THE BIOLOGY OF BETTONGIA PENICILLATA GRAY, 1837 AND MACROPUS EUGENII DESMAREST, 1804 IN RELATION TO FIRE

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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 remain within their home range areas, escaping the fire on small unburnt patches or by doubling back through the flames. Woylies generally remain within their burnt-out home range areas, living primarily on species of hypogean fungi. Despite considerable mortality during this period, some individuals survive to reproduce. Re-colonization is effected by these and other young animals from unburnt patches and from the unburnt surrounds.

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

An ordination study indicates 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-colonize 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.

1. 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 an ever-present 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 Koslowski 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 present-day Australian plant communities, is generally believed to have evolved some time before the mid-Tertiary, e.g. Crocker and Wood (1947). More recently, Lange* (personal communication) has definite evidence of Eucalyptus and other present-day genera in deposits believed to be either Oligocene or Mio-Pliocene in origin.

There is a very 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 burnable 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

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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 being the results of the 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 amongst 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: (i) survival of the adult; (ii) survival of the seed (propagule); (iii) 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 specialized 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.

The first hypothesis forms the basis of a vegetation and site study dealing with the distribution of the study species. It is 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 form 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 is based on personal observations made on woylie and tammar distribution obtained during spotlight surveys and from trapping results. Also, Havel (1975a) showed that plant associations are indicative of site characteristics. Hypothesis 2 is based on the results of an earlier study of the effects of fire on 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 burned. 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.

2. HABITAT SITE - VEGETATION STUDIES

2.1 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 eat (*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, an area where the largest known concentration of woylies is found and where the tammar is also common, suggest a clumped or discontinuous distrubution. 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 4.3), in Dryandra Forest (Table 2.1), 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 are 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.

TABLE 2.1

Dryandra Forest - Nest and digging transects

Site-vegetation type	Transect length (m)	Nest nos.	Diggings nos.	Nests/100 m	Diggings/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* sp. 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	1000	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.

2.2 Choice of methods

Methods of vegetation analysis suitable for this type of study are reviewed by Havel (1968 and 1975a). 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 1975a; Noy-Meir, 1971 and 1974). Less frequently it has been used to study the factors influencing the distribution of 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 1975a and 1975b). 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.

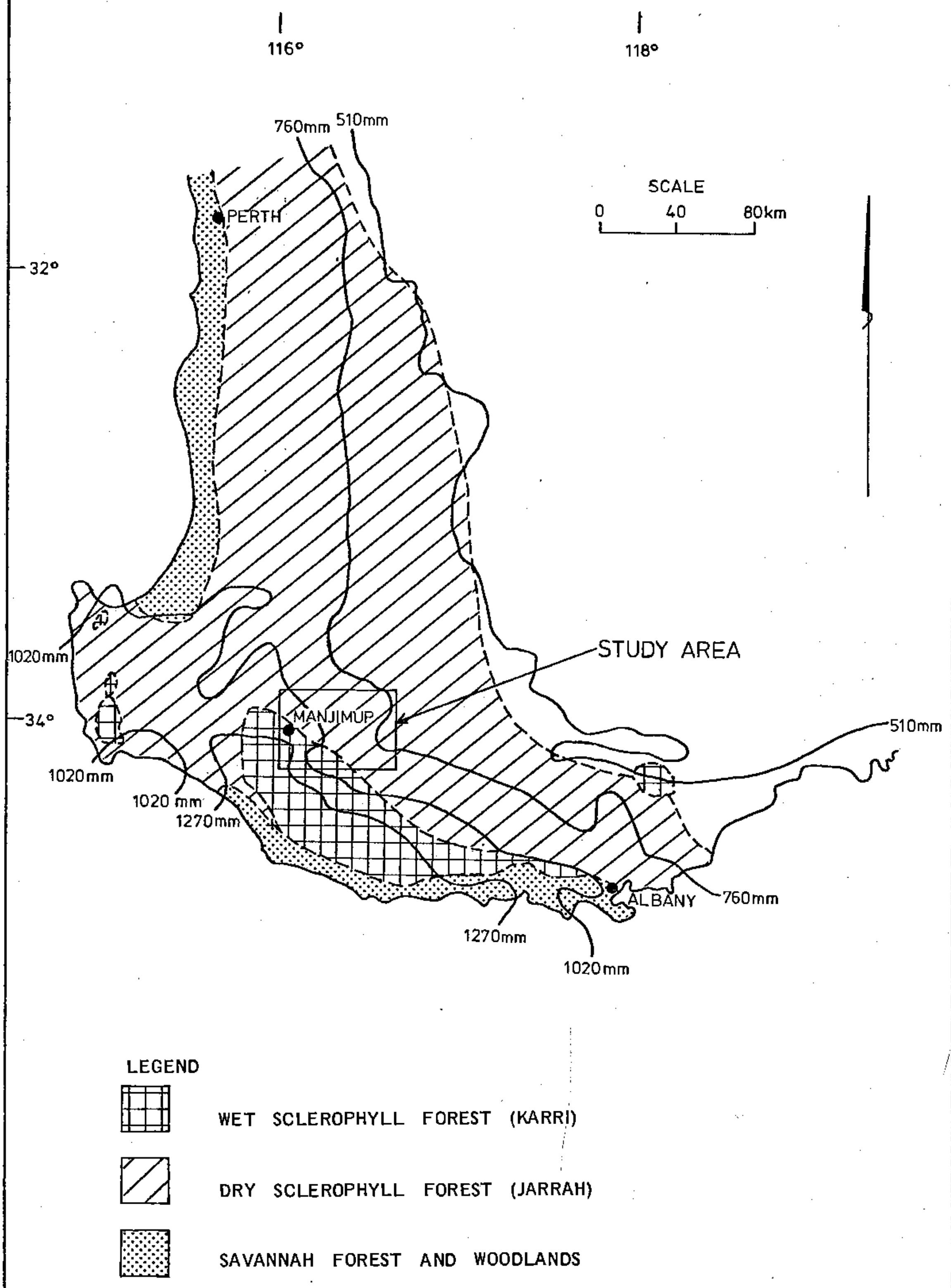
In case other methods may have provided more valuable information a hierarchial linkage analysis (McQuitty, 1964) was also tried.

2.3 Method

2.3.1 The study area

An area approximately 6000 km^2, including all known woylie and tammar populations within the State forest area east of Manjimup, was selected for the study (Figs. 2.3.1 and 2.3.2). 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 whilst the ridges are sandy gravels with occasional boulders and sheets of laterite

Fig. 2.3.1 MAP OF THE SOUTH-WEST OF WESTERN AUSTRALIA SHOWING LOCATION OF STUDY AREA.



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 Melaleuca preissii 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 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 (Eucalyptus calophylla) forest with a dense xeric to mesic understorey, dominates the ridges. Valley bottoms often have stands of blackbutt (Eucalyptus 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 north-eastern sector of the study area is similar to the Perup association but more xeric.

2.3.2 Sampling method

Data were collected for two separate analyses.

(i) 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 (Fig. 3.3.1).

(ii) A widescale study was conducted covering a range of 19 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 (Fig. 2.3.2). Two criteria were used in choosing the sites to be sampled.

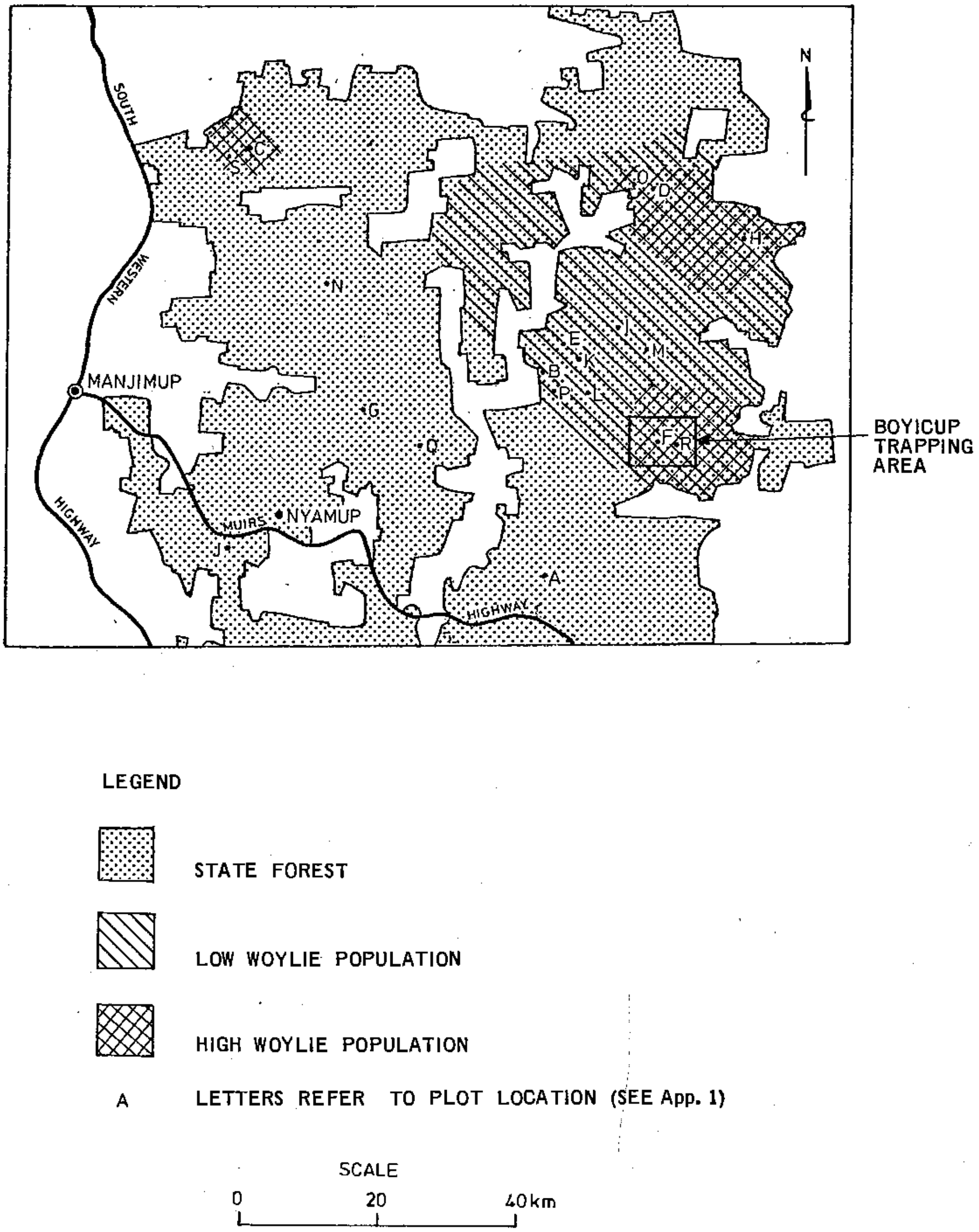
(a) They must represent the widest possible range of site-vegetation types within the study area.

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

The 19 selected sites are described in Appendix 1. These sites are not the equivalent of Havel's (1975a) site-vegetation types and should not be confused with them.

Fig. 2.3.2

MAP OF STUDY AREA SHOWING LOCATION OF BOYICUP TRAPPING AREA, VEGETATION SITE LOCATIONS AND WOYLIE DISTRIBUTION.



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 (Fig. 2.4.9) 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, 1975a). 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, 1975a). Other data relating to scrub structure, topography and soils were also recorded (Appendix 2). 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 4.3) 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.

2.4 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 factor 1. This result was not unexpected as the area sampled is small and, apart from the difference between upland and valley, it 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 (see 2.4.4).

Similarly, results of McQuitty's 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.

2.4.1 Distribution of plots within the component space

(a) Distribution of the sample plots

Ordination of the plots was accomplished using the program FACVA (Havel, 1975a). This program 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 factors 1 and 2 (Fig. 2.4.1). These two factors represent 14.0 and 8.9% 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.

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

Factors 3 and 4 account for only 7.3 and 5.4% of the total variance respectively. Hence separation is not as good, and plots tend to be clustered about the intersection of the axes. To avoid confusion, only plots from some selected sites are shown in Figure 2.4.2.

Open treeless plots with very shallow soils from the granite outcrop site (K) occur towards the +ive end of the factor 3 axis, whilst at the -ive end are clustered the plots from sites on deeper soils. Plots from seasonally droughty upland sites in the eastern sector occur towards the +ive end of the factor 4 axis, whilst plots on moist to wet sites in depressions occur towards the -ive end.

(b) Distribution of woylies within the component space

To see whether there was any correlation between woylie

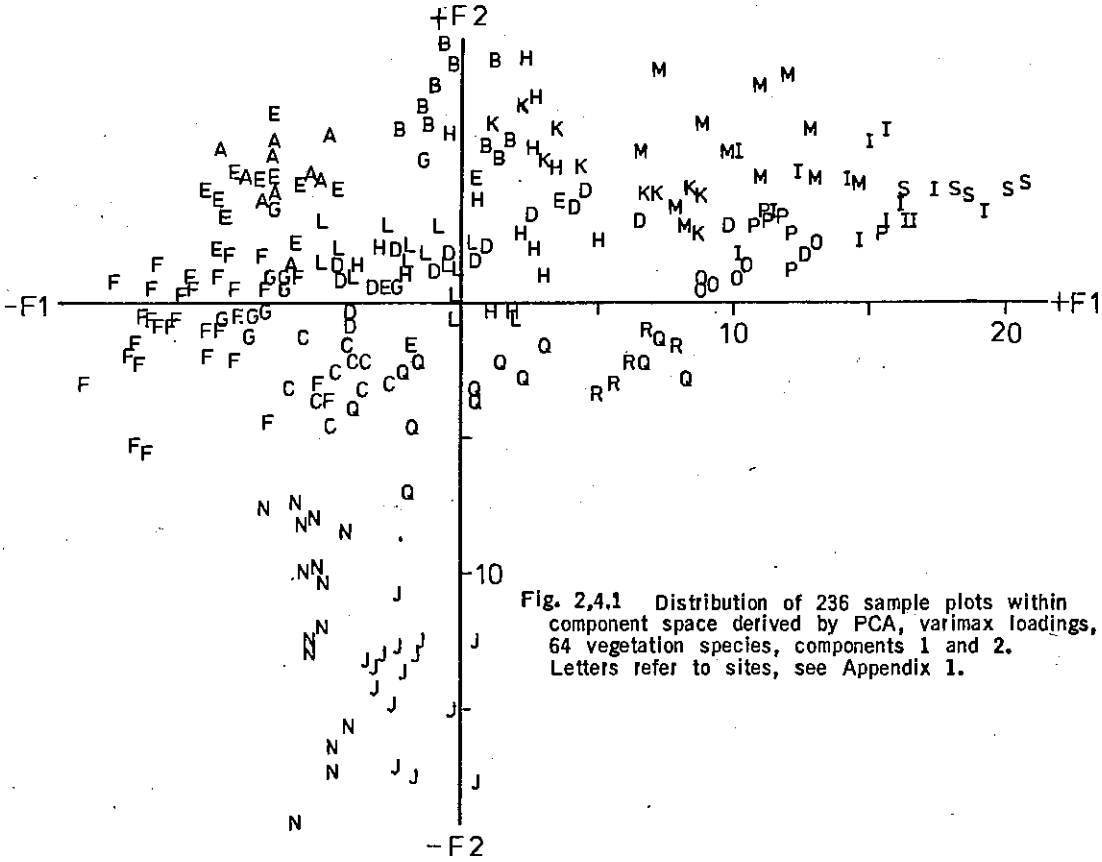


Fig. 2,4,1 Distribution of 236 sample plots within component space derived by PCA, varimax loadings, 64 vegetation species, components 1 and 2. Letters refer to sites, see Appendix 1.

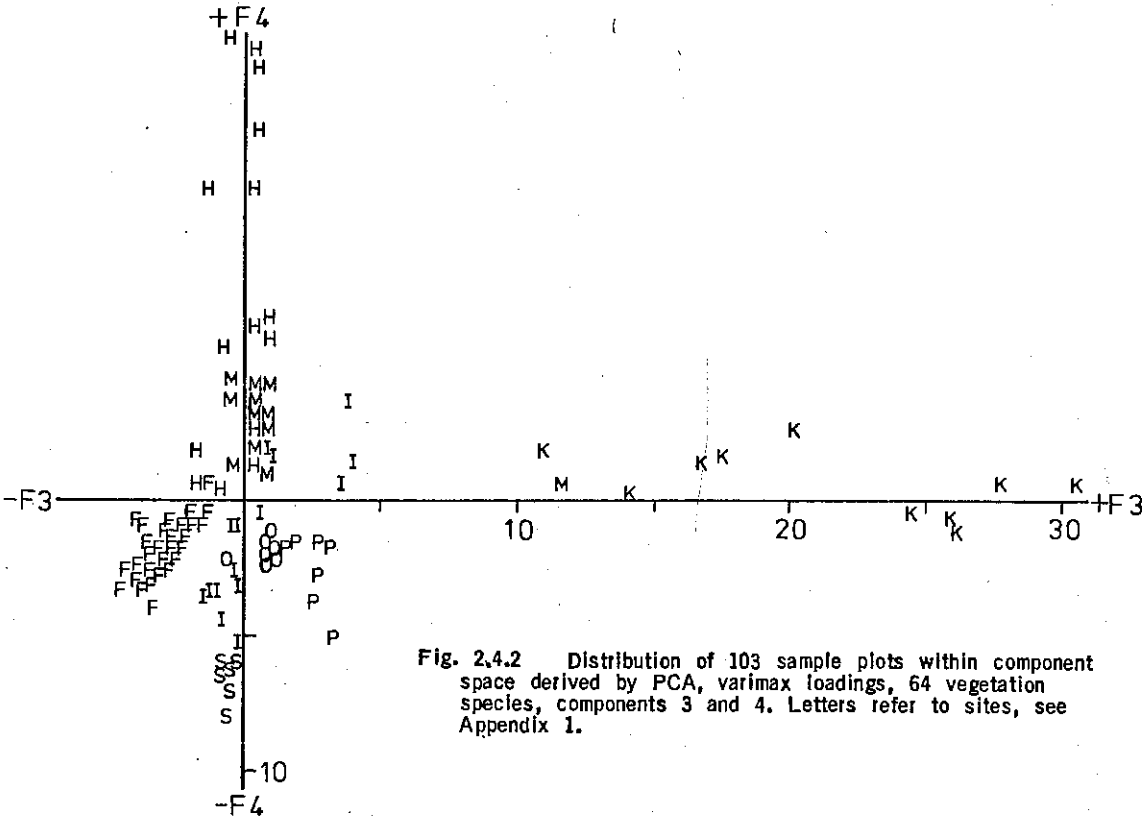


Fig. 2,4,2 Distribution of 103 sample plots within component space derived by PCA, varimax loadings, 64 vegetation species, components 3 and 4. Letters refer to sites, see Appendix 1.

distribution and vegetation plots, numbers of diggings and nests per plot were plotted within the component space using the plot scores (Figs. 2.4.3 and 2.4.4). High values for both nests and diggings show a distinct concentration at the -ive end of the F1 axis; on factor 2, the diggings in particular, tend slightly towards the -ive end also. These are the well drained upland sites tending towards the western sector. Lesser concentrations of diggings and some nests occur towards the +ive end of both F1 and F2 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 factors 3 and 4. The factor framework has been sectioned into squares of one unit each, and the mean number of nests or diggings per square is plotted (Figs. 2.4.5 and 2.4.6). The highest concentration of both nests and diggings occurs at the extreme -ive end of F3 tending towards the -ive end of F4. 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 -ive end of F3.

