Woylies**
* Not present
† Transitory
‡ Low to medium density population
§ High density population

APPENDIX II

# Site Factors Recorded in Sample Plots in Vegetation Study

**Parameters relating to overstorey tree species**

1. Canopy height—mean height of dominants
2. Basal area

**Parameters relating to understorey scrub**

3. Scrub height: mean height of dominant stratum
4. Scrub density: 0 to 60 cm
5. Scrub density: 61 to 120 cm
6. Scrub density: 121 to 240 cm
7. Scrub density: 241+ cm

(density estimated*)

8. Percentage bare ground—mineral soil or litter, no vegetation present
9. Burn age—years since last fire (Forests Department records)

**Parameters relating to the study animals**

10. Number of diggings
11. Percentage captures (tammars)
12. Number of woylie nests (nests per 1000 × 12 m transect)

**Soil parameters**

13. Soil type: 0 to 9 scale, from clay to sand
14. Soil colour: not used in analysis
15. Stoniness: 0 to 3 scale, no stones to heavy laterite or granite
16. Chemical and mechanical analysis†
    Mechanical analysis (percentages) silt, clay, fine sand, coarse sand, moisture content.
    Chemical analysis: total soluble salts ($g.kg^{-1}$); Cl, Na, K, Ca, Mg, K(HCl), P(HCl), P(avail.) (p.p.m.); N, C(%); *p*H
    Exchangeable cations—Na, K, Ca, Mg and cation exchange capacity

**Topographical features**

17. Topographical position: —0 to 5 scale, flats, valley bottoms and ridge tops
18. Slope: degree of slope.

*An estimate of the horizontal density of the vegetation at various heights above the ground. The technique used was a modified version of the method of MacArthur and MacArthur (1961). The eye of the observer standing in the middle of the plot was kept at a certain height above the ground while a white board, 30 cm wide, was placed at the edge of the plot, 6 m from the centre. The percentage of the board obscured from vision by vegetation was used as an estimate of density. Twenty such estimates per plot were found necessary to reduce the error to within 10 per cent. In view of time limitation the board was abandoned and an estimate by one observer using a 10-point scale from 0 to 100 was adopted in preference.

† Soil samples were collected from the topsoil on three plots on 16 of the 19 sites for chemical and mechanical analysis by the Soils Section of the Western Australian Forests Department.

APPENDIX III

# Methods Used in Ageing the Population

**The woylie**

Sampson (1971) published figures relating pes, tail and head measurements to the age of pouch young. No means of ageing older animals was available, so woylies captured during the first few trap sessions were therefore not aged. By September 1974 a method based on molar eruption, similar to that used by Shield (1958) on the quokka (*Setonix brachyurus*), had been developed.

As in the quokka, the final sectorial premolar, p4, is larger than p3, and in addition it has a characteristic postero-internal talon (Wood-Jones, 1924) and is thus easy to distinguish from p3. The final sectorial premolar p4 replaces p3 and dp4 when the molar eruption sequence has reached M3.2. This differs from the quokka, where M4 has fully erupted before p4 emerges (Shield, 1958) and the tammar, where M4 does not break through the gum line before p4 has erupted fully (Jones *et al.*, 1966).

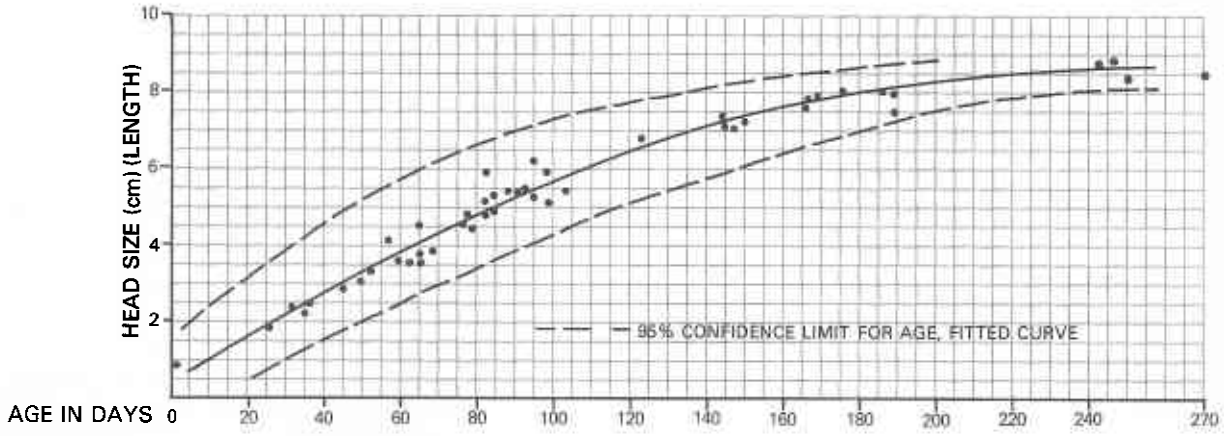


**Figure A.III (a)**

The woylie—graph showing the relationship between head size and age.