Distribution of woylie nests on plots within the component space is best visualized using a 'four-dimensional' model (Havel, 1975a). The concentration of plots with high densities of woylie nests is obvious and very striking (Photo 2.4.1).

(c). 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. 2.4.7 and 2.4.8).

The tammar occurs in a very definite area, situated towards the +ive end of the F1 axis and rather more towards the -ive end of F2 than the woylie. These are the moister, sometimes seasonally wet valley sites tending towards the more fertile western sector. Within the framework of the third and fourth components they occupy the sites towards the -ive 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 (Photo 2.4.1).

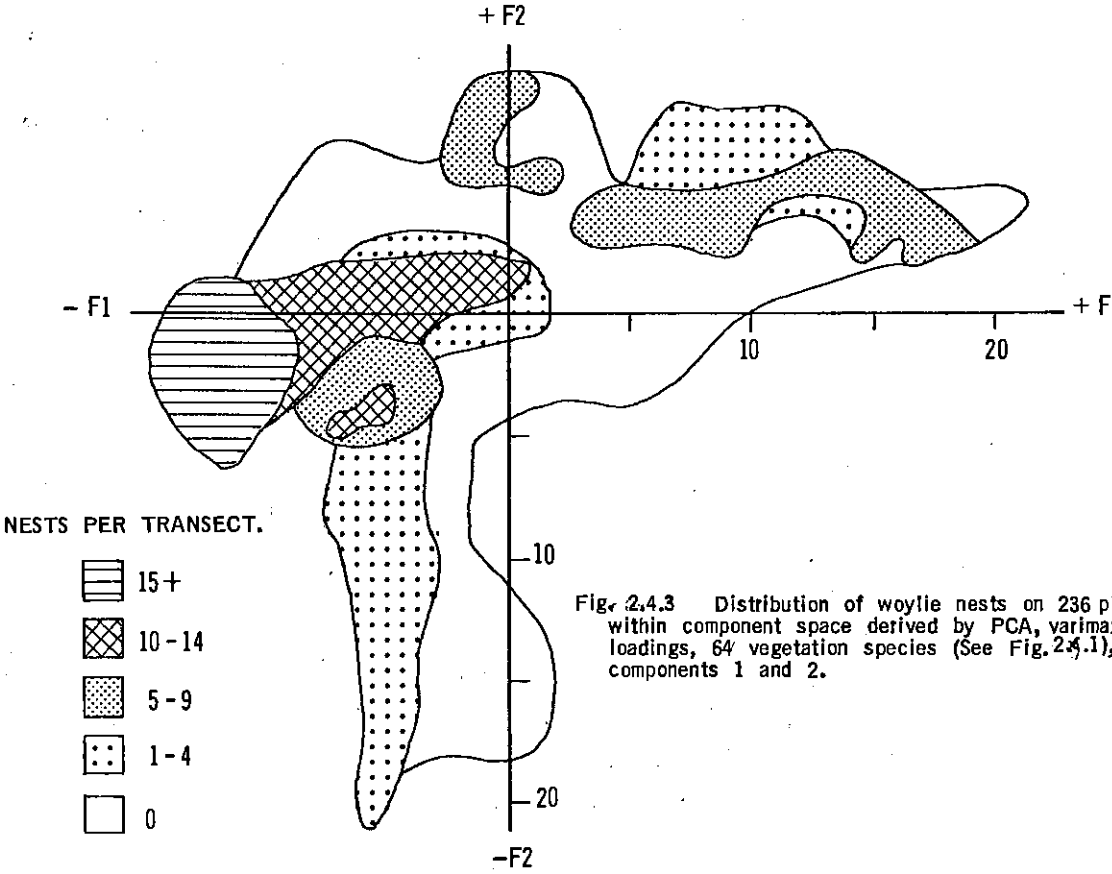


Fig. 2.4.3 Distribution of woylie nests on 236 plots within component space derived by PCA, varimax loadings, 64 vegetation species (See Fig. 2.4.1), components 1 and 2.

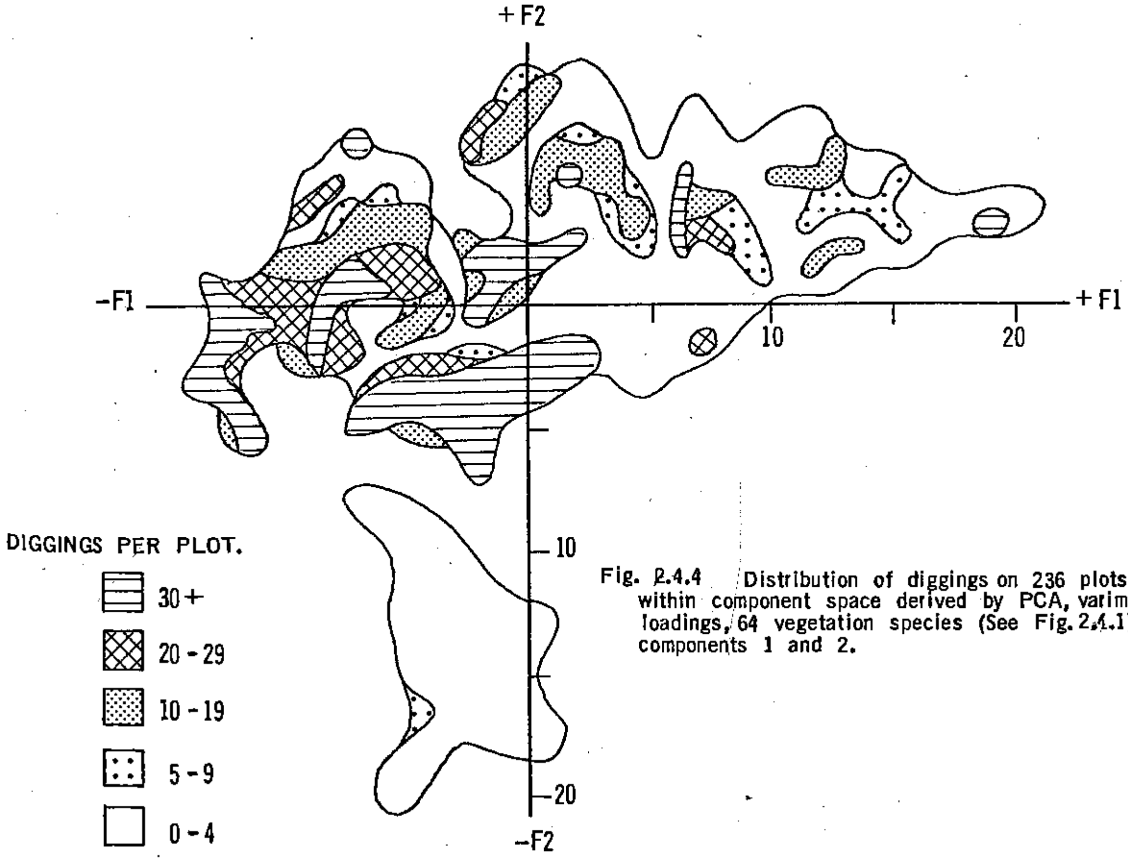


Fig. 2.4.4 Distribution of diggings on 236 plots within component space derived by PCA, varimax loadings, 64 vegetation species (See Fig. 2.4.1), components 1 and 2.

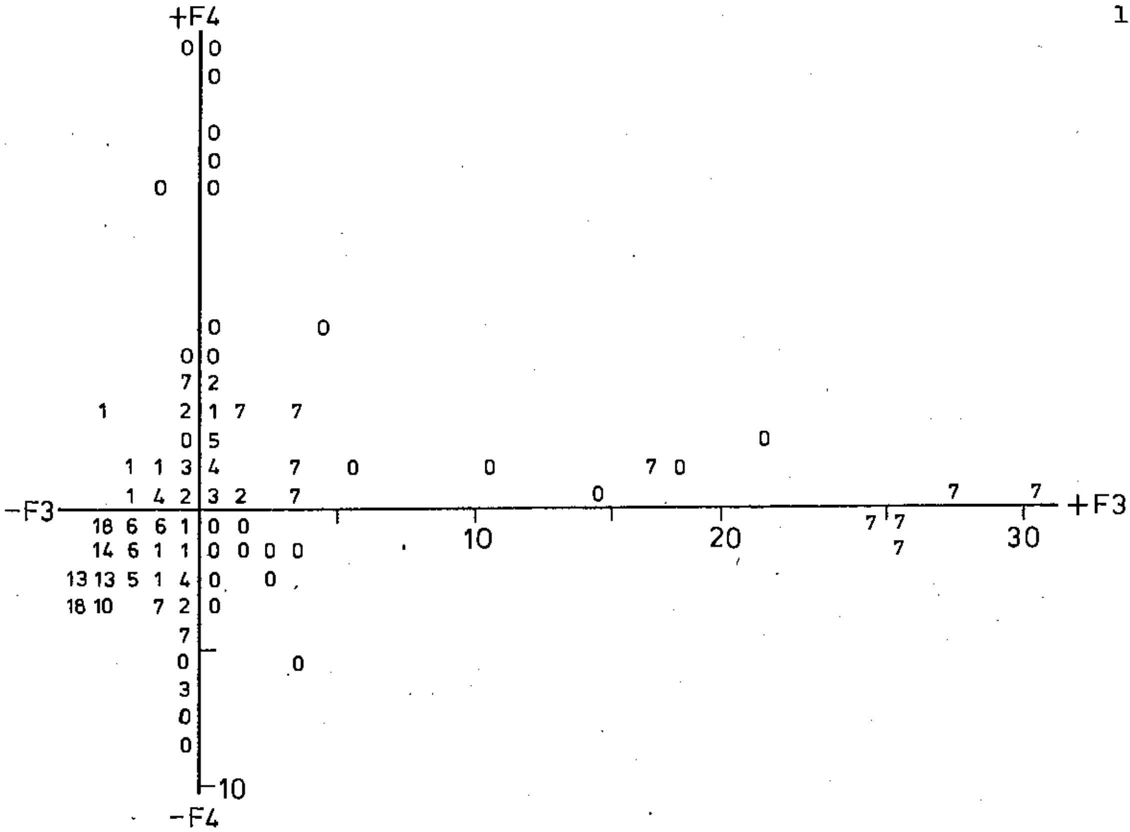


Fig. 2.4.5 Distribution of woylie nests on 236 plots within component framework derived by PCA, varimax loadings, 64 vegetation species (See Fig. 2.4.2), components 3 and 4. The component framework has been divided into segments of 1 unit each. The numbers in each represent the mean number of nests per plot for the plots within each segment.

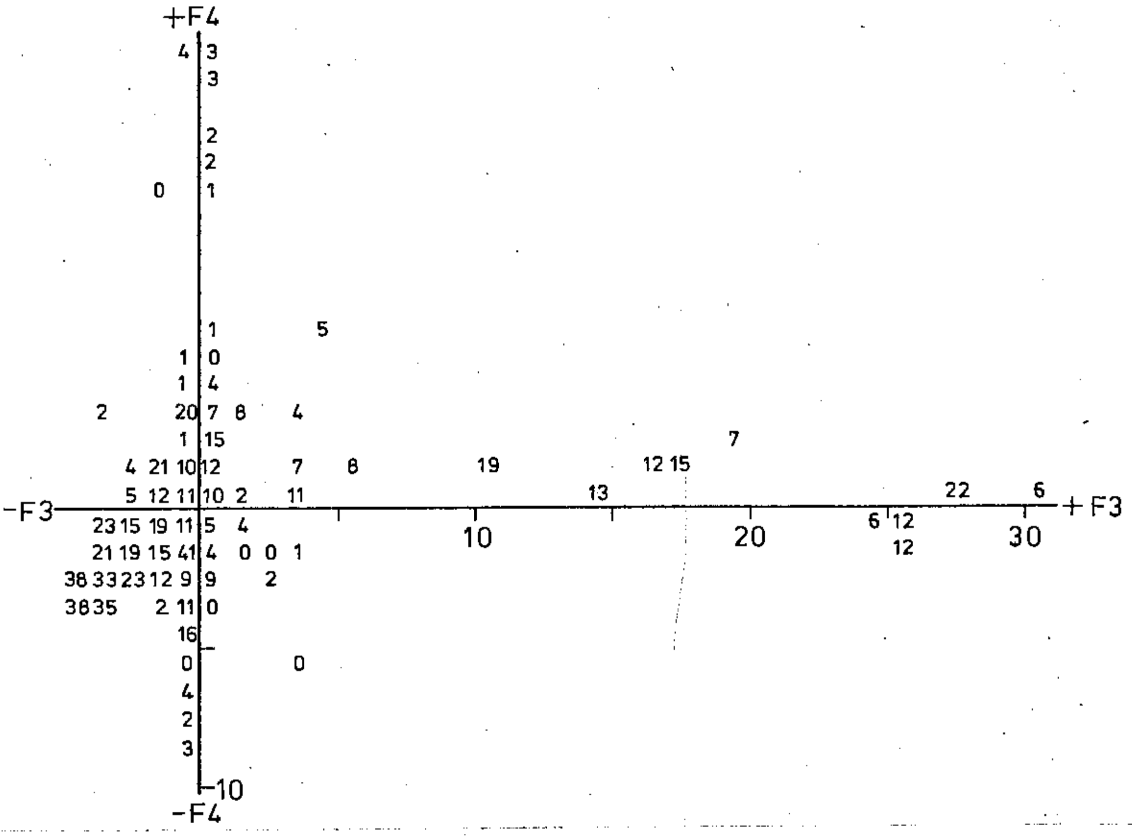


Fig. 2.4.6 Distribution of diggings on 236 plots within component framework derived by PCA, varimax loadings, 64 vegetation species (See Fig. 2.4.2), components 3 and 4. The component framework has been divided into segments of 1 unit each. The numbers in each represents the mean number of diggings per plot for the plots within each segment.

2.4.2 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.

(i) The use of 'indicator' species - thirty-three of the species used in the analysis occur in the area covered by Havel's (1975a) 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 Figures 2.4.9 and 2.4.10. Varimax loadings were used since they show the relationship between the components and vegetation species better than normal loadings (Havel, 1975a).

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

-F1 Leucopogon capitellatus, Eucalyptus marginata, Hakea lissocarpha, Leucopogon verticillatus, Macrozamia riedlei - species occurring on well drained upper slopes with deep sandy gravelly loams (Photo 2.4.2).

+F1 Drosera bulbosa, Acacia cyanophylla, Hakea prostrata, Hypocalymma angustifolium, Melaleuca preissii - species typically associated with broad, flat, seasonally swampy drainage lines (Photo 2.4.3).

-F2 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 (Photo 2.4.4).

+F2 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 (Photo 2.4.5).

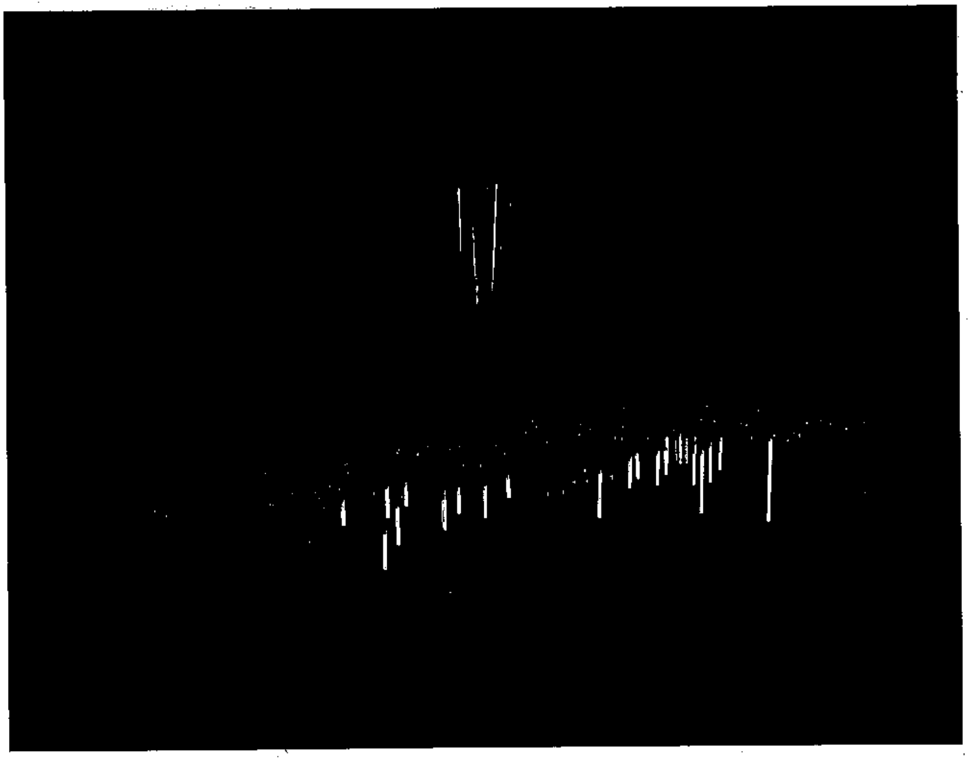


Photo 2.4.1. Four-dimensional model of ecological relationships in the study area. Each coloured stick represents an ecological sample plot. The arrangement of components derived by P.C.A. is as follows.

Left to Right –F1 to +F1, Front to back –F2 to +F2.
Up +F4, Down –F4.

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

White sticks - tammar present.
Red sticks - 15+ woylie nests/transect.
Yellow sticks - 10-14 woylie nests/transect.
Blue sticks - 1 - 9 woylie nests/transect.
Green sticks - nil woylie nests/transect.

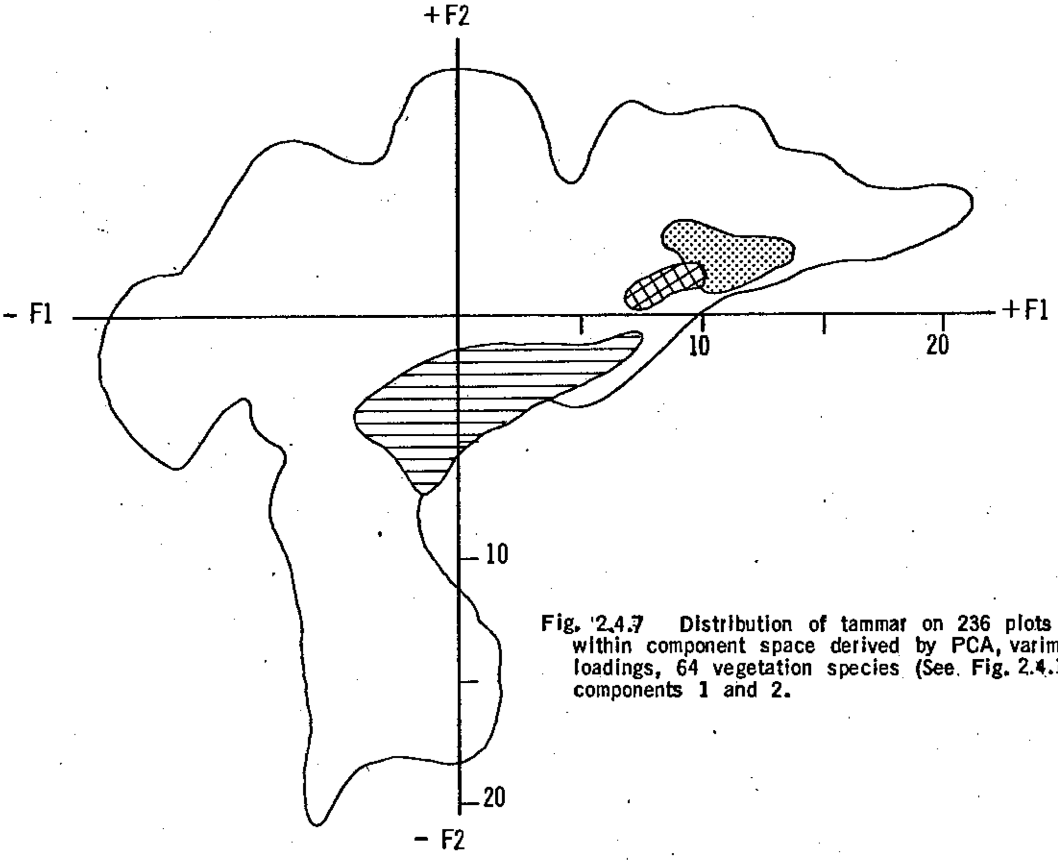


Fig. 2.4.7 Distribution of tammar on 236 plots within component space derived by PCA, varimax loadings, 64 vegetation species (See Fig. 2.4.1), components 1 and 2.

LEGEND

▤ 25 - 35 % capture

▦ 15 - 24

░ 1 - 14

☐ 0

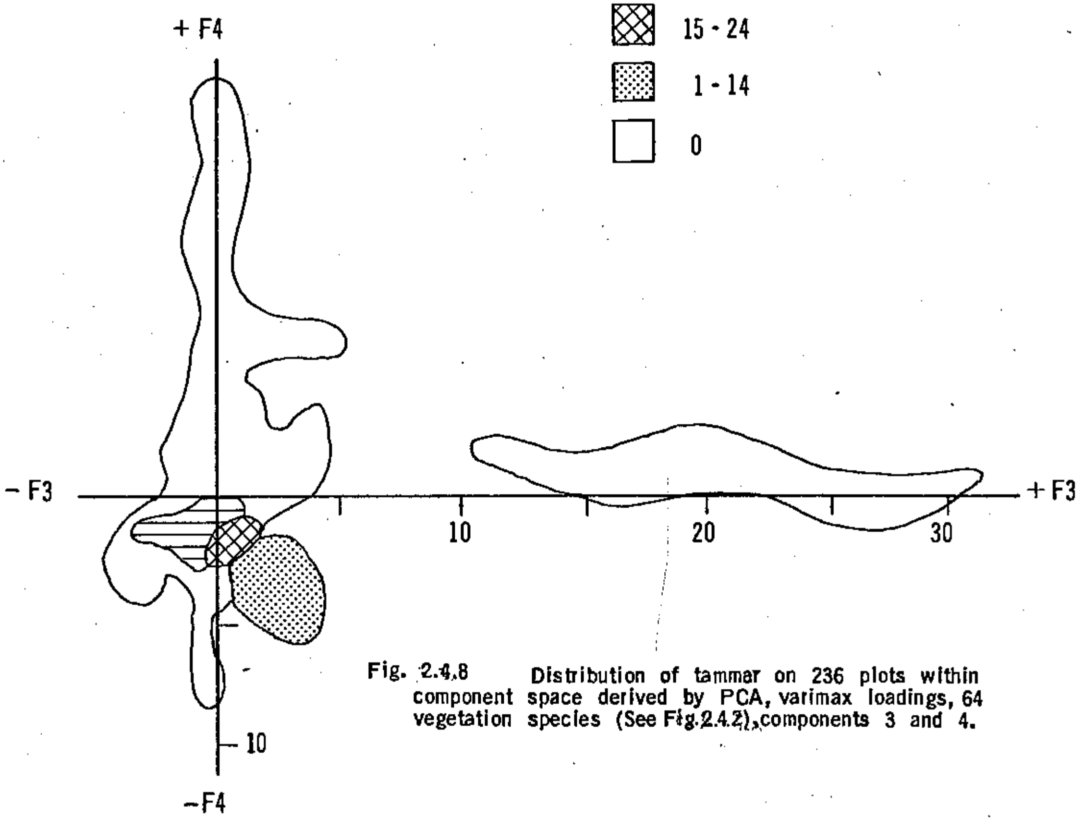


Fig. 2.4.8 Distribution of tammar on 236 plots within component space derived by PCA, varimax loadings, 64 vegetation species (See Fig.2.4.2), components 3 and 4.

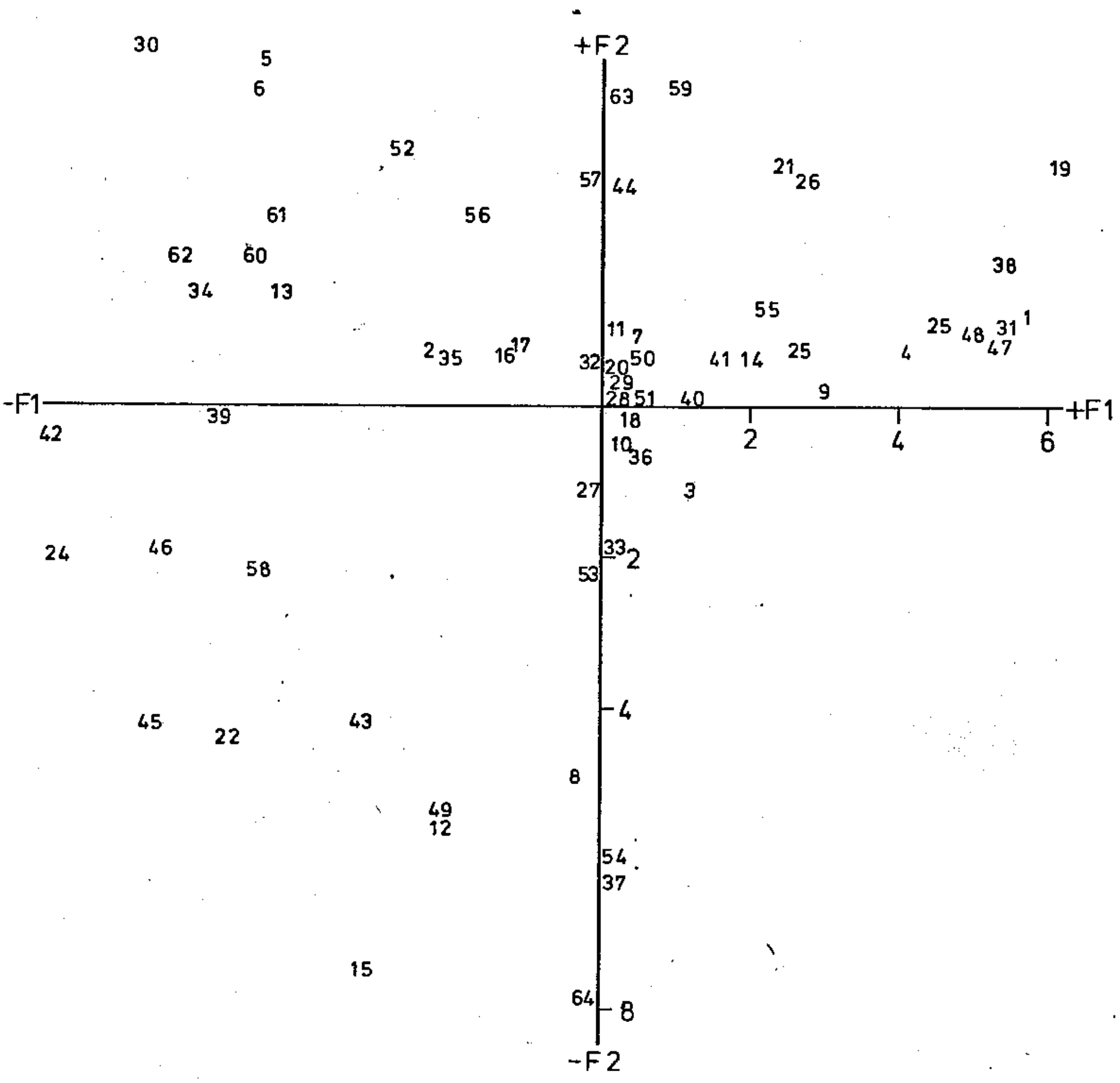


Fig. 2.4.9. Distribution of 64 individual plant species within component space derived by PCA.

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 PREISSII
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

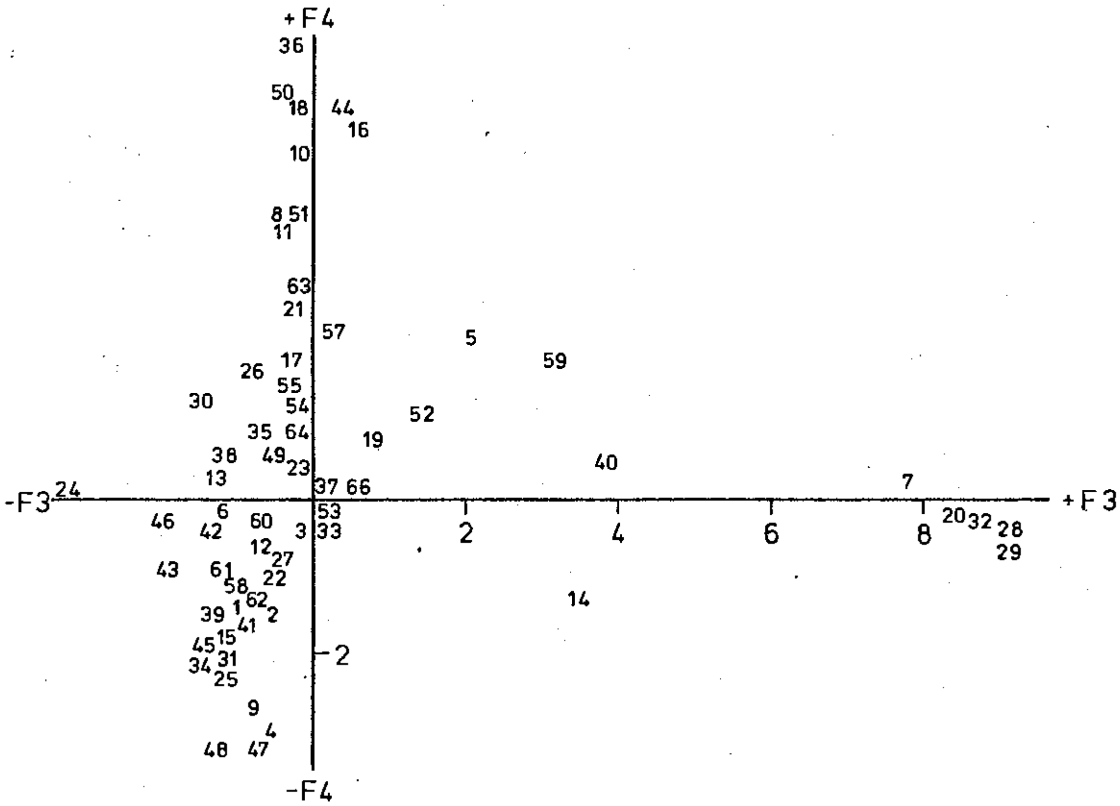


Fig. 2.4.10 Distribution of 64 individual plant species (See Fig. 2.4.9) within component space derived by PCA.

-F3	*Eucalyptus marginata*, *Macrozamia riedlei*, *Leucopogon propinquus*, *Hakea lissocarpha*, *Leucopogon verticillatus* - species commonly occurring on deep soils, very similar to -F1.
+F3	*Gastrolobium spinosum*, *Hakea incrassata*, *Hakea undulata*, *Dryandra armata*, *Baeckea camphorosmae* - species common on soils too shallow for tree growth and often overlying massive granite (Photo 2.4.6).
-F4	*Melaleuca preissii*, *Melaleuca viminea*, *Astartea fascicularis*, *Banksia littoralis*, *Eucalyptus rudis* - species occurring on moist to wet sites in depressions (Photo 2.4.7).
+F4	*Hibbertia quadricolor*, *Petrophile serruriae*, *Dillwynia cinerascens*, *Leucopogon pulchellus*, *Conostylis setigera*, *Banksia sphaerocarpa* - species occurring on dry upland sites in the eastern sector, which is subject to drought (Photo 2.4.8).

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 program (Havel, 1975a). The pattern of distribution of each of the 64 species used was thus examined and the results confirmed the conclusions reached above.

(ii) Plotting of soil data within the component space

Although a fairly detailed soil analysis was carried out on 16 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. 2.4.11). There is a tendency towards a high fine sand content in the soils on sites towards the -ive end of the F1 axis, the area with the highest woylie density. Other data relating to soil structure and composition, clay content, coarse sand and so on showed no correlation with woylie distribution.

Similarly, definite associations with soil fertility factors, phosphate content, cation exchange capacity, nitrogen content and so on were difficult to detect. The best correlation, total phosphate, is shown in Figure 2.4.12. There is a general trend towards higher phosphate levels towards the -ive end of the F1 axis. Although the wandoo sites do not conform, they correlate with woylie distribution (Figs. 2.4.3 and 2.4.4).

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

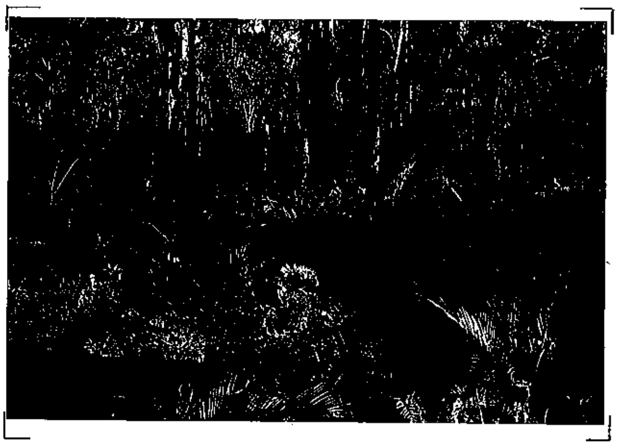


Photo 2.4.2. Extremity −F1 axis; deep sandy gravels on well-drained upper slope.

Photo 2.4.3. Extremity +F1 axis; broad flat seasonally-wet drainage line.

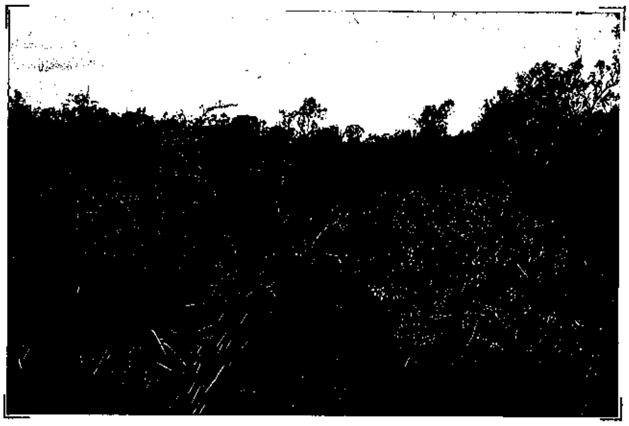


Photo 2.4.4. Extremity −F2 axis; well-drained fertile upper slopes in high rainfall western sector.

Photo 2.4.5. Extremity +F2 axis; poor infertile site in the low rainfall eastern sector.

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

Photo 2.4.6. Extremity +F3 axis; soils too shallow for tree growth overlying massive granite.

Photo 2.4.7. Extremity -F4 axis; moist wet site in a depression.

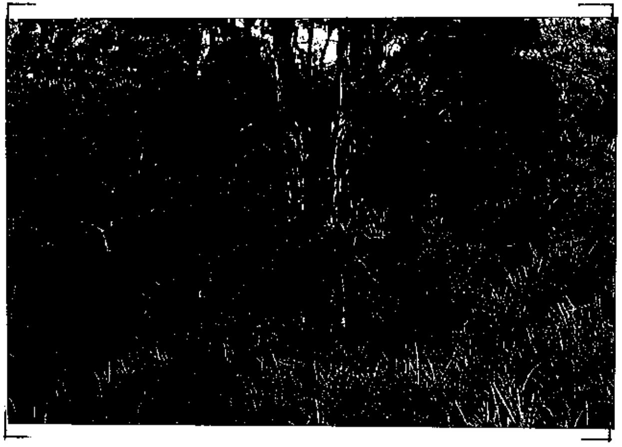


Photo 2.4.8. Extremity +F4 axis; dry upland site in eastern sector subject to drought.

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It was not possible to identify factors 3 and 4 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.

F1- 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.

F2- 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 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.

F3- 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.

F4- A drought factor - plots on drought-prone eastern sites are separated from moist valley sites with deep soils not subject to seasonal drought.

2.4.3 Correlation of individual variables with woylie and tammar occurrence

(a) 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 0-60 cm ($r = +0.347$) and between nests and bare ground ($r = +0.283$). The correlation coefficients are not high, but they are significant at the 0.001 level. These two factors show a high negative correlation with one another: $r = -0.787$ in the wide-scale survey and $r = -0.831$ in the Boyicup survey. When plotted within the component space on F1 and F2 (Fig. 2.4.13), ground cover density (scrub density 0-60 cm/bare ground) forms a pattern very similar to the woylie nest distribution (Fig. 2.4.3). The highest nest densities occur in areas with a scrub density of more than 50% at 0-60 cm and bare ground of 20-40%. Dense cover is a

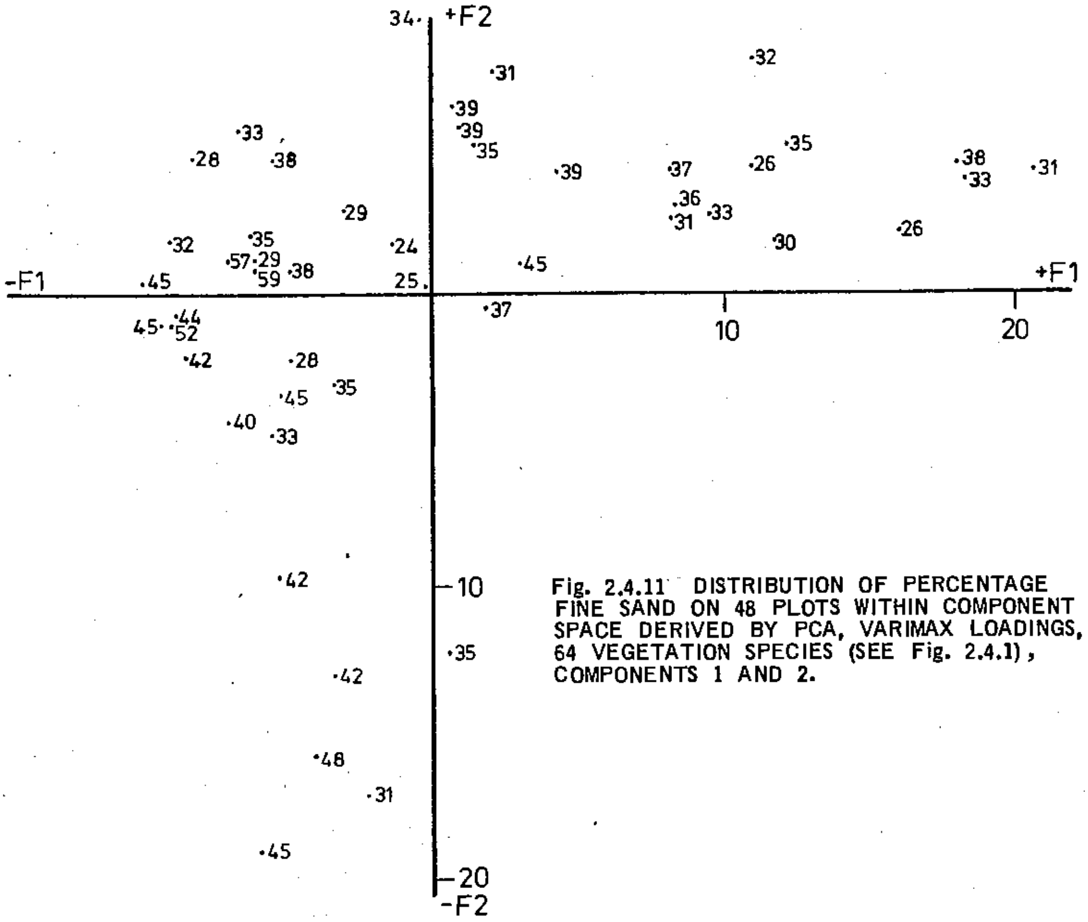

Fig. 2.4.11 DISTRIBUTION OF PERCENTAGE FINE SAND ON 48 PLOTS WITHIN COMPONENT SPACE DERIVED BY PCA, VARIMAX LOADINGS, 64 VEGETATION SPECIES (SEE Fig. 2.4.1), COMPONENTS 1 AND 2.