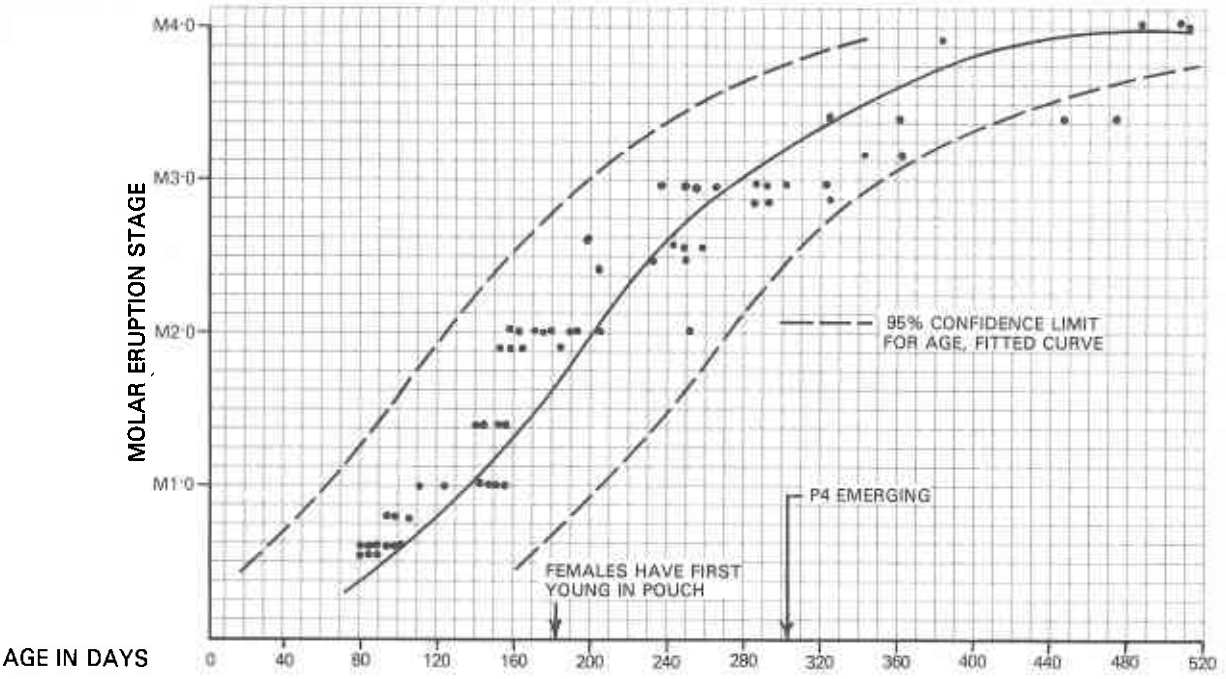


**Figure A.III (b)**

The woylie—graph showing the relationship between molar eruption and age.

Age curves based on head length data [Fig. A.III (*a*)] and tooth eruption [Fig. A.III (*b*)] obtained during the study were used in the analysis. All the curves were based ultimately on field growth data from a male joey of known age (the joey was born overnight while the mother was in a funnel trap). These data were used as a basis for determining the age and position on the graph of other animals. Accuracy was checked against Sampson's (1971) graphs.

**The tammar**

Graphs for ageing the tammar were constructed initially with the pes, tail and weight data of Jones *et al.* (1966) to age joeys. These data were used to start curves which were built on with further data from Boyicup animals [Fig. A.III (*c*) and (*d*)].

As a further refinement, a system of tooth wear categories was used to age older animals. The teeth of tammars wear from the front back, and the degree of wear may be gauged by the amount of dentine visible on each tooth. As the ridges wear, brown spots first appear at each end where the dentine shows through; these gradually increase in size until they meet and form a continuous line across both ridges on each tooth. Wear is gauged by the number of molariform teeth which are worn, and to what extent they are worn. Thus the symbol d denotes teeth with spots of dentine showing and D, teeth with the dentine showing across the length of each ridge. The tooth wear on an animal with two molariform teeth worn right across the ridges and a third with patches of dentine showing would be recorded D2 d1.

Unfortunately, only a small collection of skulls was available but comparisons with Molar index (Kirkpatrick, 1964) indicate that the tooth-wear categories may provide a reasonable guide to the age of older animals with all four molars present. In plotting Fig. A.III (*d*) problems were experienced in distinguishing between p3 and p4 (see Jones *et al.*, 1966). The large number of points which appear on the graph at this change-over stage reflect the confusion, and this age group is difficult to classify correctly.

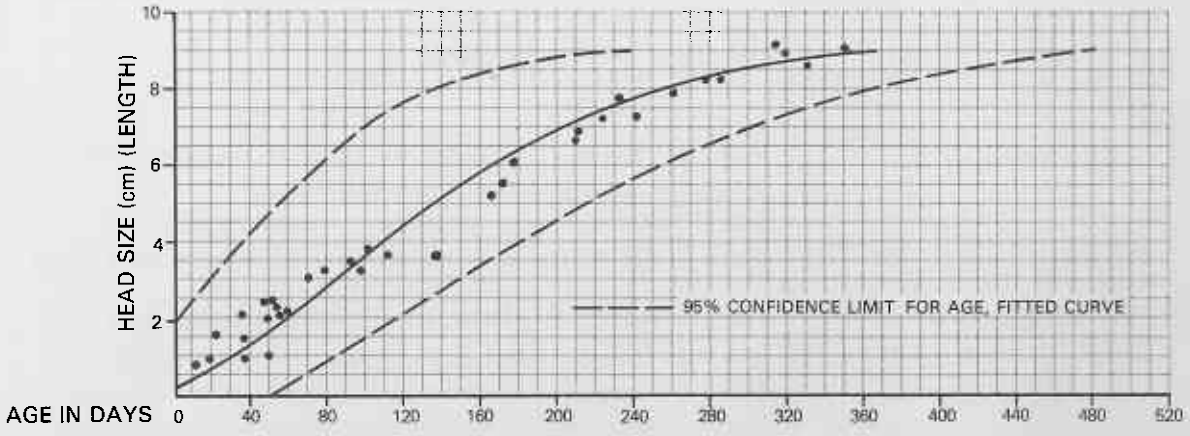


**Figure A.III (c)**

The tammar—graph showing the relationship between head size and age.