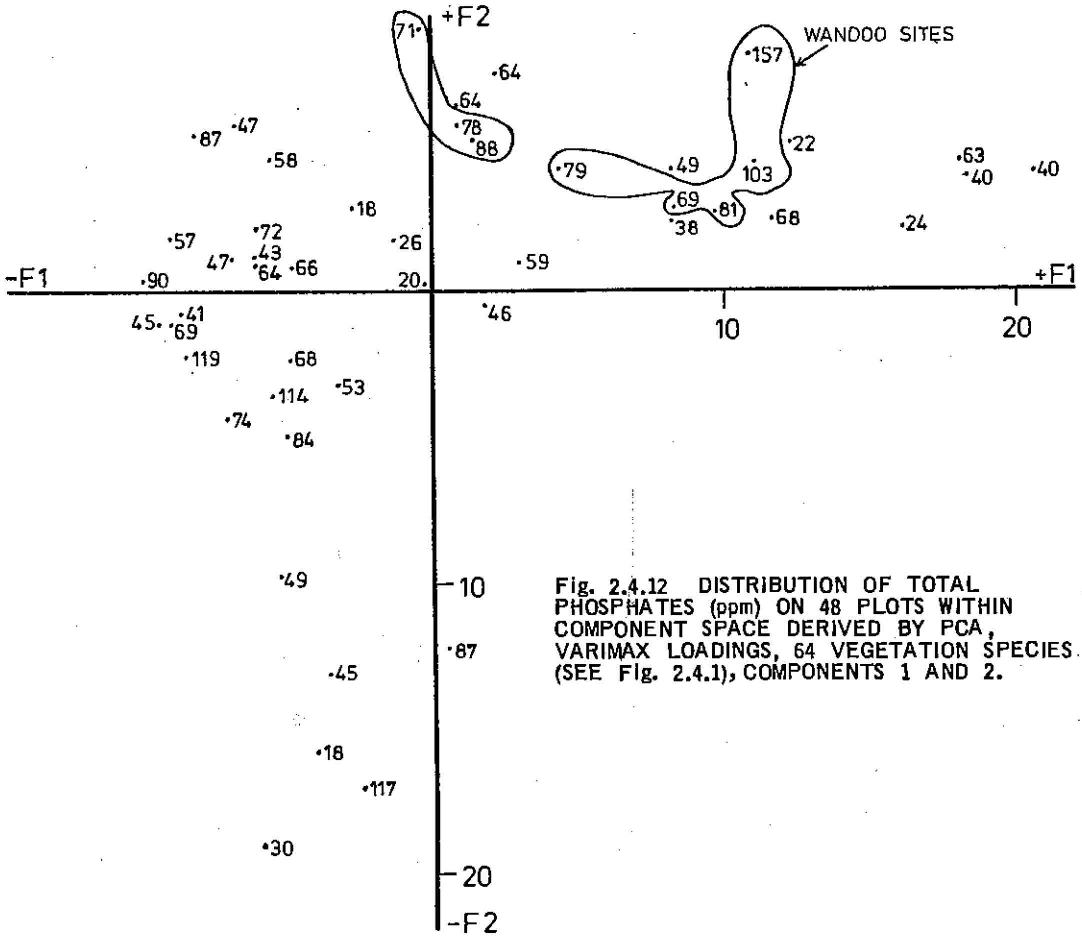

Fig. 2.4.12 DISTRIBUTION OF TOTAL PHOSPHATES (ppm) ON 48 PLOTS WITHIN COMPONENT SPACE DERIVED BY PCA, VARIMAX LOADINGS, 64 VEGETATION SPECIES (SEE Fig. 2.4.1), COMPONENTS 1 AND 2.

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 = +0.490), Leptomeria cunninghamii (r = +0.322) and Hibbertia cunninghamii (r = +0.322). These species all have moderately high -ive correlations with soil type and moderately high +ive correlations with stoniness, showing that they prefer sandy gravels. High -ive correlation with diggings are shown by Persoonia longifolia (r = -0.381) and Pteridium esculentum (r = -0.310), both on the heavier soils in the western sector. Diggings also show weaker -ive correlations with Banksia grandis and Drosera bulbosa, species which are typical of massive lateritic ridges and of seasonally wet gullies and depressions with coarse sandy soils respectively.

There is no correlation with time since fire, nor with either diggings or nest numbers.

(b) The tammar

The scrub density at 120 cm+ (mean of 120-240 and 240 cm+) plotted with percentage bare area within the component space on F1 and F2 (Fig. 2.4.14) shows a correlation with tammar distribution (Fig. 2.4.7). Tammar distribution is limited to those areas with 21-50% overhead scrub cover and with 80-100% 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.

2.5 Characteristics of woylie and tammar sites

2.5.1 The woylie

Woylies occur on quite distinct site types characterized by specific plant species and centred on a specific area within the component space (Photo 2.4.1). 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.

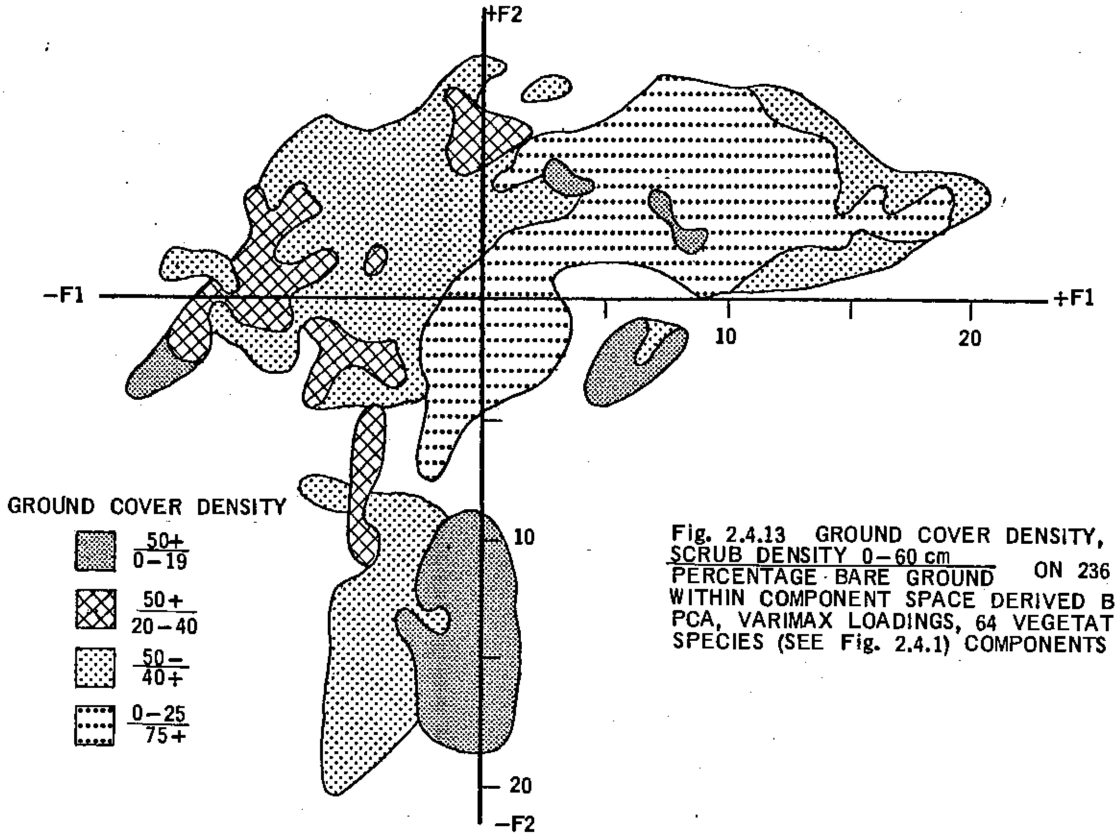

Fig. 2.4.13 GROUND COVER DENSITY, $= \frac{\text{SCRUB DENSITY 0−60 cm}}{\text{PERCENTAGE BARE GROUND}}$ ON 236 PLOTS WITHIN COMPONENT SPACE DERIVED BY PCA, VARIMAX LOADINGS, 64 VEGETATION SPECIES (SEE Fig. 2.4.1) COMPONENTS 1 AND 2

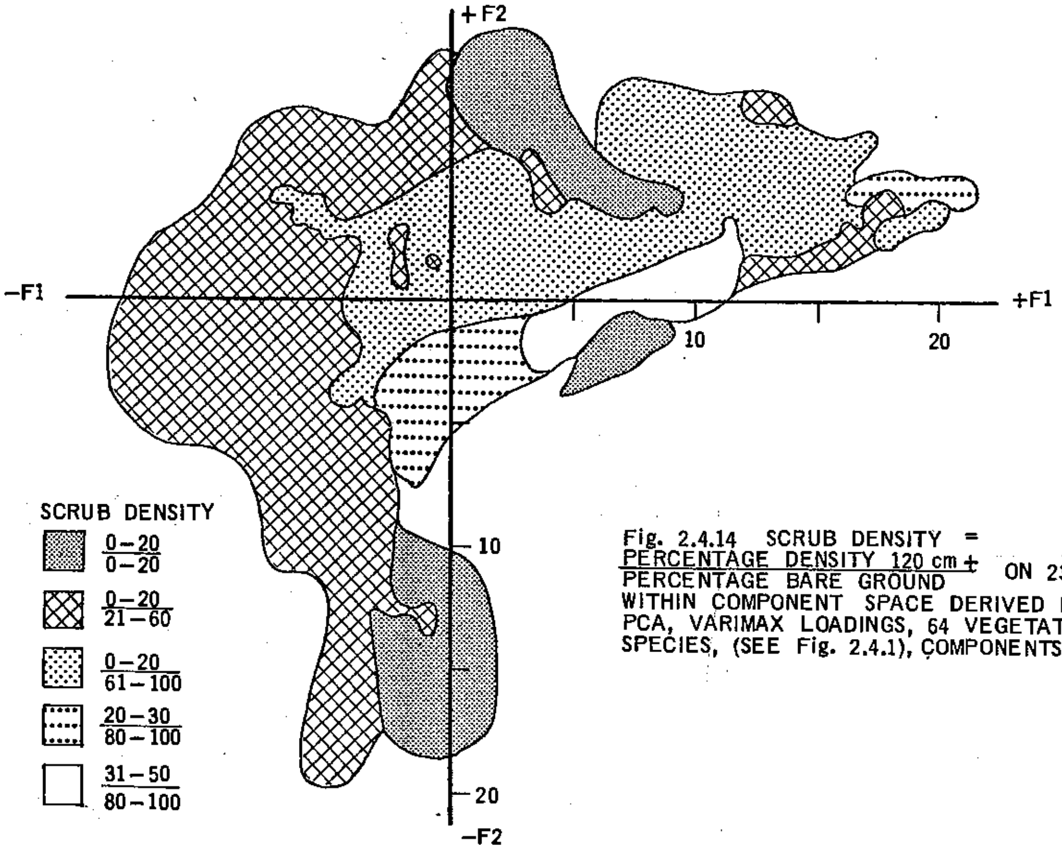

Fig. 2.4.14 SCRUB DENSITY $= \frac{\text{PERCENTAGE DENSITY 120 cm +}}{\text{PERCENTAGE BARE GROUND}}$ ON 236 PLOTS WITHIN COMPONENT SPACE DERIVED BY PCA, VARIMAX LOADINGS, 64 VEGETATION SPECIES, (SEE Fig. 2.4.1), COMPONENTS 1 AND 2.

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 rather 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.

Scrub density, more particularly the percentage of bare ground, appears to be of importance. 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% together with 20-40% bare ground in the vicinity of nesting areas, may represent an ideal density required for efficient escape from predators (Photo 2.5.1).

There is no evidence that fire is a limiting factor in the study area. Foxes are an important predator in the area (see 3.8), but the woylie still survives*. It would appear that edaphic factors and scrub cover are prime factors contributing to the present distribution of the woylie.

2.5.2 The tammar

The tammar occupies very distinct site types characterized by a few specific plant species. These sites are centred in a very restricted area within the component space (Photo 2.4.1).

Prime sites occur in close proximity to woylie areas but extend considerably further towards the moister +ive end of the F1 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% cover, and with 80-100% bare ground beneath, are a prime requirement. Overhead protection may be essential to a social species living in groups, whilst 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

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* See 5 - General discussion

(Vulpes Vulpes) are both major predators of the tammar (see 3.8).

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' (Photo 2.5.2). Grasses are a major food item of the tammar (see 4.5). 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 (Photo 4.6.1) and the grass persists as a dry food source throughout the summer months.

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 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 would appear that soils and vegetation, rather than predation*, are the prime factors contributing to the current distribution of the tammar.

2.6 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 5- to 7-year cycle. Although the mozaic effect (Christensen and Kimber, 1975) contributes to the variety, it is rare to find areas of unburnt understorey over the age of 25 years. But it is possible that fire more frequent than every 5 to 7 years or less frequent than every 25 years may have a significant effect on the distribution of the study species.

2.6.1 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 Gastrolobium calcycinum, are short-lived, hard-seeded species which require hot fires for germination (Fig. 2.6.1). In the prolonged absence of fire such species disappear. Similarly, too frequent mild fires do

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*See 5 - General discussion

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Photo 2.5.1. Typical woylie nesting area. Fairly dense understorey of B. ornata with 20 to 40 % bare ground.

Photo 2.5.2. Typical heartleaf "tammar thicket", a closed canopy but open at ground level. Note the well grazed grassy understorey.

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.

2.6.2 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 *Acacia pulchella*, a known 'fire-weed' species, in its response to heat treatment (Fig. 2.6.1). A hot fire is also essential for optimum growth and survival (Table 2.6.2 and Photo 2.6.2). 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 20-25 years. The high percentage of bare ground underneath, contributed to by the tammar's own activities, reduces the fire risk to almost neglible proportions. Only under exceptional conditions of extreme winds and high temperatures will they burn (Photo 2.6.3). After the age of about 20 years they start to degenerate and collapse (Photo 2.6.4), 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 (Table 2.6.2). Frequent cool grass fires would eliminate the thicket-forming species and encourage the grasses. Grazing by tammars and the kangaroo (*Macropus fuliginosus*) helps reduce the grass fire hazard during the first few critical years after fire (Photo 4.6.1).

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.

Fig. 2.6.1 LABORATORY SEED GERMINATION TRIALS (50 SEED PER TREATMENT) SHOWING THE EFFECTS OF VARIOUS HEAT TREATMENTS ON GERMINATION.

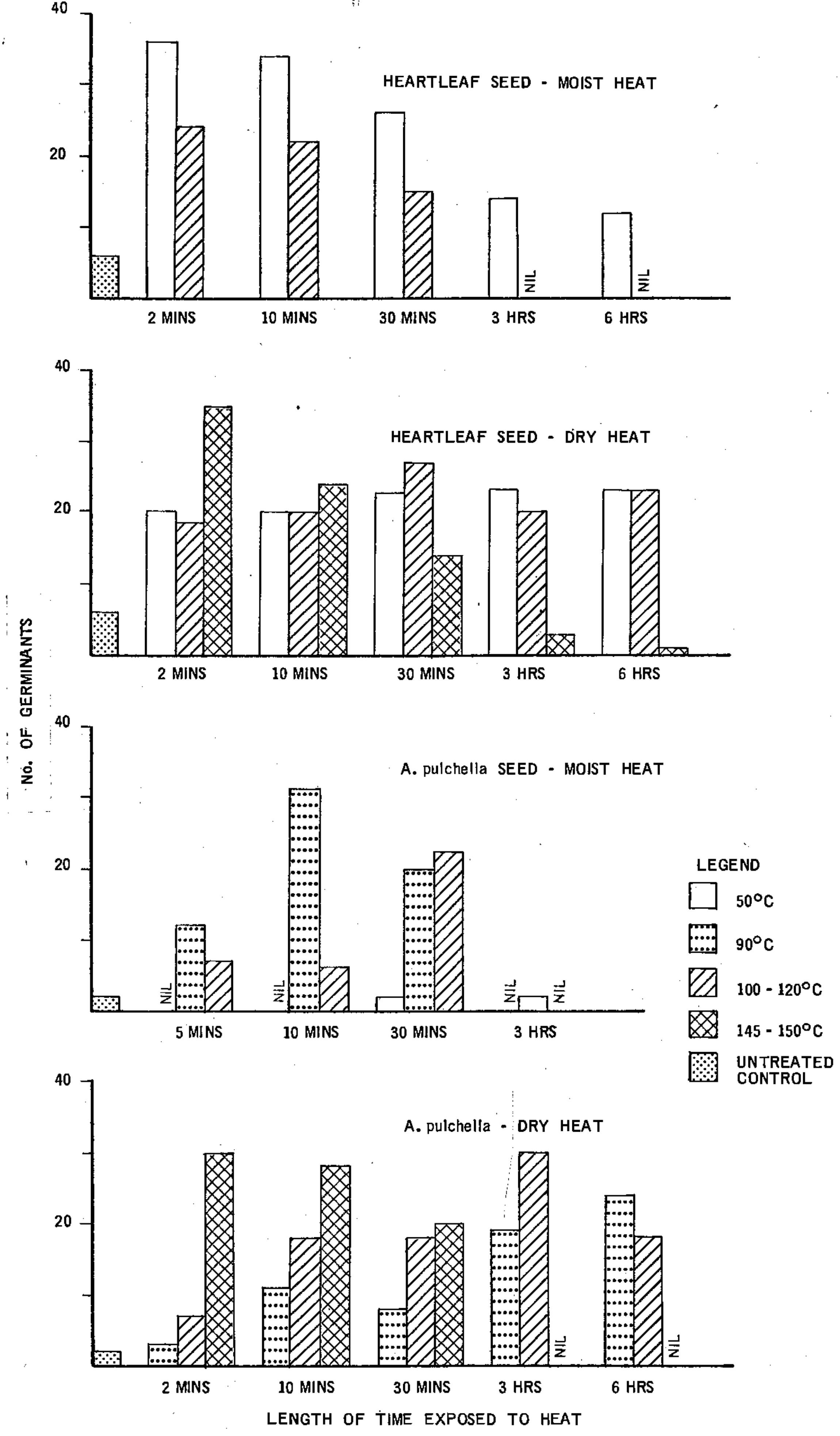


TABLE 2.6.2

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	
Seedlings 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 m^2 quadrats

* Students t test

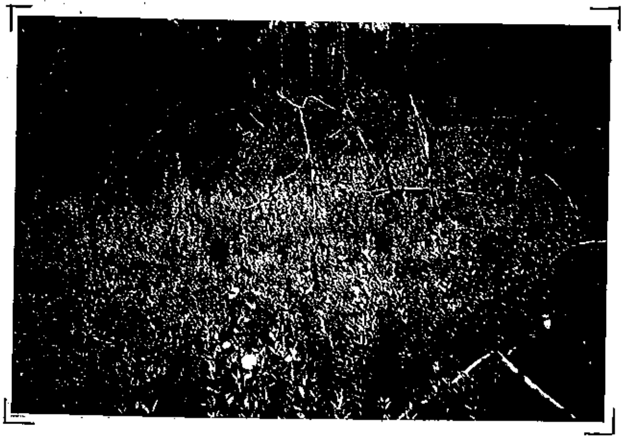


Photo 2.6.2. Vigorous heartleaf seedlings forming a dense thicket on ashbed created following a hot fire.