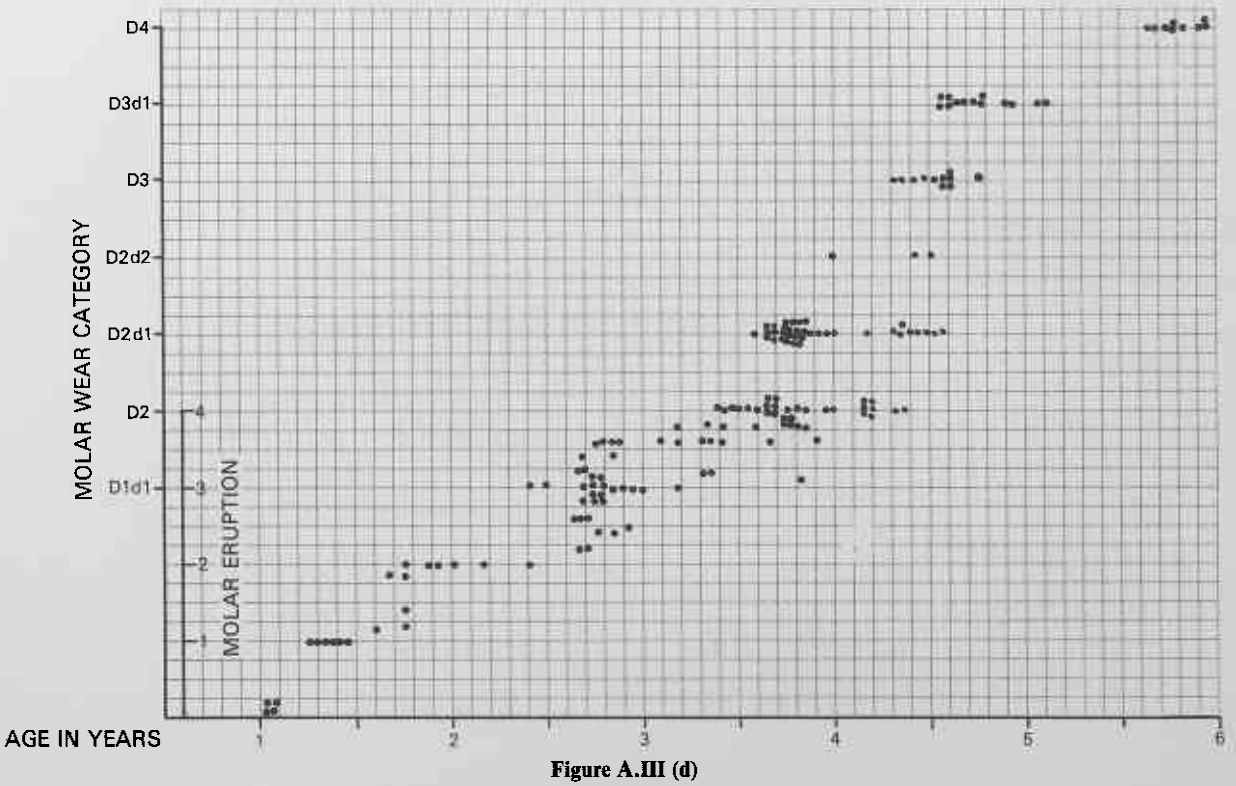


**Figure A.III (d)**

The tammar—graph showing the relationship between molar eruption, wear and age.

APPENDIX IV

# Nocturnal Activity Monitored with the Rustrak Continuous Drum Recorder

| *Channel No.* | *Species* | *No. of nights recorded* | *Mean hours per night within range** | *Month* | *Comments* |
|---|---|---|---|---|---|
| **1975 Burn** | | | | | |
| 10 | Woylie | 3 | 7·35 | April | Within range of nest area on the burn. |
| 3 | Tammar | 1 | 12·15 | June | Feeding on old home range area in the burn. (Day-time hours spent in thicket outside burn.) |
| 5 | Tammar | 1 | 11·15 | May | As above. |
| 5 | Tammar | 3 | 8·10 | May | As above. |
| **1976 Burn** | | | | | |
| 11·2 | Woylie | 1 | 5·45 | March | In feeding area (1975 burn) before 1976 burn. |
| | | 2 | 2·39 | March | (In nest area outside burn.) |
| | | 6 | 6·09 | Mar.-Apr. | In nest area now burnt, still nesting there. |
| | | 5 | 7·38 | Apr.-May | In nest area now burnt, but now nests in old feeding area, 1975 burn. |
| 8·1 | Woylie | 2 | 6·01 | Feb.-Mar. | In feeding area, 1975 burn—before burn. |
| | | 1 | 6·14 | March | In nest area, now burnt, still nesting there. |
| 2·21 | Woylie | 2 | 5·20 | March | In feeding area, 1975 burn, before 1976 burn. |
| 9·375 | Woylie | 6 | 6·24 | Apr.-June | In feeding area, 1976 burn—nest outside burn. |
| | | 3 | Nil | Apr.-June | Not in feeding area, 1976 burn. |
| 1·12 | Woylie | 9 | 9·32 | April | In feeding area, 1976 burn, nest outside burn. |
| | | 1 | Nil | April | Not in feeding area, 1976 burn. |
| **New residents 1975 burn (monitored May 1976)** | | | | | |
| 2·2 | Woylie | 5 | 12·0 | May | In range of nesting area on the 1975 burn. |
| 10·15 | Woylie | 3 | 10·15 | May | As above. |

* Range of recorder = 200 to 250 m

APPENDIX V

# Dates Referring to Numbers on Radio Location Maps

(Figs. 28, 29, 33 and 37)

**1975 Burn**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 25 February | 12 | 14 March | 23 | 30 March | 34 | 24 April | 45 | 28 May |
| 2 | 26 February | 13 | 17 March | 24 | 1 April | 35 | 29 April | 46 | 30 May |
| 3 | 27 February | 14 | 18 March | 25 | 3 April | 36 | 31 April | 47 | 3 June |
| 4 | 28 February | 15 | 19 March | 26 | 7 April | 37 | 5 May | 48 | 5 June |
| 5 | 3 March | 16 | 20 March | 27 | 10 April | 38 | 8 May | 49 | 9 June |
| 6 | 4 March | 17 | 21 March | 28 | 14 April | 39 | 9 May | 50 | 10 June |
| 7 | 6 March | 18 | 24 March | 29 | 17 April | 40 | 12 May | 51 | 17 June |
| 8 | 10 March | 19 | 25 March | 30 | 18 April | 41 | 19 May | 52 | 20 June |
| 9 | 11 March | 20 | 26 March | 31 | 21 April | 42 | 23 May | 53 | 25 June |
| 10 | 12 March | 21 | 27 March | 32 | 22 April | 43 | 25 May | 54 | 27 June |
| 11 | 13 March | 22 | 28 March | 33 | 23 April | 44 | 27 May | 55 | 2 July |