Photo 2.6.3. Within minutes of ignition under hot dry conditions, flames leap from <u>Melaleuca viminea</u> thicket fanned by strong winds.

Photo 2.6.4. Heartleaf thicket 15 to 20 years old in early stages of "degeneration". Note the large numbers of dead and collapsing bushes.

3. POPULATION STUDIES

3.1 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, (e.g. 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 therefore may 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.

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

3.2 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 (Fig. 2.3.2). 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 (Photo 2.5.1) and the latter by site R (Photo 2.5.2) in the wide-scale survey (Appendix 1). The major understorey communities are shown in Figure 3.2.1.

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 5- to 7-year basis since 1955. This has resulted in a mozaic pattern of different ages of understorey scrub (Fig. 3.2.2). Such a pattern is a natural consequence of frequent fires, but the network of logging tracks has accentuated it.

3.3 Methods

Two separate experimental burns were carried out.

(i) The 1975 burn - designed to test the second hypothesis, 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 large unburnt patches within the burnt area itself.

(ii) The 1976 burn - designed to test the third hypothesis, 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 (Photo 3.3.1) 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 3), and joeys were weighed, measured and tagged when possible.

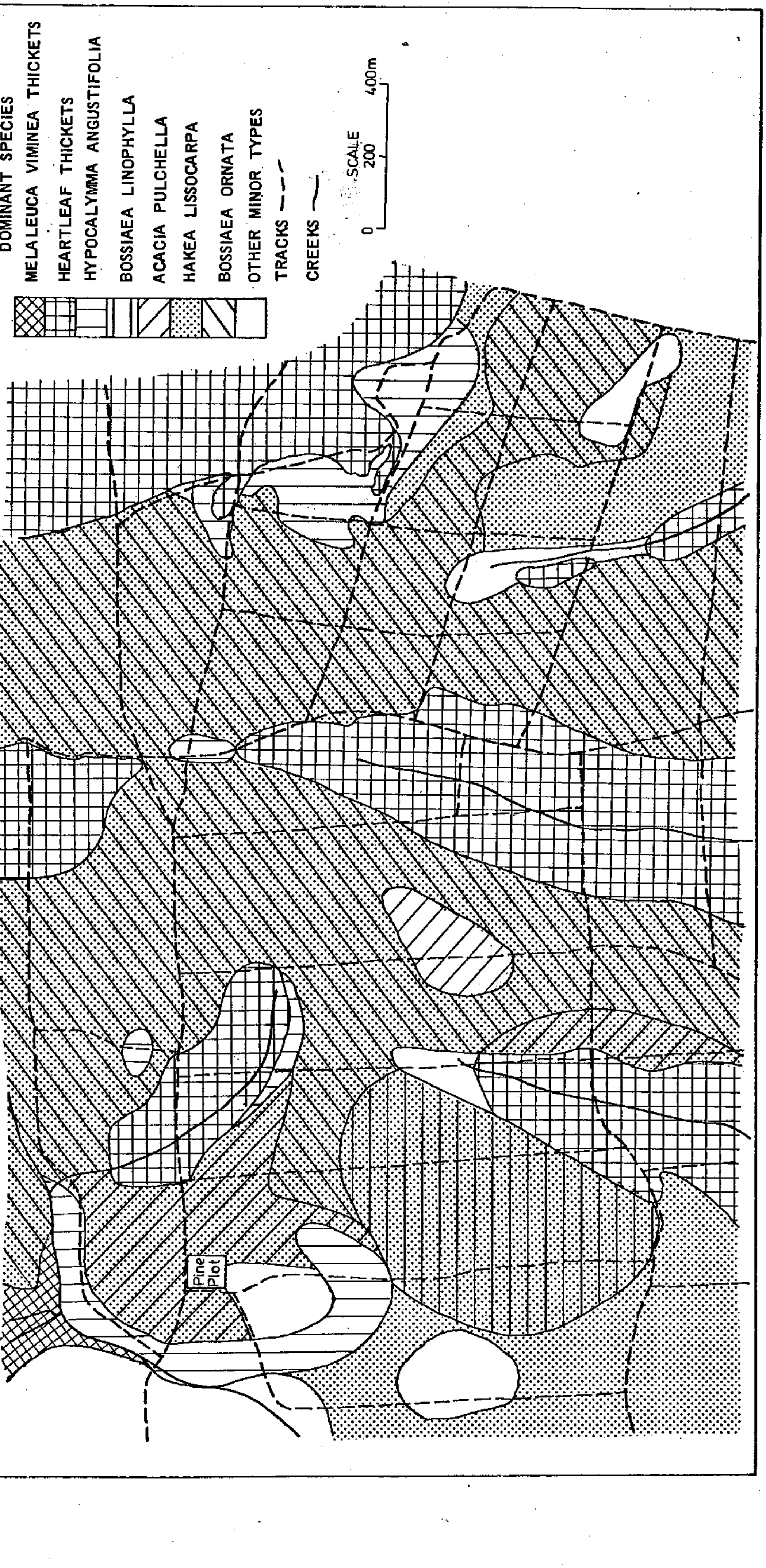
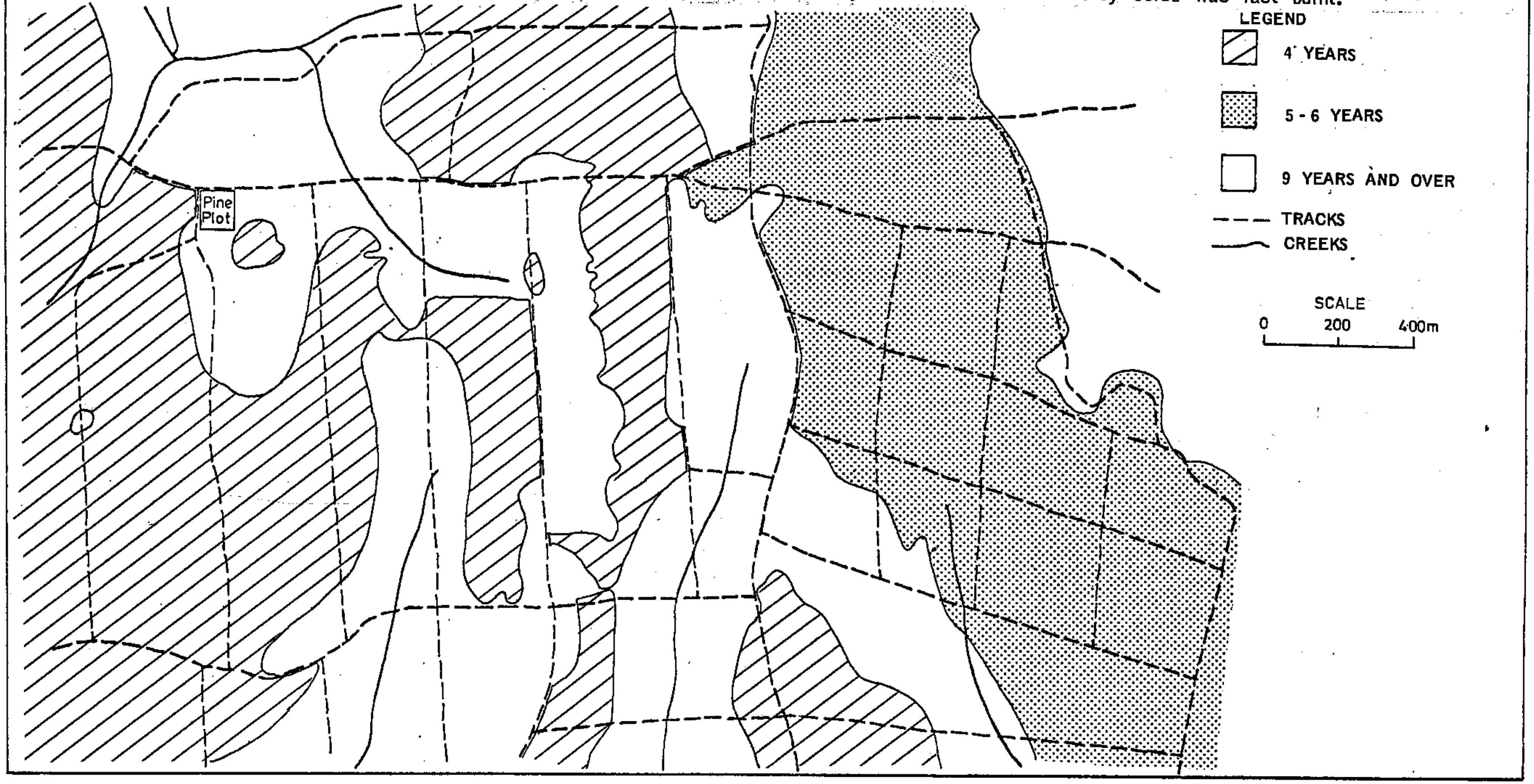


Fig. 3.2.1 BOYICUP TRAPPING AREA - DISTRIBUTION OF MAJOR UNDERSTOREY SCRUB COMMUNITIES.

Fig. 3.2.2 BOYICUP TRAPPING AREA - Burn age map, showing the number of years since the understorey scrub was last burnt.



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 hand-held yagi antenna (Photo 3.3.2). AVM transmitters were attached to the animals by means of a collar, (Photo 3.3.3, and AVM publication).

Radio-tracked animals were located by means of triangulation both during the day and at night. The trapping grid (Fig. 3.3.1) 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 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 15-20 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 is recorded continuously (Photo 3.3.4) whilst the animal is within range of the recorder (approximately 200-250m).

3.3.1 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 (Fig. 3.3.1).

The tammar was trapped on a separate grid of 39 permanently located funnel traps in heartleaf thickets in two adjacent valleys (Fig. 3.3.1).

3.3.2 The 1976 burn

An area of 190 ha adjacent and to the east of the burn was

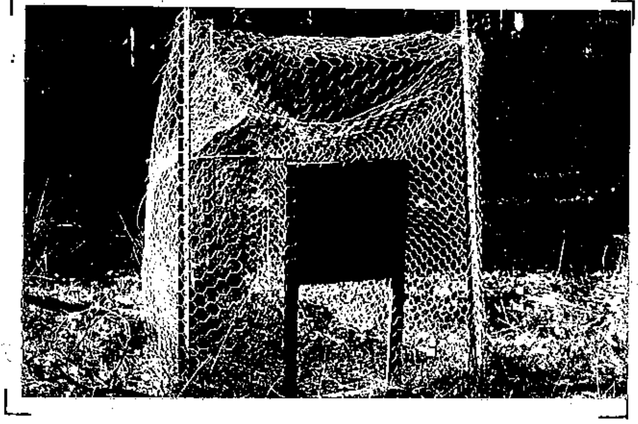
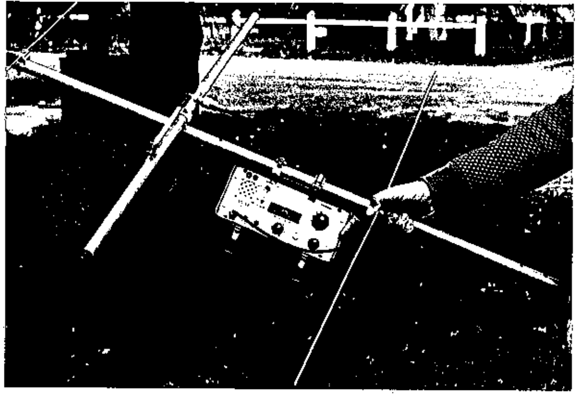


Photo 3.3.1. Funnel trap. The hanging wire trip mechanism is barely visible at the rear of the enclosure.

Photo 3.3.2. A V M Receiver with hand held yagi directional antenna.



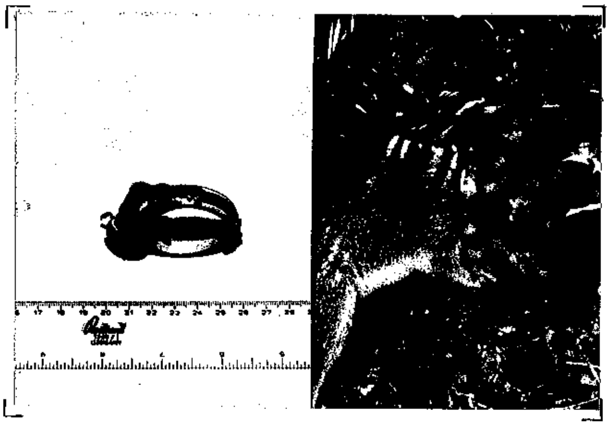
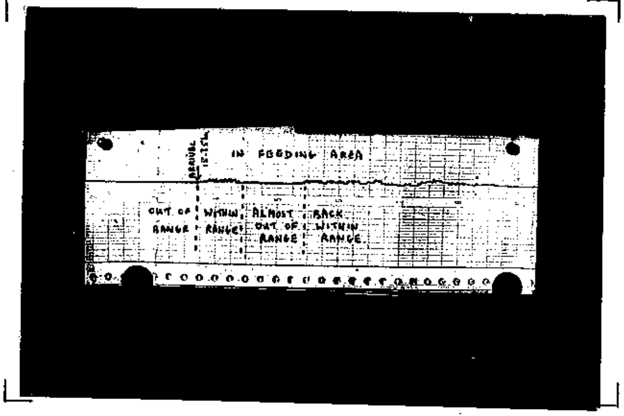


Photo 3.3.3. A V M collar type transmitter showing size and attachment to woylie.

Photo 3.3.4. Typical trace on Rustrak recorder showing transmitter animal within and out of range of the recorder.



selected for this study. The western portion was set aside for burning whilst the eastern sector served as an unburnt control area (Fig. 3.3.2). Thirty-six permanently located funnel traps on a 400 x 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 (Table 3.4.2). 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. In order to also obtain information on the distance from which transported woylies will return to their home range areas, individuals were released at distances varying between 2500 m 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 18 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 prior to, 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.

3.3.3 Data analysis and presentation

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

(i) 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 in 1975.

(ii) Woylie captures in the funnel traps set for the tammar were exceedingly high (Table 3.4.1). 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).

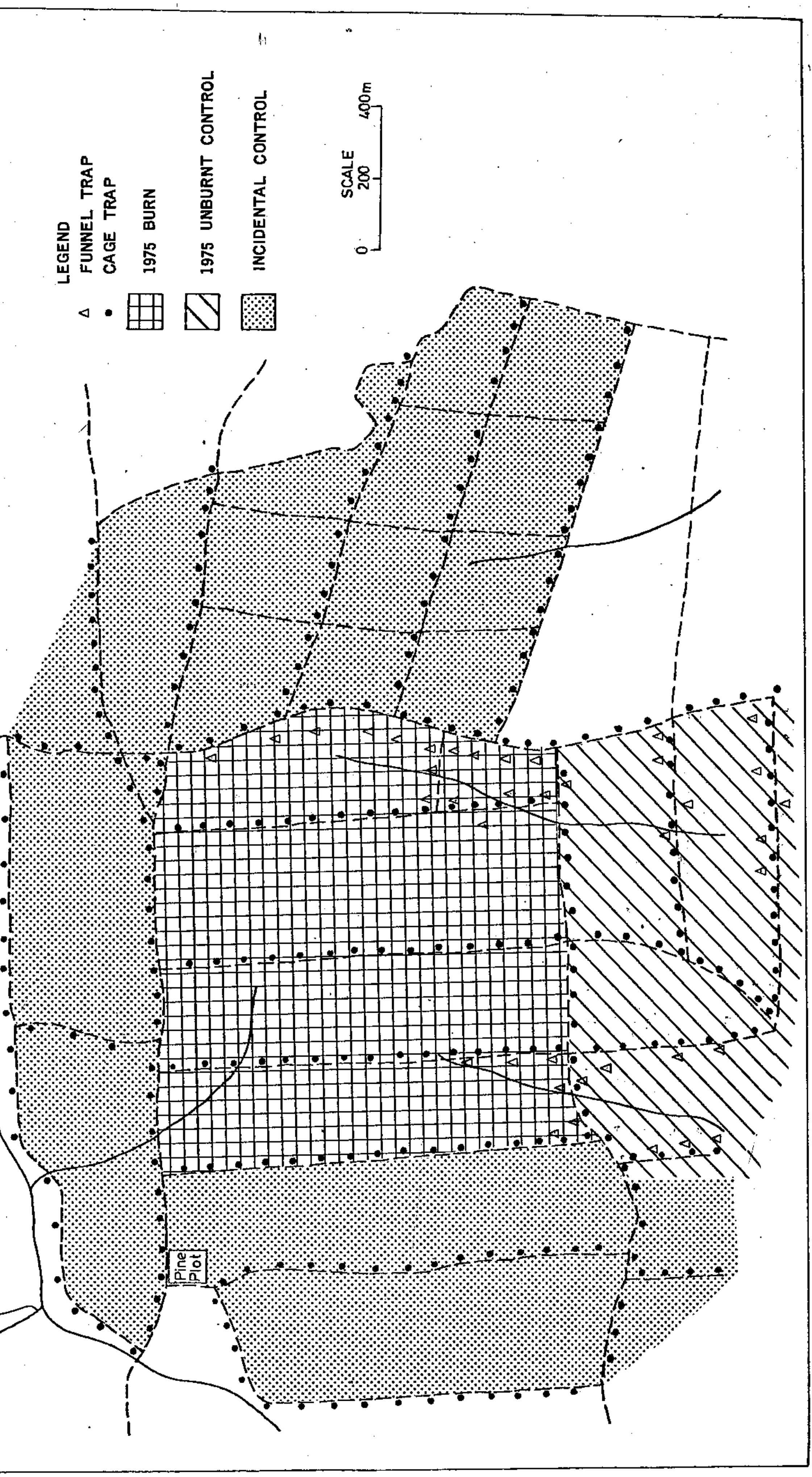
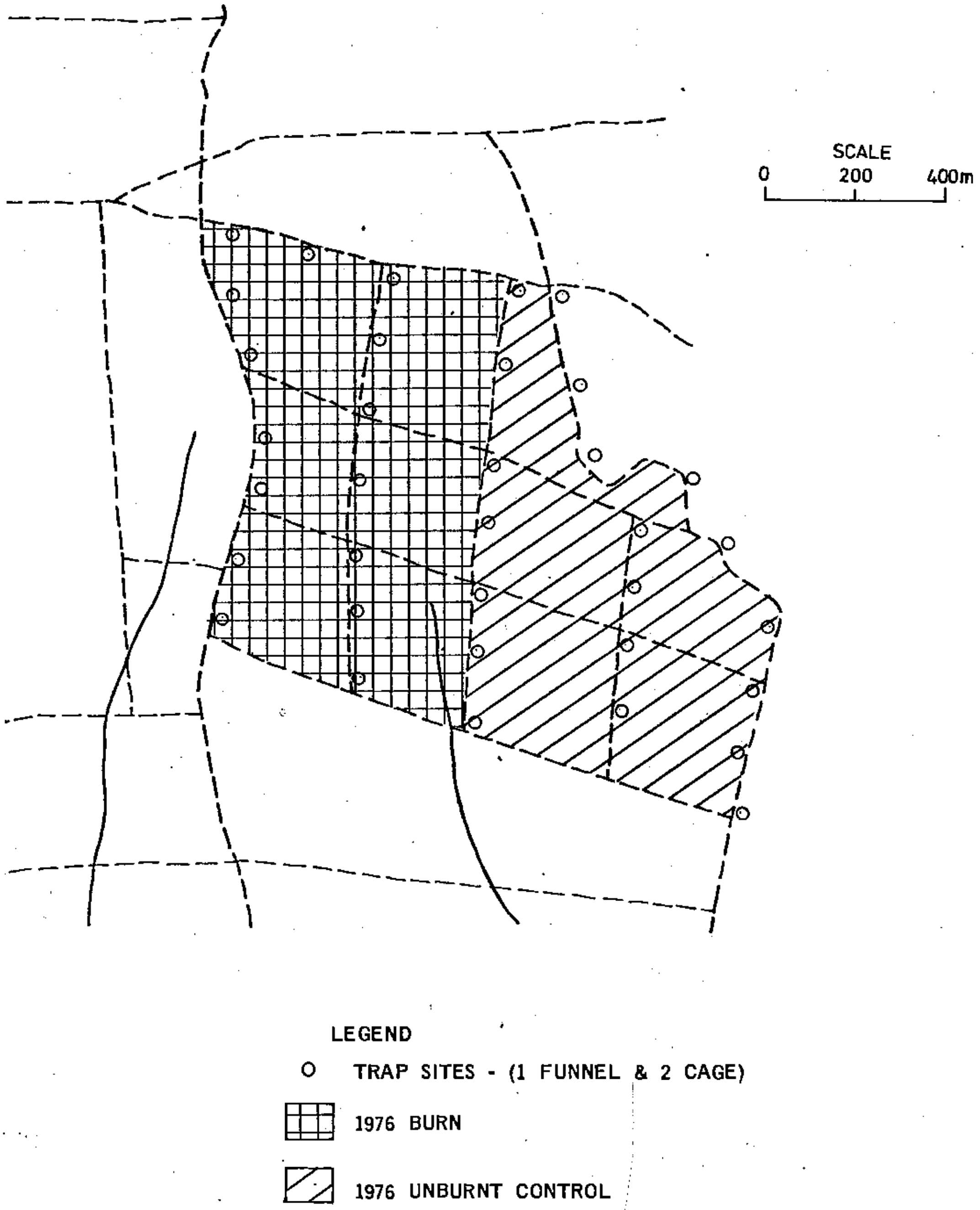


Fig. 3.3.1 BOYICUP TRAPPING AREA - TRAPPING SEQUENCE AND TRAP POSITIONS, 1975 BURN AREA.