**1976 Burn, day-time location**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 20 February | 10 | 10 March | 20 | 1 April | 29 | 28 April | 38 | 10 June |
| 2 | 23 February | 11 | 11 March | 21 | 5 April | 30 | 29 April | 39 | 14 June |
| 3 | 24 February | 12 | 15 March | 22 | 7 April | 31 | 30 April | 40 | 17 June |
| 4 | 25 February | 13 | 17 March | 23 | 9 April | 32 | 7 May | 41 | 5 July |
| 5 | 26 February | 14 | 18 March | 24 | 13 April | 33 | 12 May | 42 | 29 July |
| 6 | 27 February | 15 | 19 March | 25 | 15 April | 34 | 17 May | 43 | 19 August |
| 7 | 2 March | 16 | 22 March | 26 | 20 April | 35 | 24 May | 44 | 25 August |
| 8 | 4 March | 17 | 24 March | 27 | 22 April | 36 | 28 May | 45 | 26 August |
| 9 | 8 March | 18 | 26 March | 28 | 27 April | 37 | 2 June | 46 | 27 August |
| | | 19 | 29 March | | | | | | |

**Nocturnal location**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 26 February | 4 | 18 March | 8 | 27 April | 11 | 28 May | 14 | 29 July |
| 2 | 8 March | 5 | 30 March | 9 | 7 May | 12 | 16 June | 15 | 23 August |
| 3 | 11 March | 6 | 1 April | 10 | 17 May | 13 | 5 July | 16 | 26 August |
| | | 7 | 14 April | | | | | | |

More than one location during the same night is recorded as 3*a*, 3*b*, etc.

APPENDIX VI

# List of Spore Types from Hypogean Fungi in Collection and from Scat and Stomach Analysis

| *Spore type* | *Specimens in fungus collection* | *Estimated frequency of occurrence of spores and origin* | | | | | *Description of spores as seen under light microscope 400 to 600 magnification (Sizes in μ approximate only)* |
|---|---|---|---|---|---|---|---|
| | | *Boyicup study area* | | | *Tutanning* | | |
| | | *Woylie scats* | *Woylie stomachs* | *Bandicoot scats* | *Woylie scats* | *Woylie stomachs* | |
| 2 | Yes | 5 | 5 | 5 | 4 | — | 7 to 8 × 5—hyaline and smooth |
| 3 | Yes | — | — | — | — | — | 10 × 5—hyaline and smooth |
| 5 | Yes | — | — | — | — | — | 10 × 5—hyaline and slightly knobbly in appearance |
| 7 | Yes | — | — | — | — | — | 12 to 13 × 5—hyaline, oval, scar of attachment |
| 13 | Yes | — | — | — | — | — | 12 to 14 × 5—hyaline, oval and smooth |
| 4 | Yes | 3 | 3 | 1 | — | — | 12 × 5—brownish yellow, longitudinal flanges, twisted |
| 1 | Yes | 2 | 2 | 1 | 1 | — | 9 to 15 diameter—hyaline, spherical, knobbly |
| 6 | Yes | 2 | — | — | — | — | 12 diameter—dark, spherical, well pronounced flanges |
| 9 | Yes | 2 | — | 1 | 3 | — | 20 to 30 diameter—dark, spherical, thick-walled, marked like a golf ball |
| 18 | Yes | 1 | — | — | 1 | — | 6 to 8 diameter—hyaline, spherical, knobbly |
| 11 | Yes | — | — | — | 1 | — | 12 × 5—hyaline, oval, looks like a spindle |
| 12 | Yes | 3 | 1 | — | — | — | 8 × 5—hyaline, lemon shaped |
| 14 | Yes | 2 | 2 | — | 2 | — | 15 × 30—dark, oval with pointed ends |
| 15 | Yes | 3 | 1 | — | — | 1 | 4 × 5—greenish brown, oval, knobbly |
| 16 | Yes | — | — | — | — | — | 10 × 5—golden brown, oval, pointed one end and collapsed sides |
| 32 | Yes | 2 | 1 | — | 1 | — | 10 diameter—hyaline, spherical, flanges |
| 33 | Yes | — | 1 | — | — | — | 8 to 9 diameter—hyaline, spherical, bumpy appearance |
| 38 | No | 2 | — | — | — | — | 20 diameter—light brown, spherical, very thick walled |
| 39 | No | 1 | — | — | — | — | 45 diameter—dark very thick walled |
| 40 | No | 1 | — | — | — | 1 | 10 × 5—yellow brown, banana shape, thick walled, with stalk |
| 17 | Yes | 2 | — | — | — | — | 12 × 7—hyaline, slightly opaque, rounded oval with bumpy surface |
| 41 | No | 3 | 2 | — | 2 | — | 3 × 1—hyaline, oval |
| 42 | No | 1 | — | — | — | — | 7 × 5—dark, irregular pear shape |
| 43 | No | — | — | 1 | — | — | 20 × 10—brownish yellow, oval, with stalk, thick walled |
| 45 | No | — | — | — | — | 1 | — |