Fig. 3.3.2 BOYICUP TRAPPING AREA - TRAP LAYOUT, 1976 BURN AREA.



(iii) 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 is no great advantage in keeping them separate.

3.4 The pre-burn population - the woylie

A summary of trapping results over the three-year period of the study is presented in Table 3.4.1.

3.4.1 Ageing the population

Details of the methods used are presented in Appendix 3.

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

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

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

(iii) 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.

(iv) 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.

3.4.2 Population analysis

(a) Population structure

Mean capture percentages by trap types for the entire duration of the study are given in Table 3.4.2. Funnel trap percentage captures are consistently higher than those of the cage traps. This is believed to be because the woylies are less reluctant to enter the

TABLE 3.4.1

Summary of trapping

	Woylie	Tammar	Quenda	Brushtailed 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	4 725	1 808
	Funnel	1 423	1 053
% Capture - Woylie	- Cage	7.17	6.64
	- Funnel	15.81	17.66
% Capture - Tammar	- Funnel	18.41	5.60

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

TABLE 3.4.2

The woylie -
Comparison of pre- and post-burn capture percentages

3.4.2 (a)

Treatment	Trap type	1975 Burn					
		Pre-burn			Post-burn		
		C	T/N	%	C	T/N	%
Control	Cage	79	861	9.18	61	901	6.77
	Funnel	18	130	13.85	67	331	20.24
Burn	Cage	90	1450	6.21	109	1603	6.80
	Funnel	79	551	14.34	61	401	15.21

3.4.2 (b)

Treatment	Trap type	1976 Burn					
		Pre-burn			Post-burn		
		C	T/N	%	C	T/N	%
Control	Cage	28	378	7.41	5	336	1.49
	Funnel	58	252	23.02	14	168	8.33
Burn	Cage	68	610	11.15	19	484	3.93
	Funnel	73	391	18.67	41	242	16.94

C = Captures

T/N = Trap nights

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. 3.4.1). A chi-square test comparison of pre-fire individual numbers of males and females reveals that this is due to a higher re-capture rate of males and that there is no significant difference in numbers of individuals.

Pre-fire captures and re-captures of adults were consistently higher than those of non-adults in both the 1975 and the 1976 burn areas (Fig. 3.4.2). Chi-square tests on comparisons of the actual numbers of adults and non-adults reveal 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 due to the effect of the adjacent 1975 burn and also to the removals. Both treatments resulted in increased numbers of young males (see 3.6.3).

After the first few trap sessions, when most of the resident woylies had been tagged, new captures tended to be non-adult animals (**Figs. 3.4.3 and 3.4.4**). This indicates that there is little immigration of adult animals.

(b) 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, on the burn edge and on the burn area (Table 3.4.3). 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 are included, and the age of animals when first caught was not known. Furthermore, loss may be due not to death but to emigration. However, the study revealed that very little adult movement occurred, and loss in most cases could be attributed to death.

Females appear to survive slightly longer than males on the control and burn area, but the position is reversed on the edge. None of these differences are significant, however. Surprisingly, there is

Fig. 3.4.1 THE WOYLIE-COMPARISON OF TOTAL MALE AND FEMALE CAPTURES AND RECAPTURES.

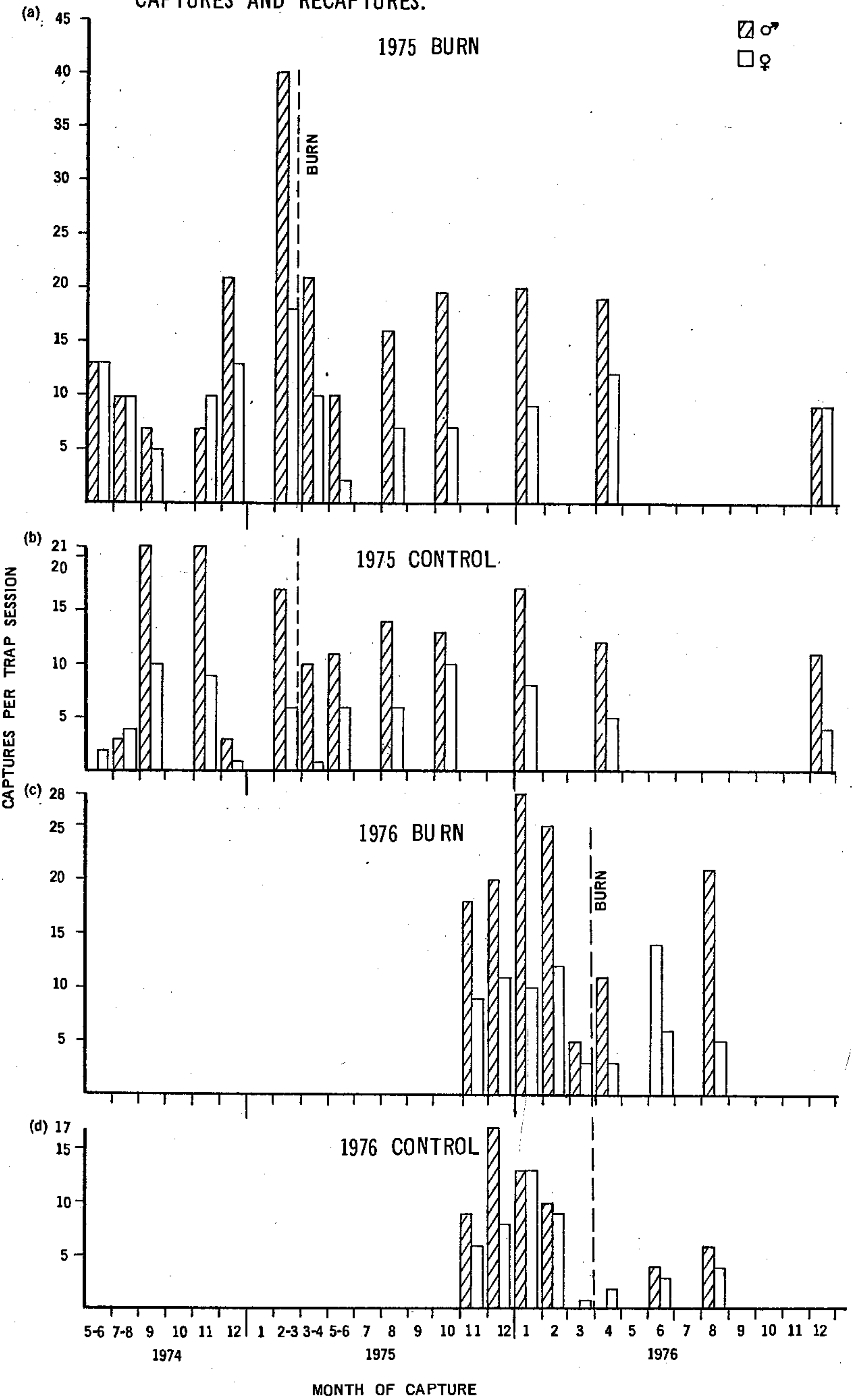


Fig. 3.4.2 THE WOYLIE - COMPARISON OF ADULT AND NON-ADULT CAPTURES AND RECAPTURES.

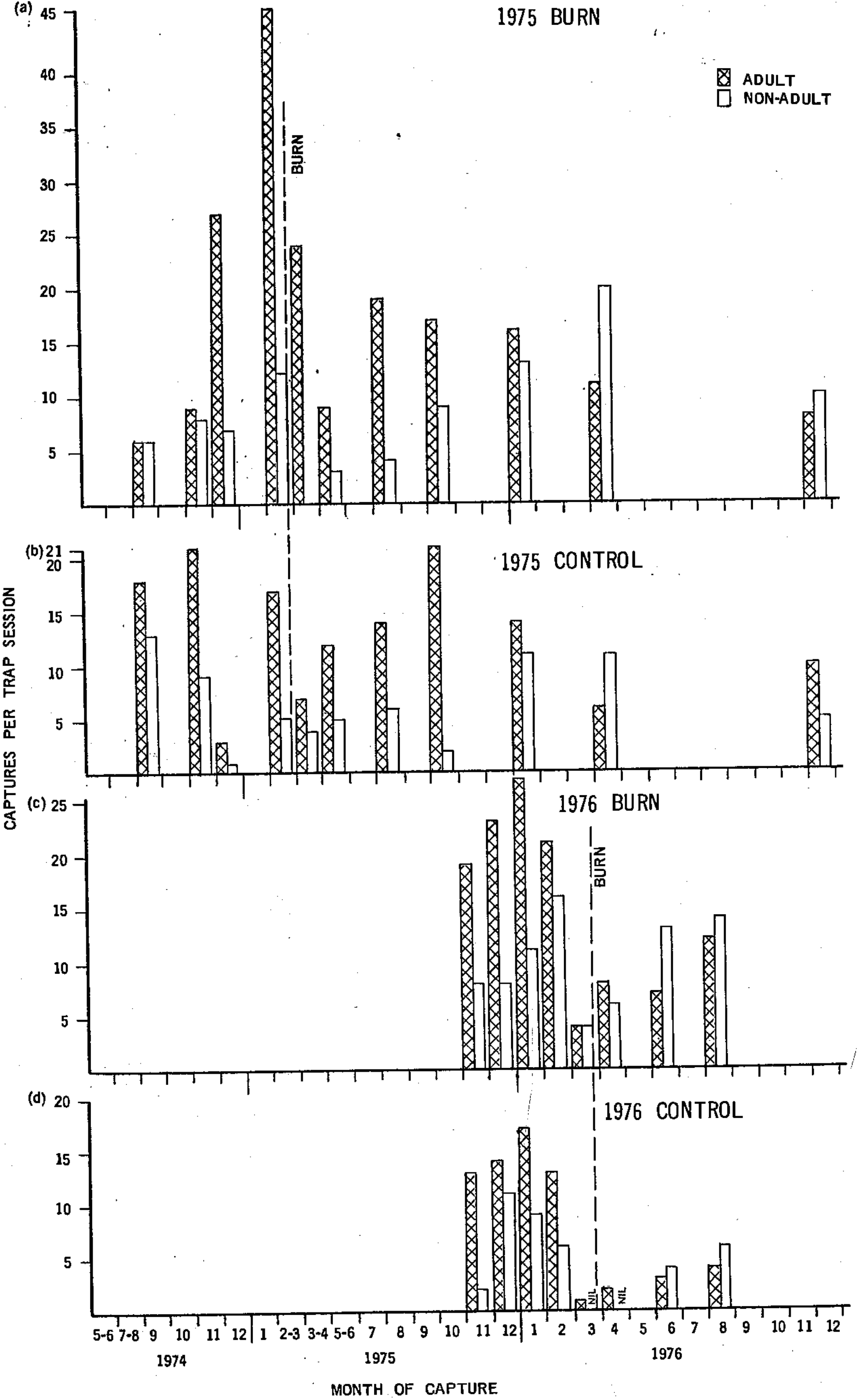


Fig. 3.4.3 THE WOYLIE - ADULTS, A COMPARISON OF TAGGED ANIMALS AND NEW CAPTURES (UNTAGGED).

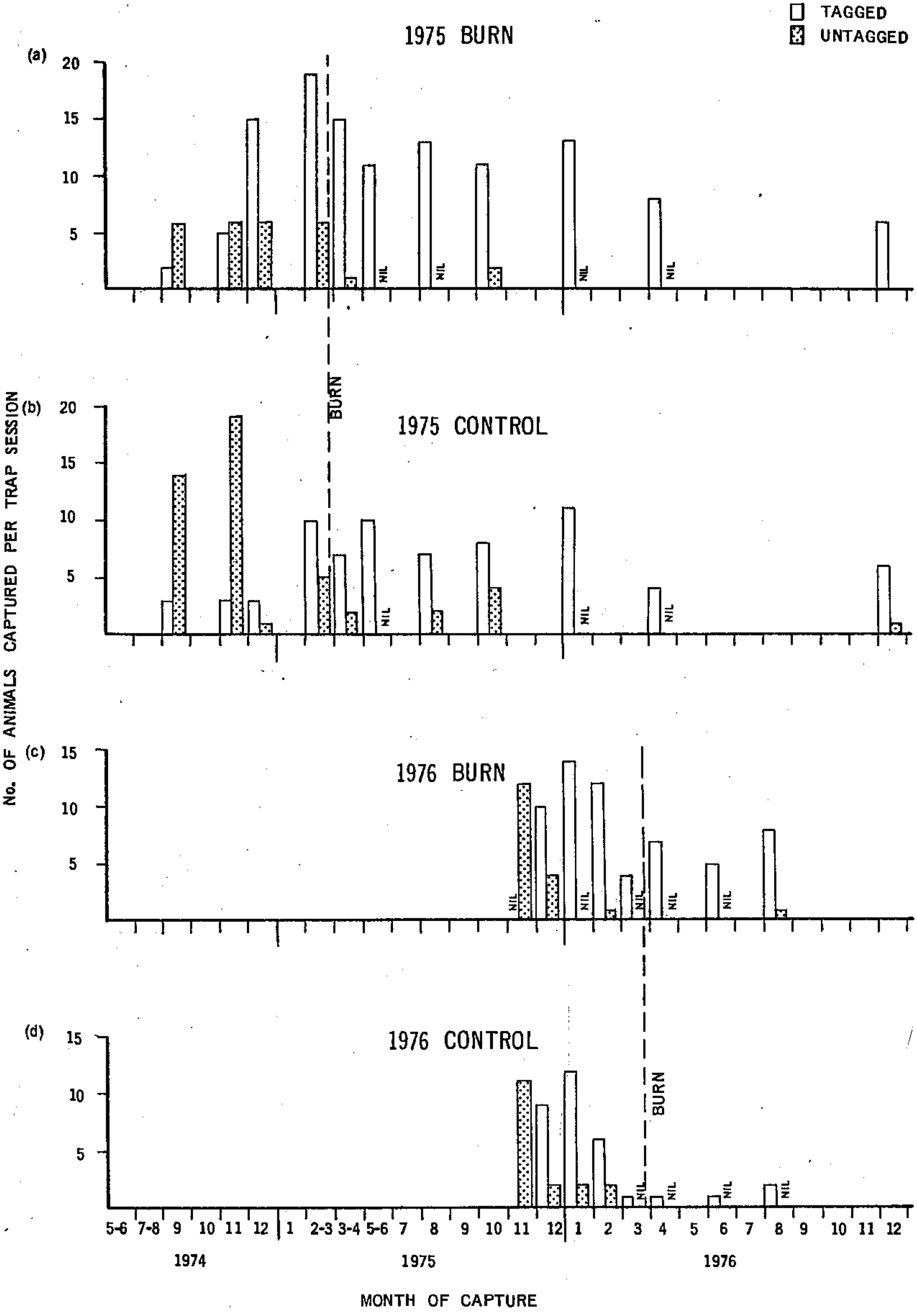
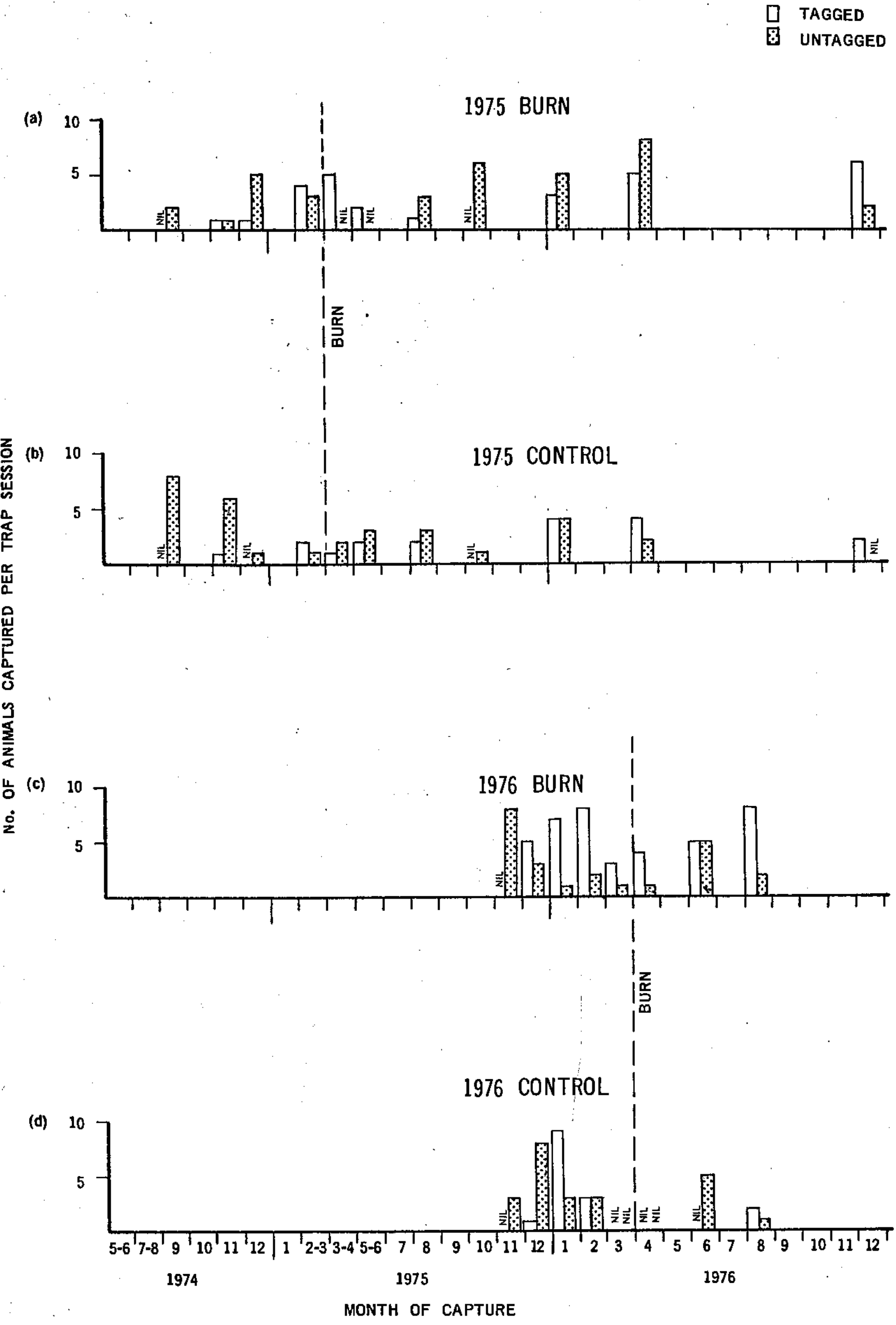


Fig. 3.4.4 THE WOYLIE - NON-ADULTS, A COMPARISON OF TAGGED ANIMALS AND NEW CAPTURES (UNTAGGED).