| Spore type | Specimens in fungus collection | Estimated frequency of occurrence of of spores and origin | | | | | Description of spores as seen under light microscope 400 to 600 magnification (Sizes in $\mu$ approximate only) |
|---|---|---|---|---|---|---|---|
| | | Boyicup study area | | | Tutanning | | |
| | | Woylie scats | Woylie stomachs | Bandicoot scats | Woylie scats | Woylie stomachs | |
| 44 | No | — | 1 | — | — | — | 16 diameter—dark, spherical, with numerous very long spines |
| 28 | No | — | — | — | — | 1 | 15 × 8—dark, oval, with stalk, smooth thick wall |
| 29 | No | — | — | — | 2 | — | 15 × 5—dark, oval, thick wall with septa |
| 46 | No | — | — | — | 2 | — | 18 × 8—yellow brown, oval, scar of attachment knobbly |
| 37 | No | 2 | — | — | — | — | 7 × 7—brownish yellow spherical thick wall |

Scale of increasing frequency 0-5 (see Section IV, scat and stomach content analysis—the woylie)
4 = *Australasia chlorospora*
Spore types 2, 3, 5, 7 and 13 = *Mesophellia* sp. (Own identification)
9 = *Labyrinthomyces varius*
18 = *Martellia* sp. nov. ≠ 2.
6 = *Martellia* sp. nov. ≠ 1.
24 = *Melanospora episphaerium* (parasitic on other fungi)
All identification by J. M. Trappe, U.S. Department of Agriculture.

APPENDIX VII

# Concentrations of Elements in Selected Green and Senescent Leaves and Fungi

| *Species* | *Element* | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *N* (%) | *P* (%) | *K* (%) | *Ca* (%) | *Mg* (%) | *Na* (%) | *Si* (%) | *Al* (%) | *S* (%) | *Mn* (*p.p.m.*) | *Zn* (*p.p.m.*) | *Cu* (*p.p.m.*) | *Cl* (*p.p.m.*) | *Ni* (*p.p.m.*) | *Fe* (*p.p.m.*) |
| Jarrah *Eucalyptus marginata* leaves (green) | 0·84 | 0·041 | 0·57 | 0·58 | 0·43 | 0·29 | — | — | 0·103 | 117 | 5·6 | 2·9 | — | — | — |
| Jarrah *E. marginata* leaves senescent | 0·30 | 0·009 | 0·26 | 0·74 | 0·40 | 0·29 | — | — | 0·085 | 192 | 3·0 | 2·5 | — | — | — |
| *Acacia pulchella* leaves (green) | 2·15 | 0·039 | 0·86 | 1·19 | 0·24 | 0·03 | — | — | 0·209 | 47 | 8·0 | 4·5 | — | — | — |
| *Mesophellia* sp. central core. Spores* | 1·64 *3·52 | 0·085 | 0·26 | 0·042 | 0·060 | 0·047 | 0·088 | 0·105 | 0·30 | 9·4 | 35·8 | 14·3 | 0·029 | 2·0 | 127 |
| *Agaricales* sp. | 2·8 | 0·34 | 2·6 | 0·028 | 0·09 | 0·13 | — | — | 0·283 | 21 | 47 | 24 | — | — | — |

*Nitrogen concentration of *Mesophellia* sp. supplied by J. Kinnear, Zoology Department, University of W.A. (personal communication).

Other data supplied by Dr. N. Malajczuk, C.S.I.R.O., Perth (personal communication).

All percentages refer to percentage dry weight. All element concentrations except N obtained using X-ray fluorescent analysis.