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 is significantly higher than that of non-adults. This difference is caused partly by an increase in the mean survival time of the adult 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 3.4.4 shows survival of pouch young over the study as a whole. Joeys that reached the age of 85 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 85 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 due to 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% at the maximum and 8.8% at the minimum. This compared favourably with mortality rates of pouch young in the red kangaroo (Megaleia rufa) (Frith and Calaby, 1969).

(c) Reproduction

Approximate birth dates of joeys were calculated using curves for pes and head measurements (Appendix 3). No differences were detected between years or areas so the data were pooled (Figs. 3.4.5). The apparent seasonal difference is due to uneven trap effort, most trapping being carried out during the summer months. As in Tutanning (Sampson, 1971), breeding is continuous. Females may have their first joeys at the age of approximately 170 to 180 days (the M2.0 tooth eruption stage). They then continue 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 4 years, still bear young. Females without joeys in the pouch comprised 10.7% of the population. These were mostly females in the "between joeys" stage.

There seems to be a seasonal change in the sex ratio of births.

TABLE 3.4.3

The woylie - known survival

	Control		
	No. of animals	Total survival (months)	Mean survival (months)
Male	22	128	5.81
Female	10	96	9.60
Non-adult	18	126	7.0
Adult	14	96	7.0

	Burn edge		
	No. of animals	Total survival (months)	Mean survival (months)
Male	33	233	7.10
Female	21	133	6.33
Non-adult	32	145	4.53
Adult	22	221	10.04*

	Burn		
	No. of animals	Total survival (months)	Mean survival (months)
Male	17	125	7.35
Female	12	109	9.10
Non-adult	16	87	5.43
Adult	13	147	11.30**

* Significant diff. @ 0.01 level (Students t test)
** Significant diff. @ 0.05 level (Students t test)

TABLE 3.4.4

The woylie - survival of pouch young

	Known survivals	Probable survivals	Unknown fate	Mortalities
No. 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

If the data in Figure 3.4.5b are combined by 3-month periods, and analysed as a contingency table, the resulting X_2 is 12.58 (n = 3), so that the proportion of male births ranges from a maximum in mid-summer to a minimum in mid-winter.

(d) Weights

There were no significant weight differences between males and females caught during this study. Both sexes exhibit significant season fluctuations in body weight (Fig. 3.4.6). Weight losses are relatively small; male weights fall 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%. However, so consistent are these seasonal changes that they are highly significant for both males and females. They become even more significant if examined in conjunction with Sampson's data (Sampson, 1971) on body fluids, 68 and 81% respectively for summer and winter. The 118.7 g drop in body weights from the summer peak to the late winter low represents a total drop in body solids of 45.7%.

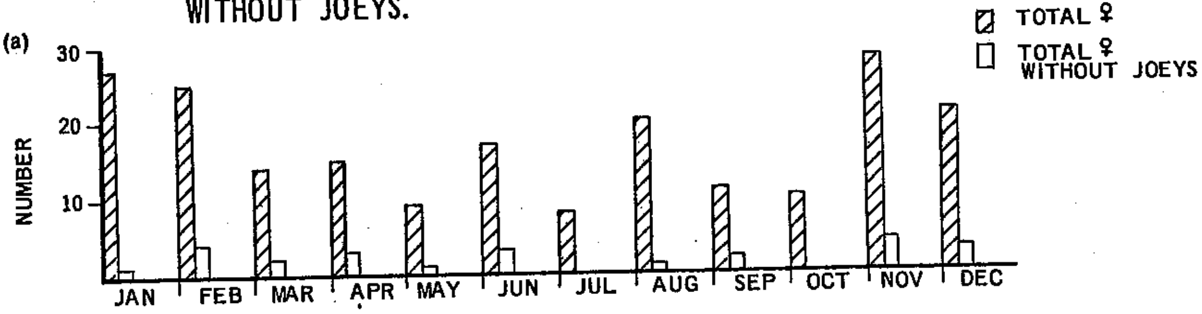
3.4.3 Movements

The woylies' movements seem to fall into the typical home range pattern with a territorial nesting area. 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.

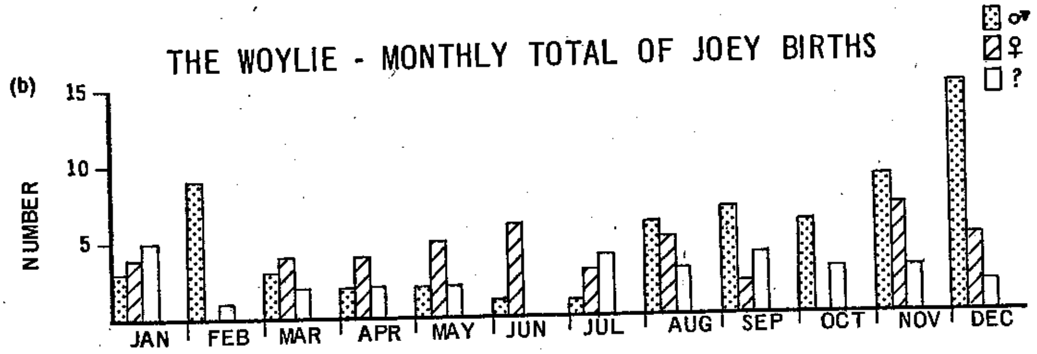
Home range areas from trap data were calculated using the exclusive boundary strip method (Stickel, 1954) (Table 3.4.5). As trap-measured home range areas are known to increase with the number of captures (Burt, 1943), some selection of individuals was necessary if comparisons were to be valid. A further restriction was set by the limited number of multiple captures. Accordingly, only animals captured more than 4 times but less than 10 were used for comparison.

Home range areas were also calculated using the minimum area method (Stickel, 1954) on the radio location maps for the 1976 burn (Table 3.4.5). The minimum method was used because it is not possible to use the more accurate exclusive boundary strip method on this type of data. As a 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

Fig. 3.4.5 THE WOYLIE - MONTHLY TOTAL OF FEMALES WITH AND WITHOUT JOEYS.



THE WOYLIE - MONTHLY TOTAL OF JOEY BIRTHS



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 (Table 3.4.5) are somewhat smaller than those reported for the Tutanning woylie (Sampson, 1971).

Animals caught 3 or more times were used to construct a table of movements (Table 3.4.6): 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 4 months, i.e. the time needed to engage in successful reproduction. No such shifts 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 daytime locations, and a feeding area shown by nocturnal locations (Figs. 3.4.8a and b)*. The woylie has several nests in use at any one time: Channel 4.35 illustrates this particularly well (Fig. 3.4.8a).

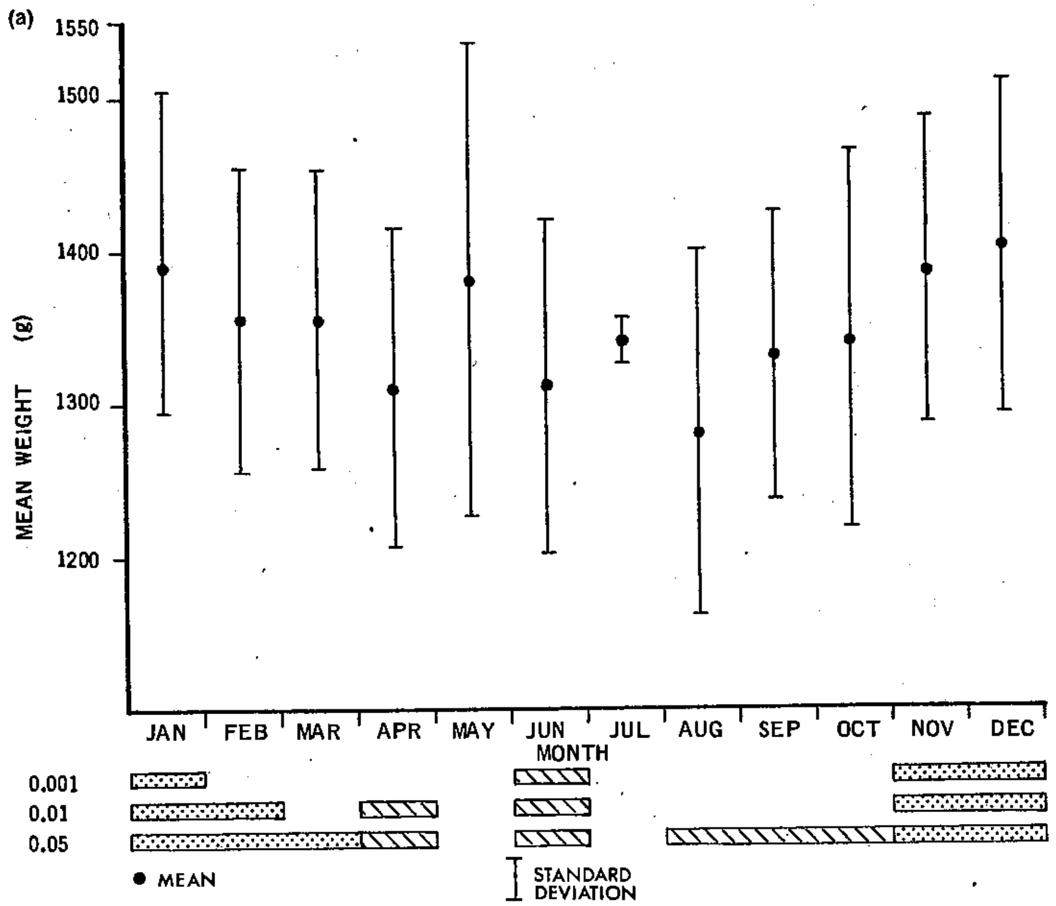
A cluster of locations on the map (Fig. 3.4.8a) represents a nest; each location in a cluster should fall on the same point, but tracking and mapping errors all contribute towards inaccuracies. It can be seen that 3 or 4 nests are used alternatively and in a random manner over a period of weeks. Nests (clusters) are less obvious amongst the radio tracking data for the 1975 burn because aerial interpretation maps were used. The map of the 1976 burn was accurately surveyed using compass and chain.

The nest areas (Fig. 3.4.8a) appear to be almost exclusive to individuals. Any overlap that exists (Table 3.4.5) is largely between adjacent males and females; nest areas of males do not overlap one another. Feeding areas of both sexes, however, overlap considerably (Fig. 3.4.8b and Table 3.4.5).

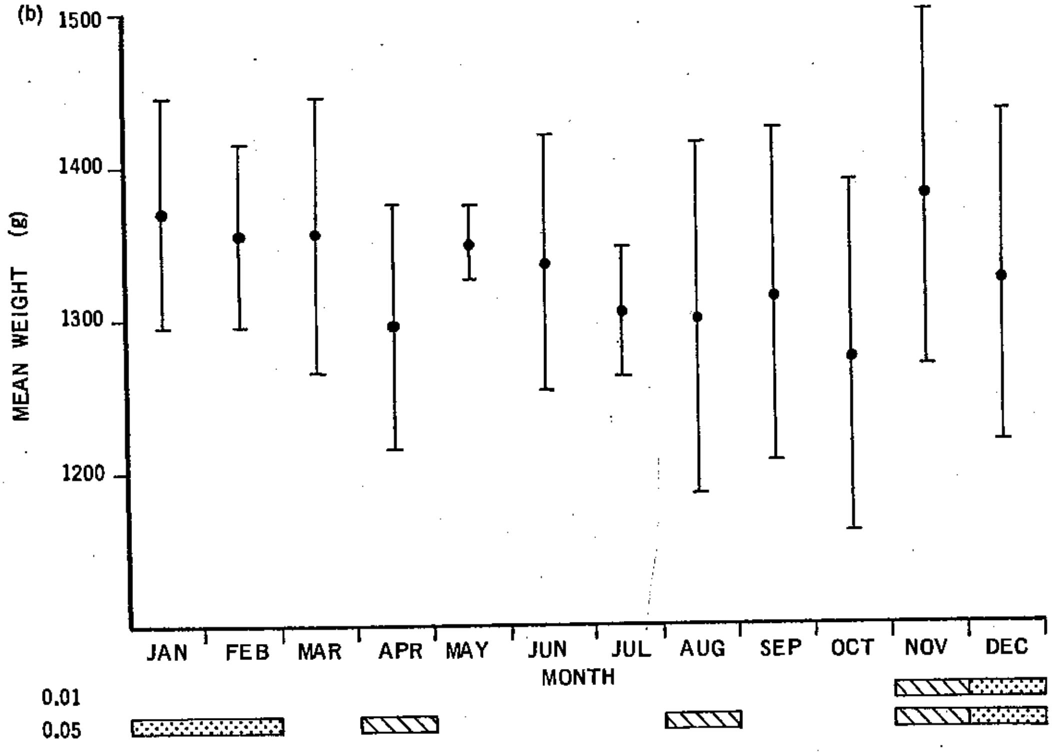
These results are partly in agreement with Sampson (1971), who suggests that the males only are totally territorial. However, territoriality seems to be confined to the nesting area. There is evidence that the woylie may possess well developed scent-marking glands (Nick Allen, personal communication) (Photo 3.4.1); the duct from the scent glands ends in a cloacal appendage which may be used in deposition of scent (Photo 3.4.2). These glands are morphologically

* Figures 3.4.7, 3,4,8, 3.5.4 and 3.6.3, the radio location maps, are inserted in a pocket inside the back cover.

Fig. 3.4.6 THE WOYLIE - MEAN MONTHLY WEIGHTS, MALES



THE WOYLIE - MEAN MONTHLY WEIGHTS, FEMALES



MEAN MONTHLY WEIGHTS DIFFER SIGNIFICANTLY BETWEEN MONTHS UNDERLINED ⁙⁙ AND \\\ AT THE LEVEL INDICATED (STUDENTS 't' TEST)

TABLE 3.4.5

The woylie - home range sizes calculated from trapping and radio-tracking data

	Trapping			
	Pre-burn		Post-burn	
	♂	♀	♂	♀
Number of animals	18	14	5	-
Mean area (ha)	27.31	19.64	41.88	-
Standard deviation	8.35	9.94	23.4	-
Mean per cent overlap*				

	Radio tracking - pre-burn			
	Nest area		Feeding area	
	♂	♀	♂	♀
Number of animals	12	5	9	4
Mean area (ha)	2.09	2.73	8.67	7.51
Standard deviation	1.79	1.21	4.79	3.35
Mean per cent overlap	19.54		63.85	

	Radio tracking - post-burn			
	Nest area		Feeding area	
	♂	♀	♂	♀
Number of animals	12	6	9	4
Mean area (ha)	2.89	2.53	8.59	11.75
Standard deviation	11.02	1.39	3.71	5.44
Mean per cent overlap	21.46		60.25	

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

TABLE 3.4.6

The woylie - table of movement

Animals shifting their home range

Treatment	Sex	Age class	Successful	Not successful
Control	Male	Non-adult		
		Adult		
	Female	Non-adult		
		Adult		
Edge	Male	Non-adult	1	(1)
		Adult		(1)
	Female	Non-adult		
		Adult		
Burn	Male	Non-adult	(2)	
		Adult	3 (2)	(1)
	Female	Non-adult		1
		Adult	3	(1)

Animals not shifting their home range

Treatment	Sex	Age class	Successful	Not successful
Control	Male	Non-adult	2	1
		Adult	7	1
	Female	Non-adult	1	
		Adult	1 (1)	2
Edge	Male	Non-adult	2 (2)	1
		Adult	7 (3)	3 (1)
	Female	Non-adult	1 (2)	2
		Adult	6 (1)	2 (1)
Burn	Male	Non-adult	1	3 (1)
		Adult	1	(1)
	Female	Non-adult	1	1
		Adult	1	(2)

( ) 1976 burn; other figures are 1975 burn.

similar to those in the brushtailed 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).

Data obtained using the Rustrak continuous recorder, showing the mean number of hours per night spent within its range, suggest that the woylie moves and feeds within a fairly restricted area on any one night (Appendix 4). The greater part of most nights is spent within the 200-250 m radius range of the recorder.

Further indication of the woylies' limited range of movement is provided by results from the transportation experiment (Table 3.4.7). 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.

3.5 The pre-burn population - the tammar

A summary of the trapping results over the three-year period is presented in Table 3.4.1.

3.5.1 Ageing the population

Details of the method used are presented in Appendix 3. For the purpose of this study four age categories are recognized.

(i) Joeys - pouched joeys from birth to approximately 7 to 8 months. Tooth eruption: M1.0 is just starting to rise.

(ii) Juveniles - approximately between the ages of 7 to 8 months and 15 months. Tooth eruption: M1.0 to M2.0.

(iii) Sub-adults - from approximately 15 months to 2 years. Tooth eruption: M2.0 to M3.0, before p4 replaces p3 and dp4.

(iv) Adults - from approximately 2 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 has been used in most of the analyses.

3.5.2 Population analysis

(a) 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 are used.

Trapping in the unburnt control block was not properly

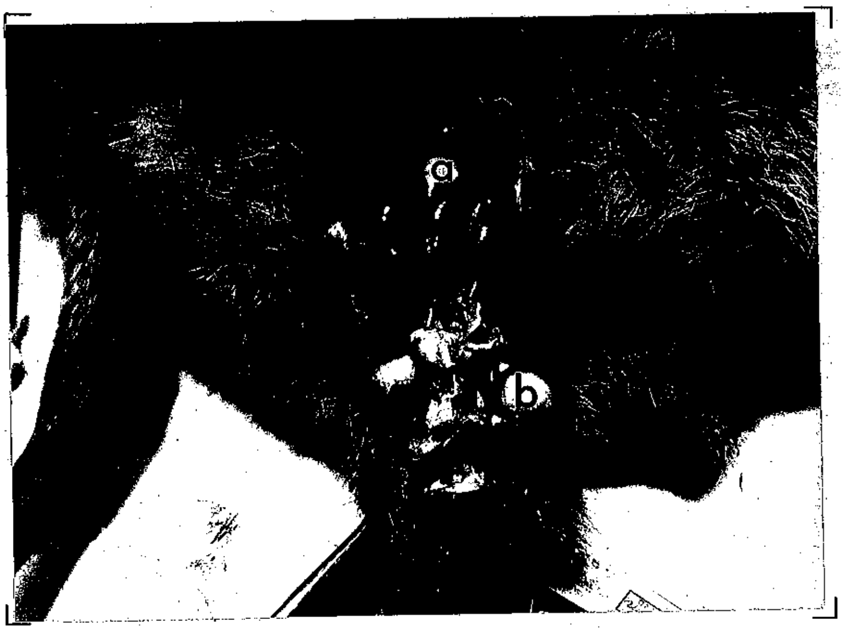


Photo ~~Fig.~~ 3.4.1. Male woylie dissected to show paired scent or oil glands (Photo Nick Allan)
a - prostate gland.
b - scent or oil gland.

Photo ~~Fig.~~ 3.4.2. A droplet of fluid exuding from the tip of the cloacal appendage after application of pressure to the scent gland. (Photo Nick Allan)

TABLE 3.4.7

Fate of woylies transported from their home range areas

Sex	Maturity	Distance released from home range area (m)		
		2000-2500	2600-3000	3100-3500
Males	Non-adult	1	5 (2)	1
	Adult	1 (1)	3 (1)	1
Females	Non-adult	1	1	2
	Adult	1	1	1

Sex	Maturity	Distance released from home range area (m)		
		3600-4000	4100-4500	4600-5000
Males	Non-adult	6 (1)	1	1
	Adult	3	6	
Females	Non-adult	1	3	1
	Adult	2	2	

( ) number of animals that returned to their home range areas

Fig. 3.5.1 THE TAMMAR - PERCENTAGE CAPTURES 1975 BURN

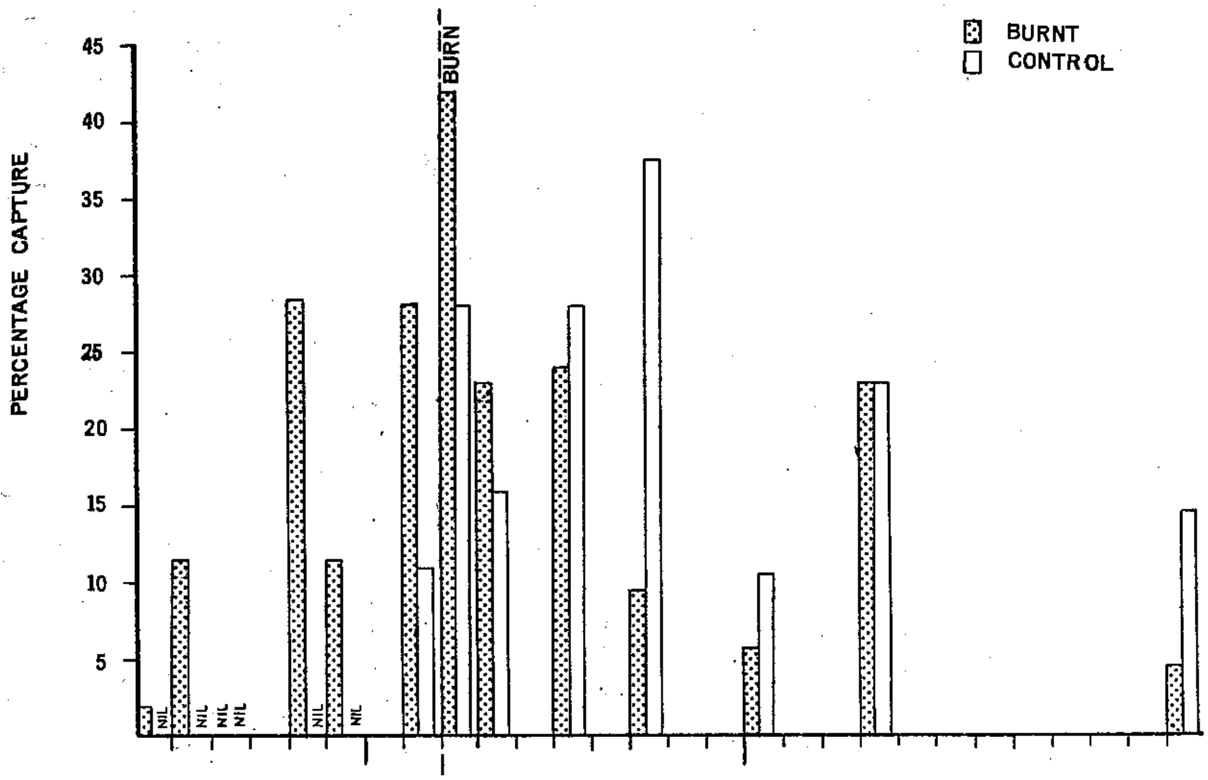
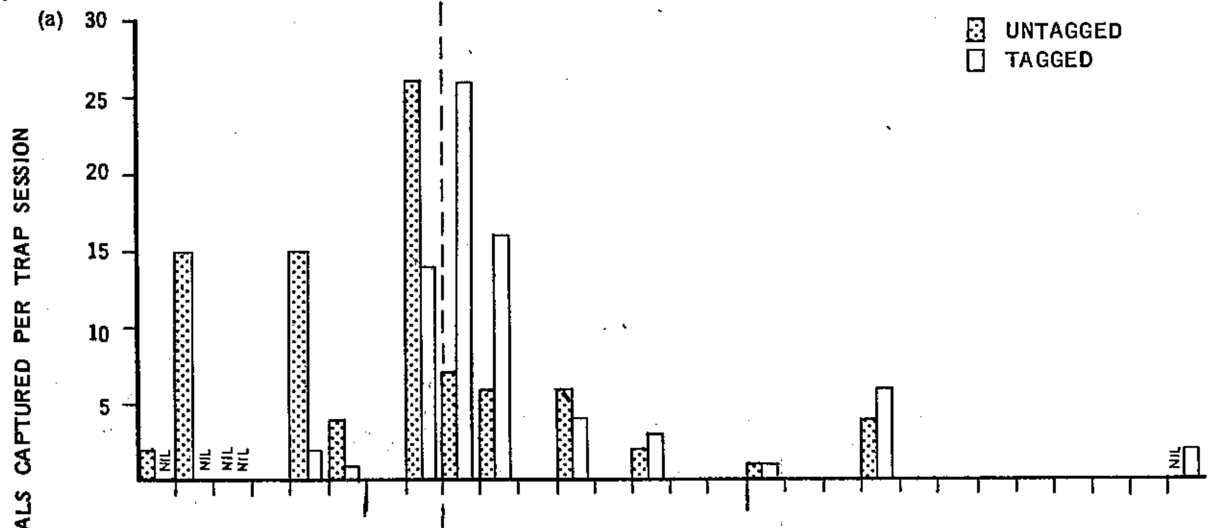
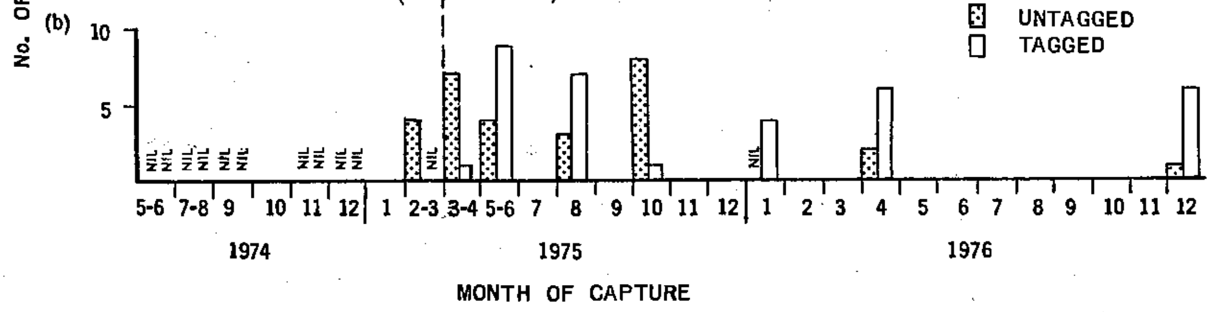


Fig. 3.5.2 THE TAMMAR - COMPARISON OF TAGGED ANIMALS AND NEW CAPTURES (UNTAGGED). 1975 BURN



THE TAMMAR - COMPARISON OF TAGGED ANIMALS AND NEW CAPTURES (UNTAGGED). 1975 CONTROL



organized until just before burning. Consequently, capture percentages before burning are largely provided by the burn area (Fig. 3.5.1). 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. 3.5.2).

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% of the population.

(b) Survival

A table of known survival, similar to that constructed for the woylie, was made up for the tammar (Table 3.5.1). 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.

(c) Reproduction

Birth dates of tammar joeys were estimated using head and pes length (Appendix 3). Data from three years of trapping were combined (Table 3.5.2).

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).

(d) 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 @ 0.001 level, Students t test). Only the data for males are sufficient for analysis, and these show considerable seasonal variation. As with the woylie, weights taken from the time when they are heaviest (October to February) differ significantly from weights during the period March to August (Fig. 3.5.3). The mean weight of adult males falls 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%, somewhat higher than that of the woylie.

TABLE 3.5.1

The tammar - known survival

	Control		
	No. of animals	Total survival (months)	Mean survival (months)
Male	13	58	4.46
Female	11	32	2.91
Non-adult	12	52	4.33
Adult	12	38	3.17

	Burn edge		
	No. of animals	Total survival (months)	Mean survival (months)
Male	27	161	5.59
Female	23	81	3.52
Non-adult	14	57	4.07
Adult	36	175	4.86

	Burn		
	No. of animals	Total survival (months)	Mean survival (months)
Male	11	53	4.82
Female	11	20	1.82
Non-adult	4	1	0.25
Adult	18	72	4.00

TABLE 3.5.2

The tammar - joey births 1974 to 1976
combined data

Month	December					January				February				March			
Weekly births	-	--	4	7	8	5	6	4	7	9	-	1	-	1	-	-	1

3.5.3 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 are occupied by surprisingly large numbers of tammar. Trapping data indicate that on a good site approximately 30 to 40 tammars may occupy a thicket area of only 40 ha. How many separate groups these animals comprised is not known.

A table of movements, similar to that constructed for the woylie, was made up for the tammar (Table 3.5.3). Unlike the woylie , there is considerable movement of tammars in the control area. Most of the animals that move are mature males.

Radio-tracking data on the tammar are limited to those obtained from five individuals and hence are not as comprehensive as the woylie data (Fig. 3.5.4).

The tammar lives 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 occasionallycaught together in the traps. Observations on tammars at a feeding station suggest 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-optimal habitat, close to other groups. This may indicate a degree of hostility between members of different groups. Certain individuals, usually males, appear 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.

Fig. 3.5.3 THE TAMMAR - MEAN WEIGHT PER TRAP SESSION

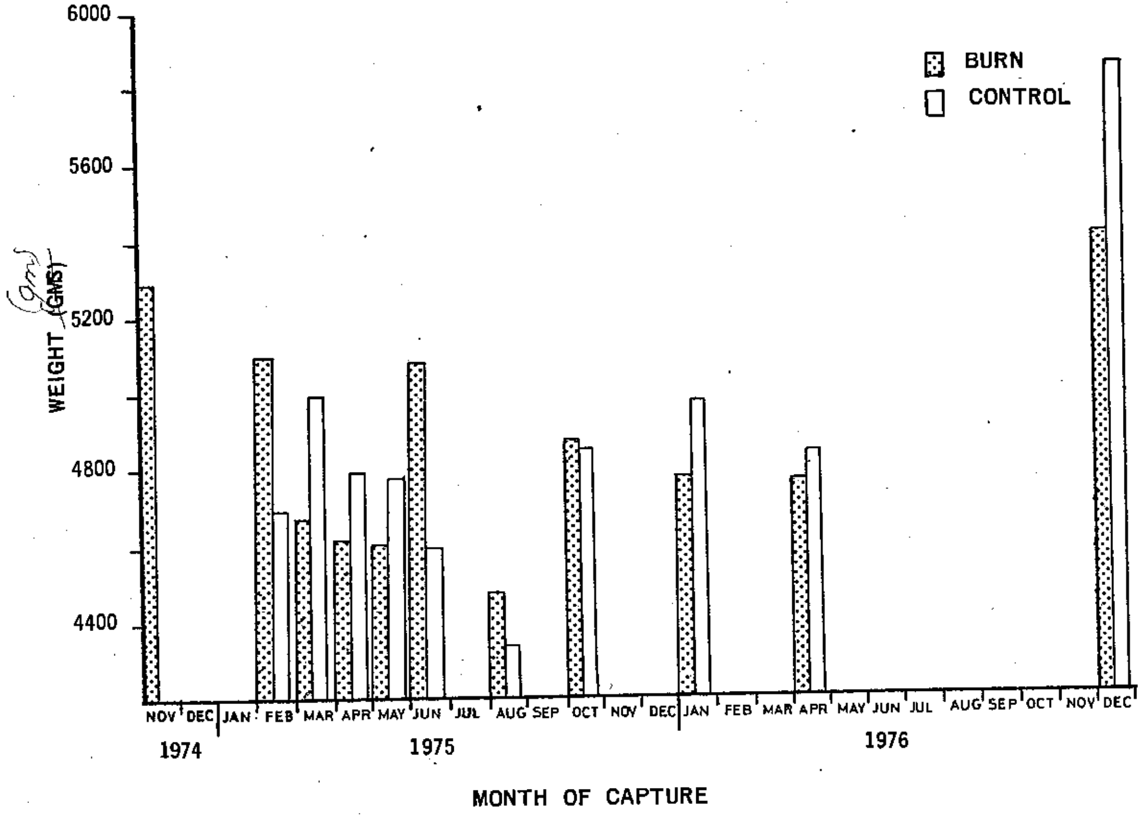


TABLE 3.5.3

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

3.6 Fire effects - the woylie

3.6.1 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 complete 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 heart-leaf thickets were burnt. Fire intensity was not uniform over the area and various intensities of burn could be recognized (Fig. 3.6 and Photos 3.6.1 to 3.6.3).

3.6.2 Animal behaviour during the fires - woylie and tammar

Animals with radio transmitters, both woylie and tammar, were monitored during the fires. Results are given in Table 3.6.1. In no instance did any of the animals leave their known home range areas during the burn (Figs. 3.4.7, 3.4.8a and b and 3.5.4). Only one animal, radio transmitter Channel 8.3, died as a direct result of the fires. 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(Channel 6.15) were recorded in some detail (Fig. 3.6.1). This animal's behaviour is fairly typical of that exhibited by other individuals of both species. Woylies stay in their nests, and tammars in their resting places, until the very last minute when they vacate them to move in front of the flames until an unburnt patch becomes evident. Such unburnt patches are common in most fires (Fig. 3.6), and even a small one will provide sufficient refuge.

Tammar Channel 7 sheltered underneath a log in an unburnt patch no more than 20 m^2 in extent while the fire raged all about it, scorching the leaves on trees 40 m in height.

In cases where no suitable unburnt patches remain before the fire has pushed the animal to the limits of its home range area, an animal will 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 approach after the fire. They are thought to have been suffering from a form of shock (see 3.8).

Fig. 3.6 BOYICUP TRAPPING AREA - MAP SHOWING FIRE INTENSITY ON THE 1975 AND 1976 BURNS.

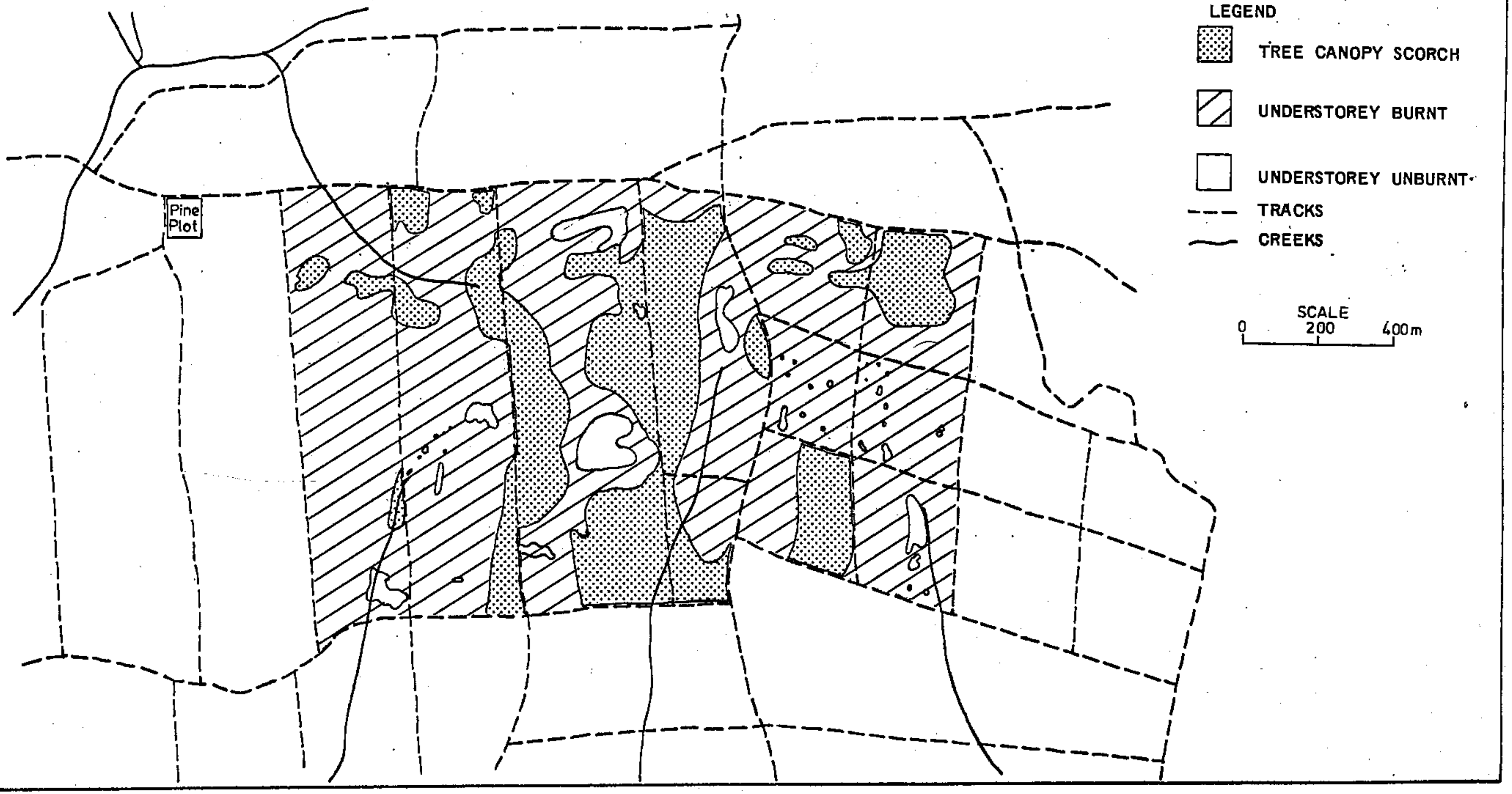


Photo 3.6.1. Tree canopy scorch. Note the blackened trunks and dead leaves of the overstorey trees. The ground vegetation has been completly removed by the fire.

Photo 3.6.2. Understorey burnt. Note green leaves on the overstorey trees. Clumps of dead understorey remain.

Photo 3.6.3. Understorey burnt. Areas of ground vegetation remain unburnt in some places.

Photo 3.6.4. Regeneration of forest in area of canopy scorch 8 months after the fire.

TABLE 3.6.1

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

TABLE 3.6.6

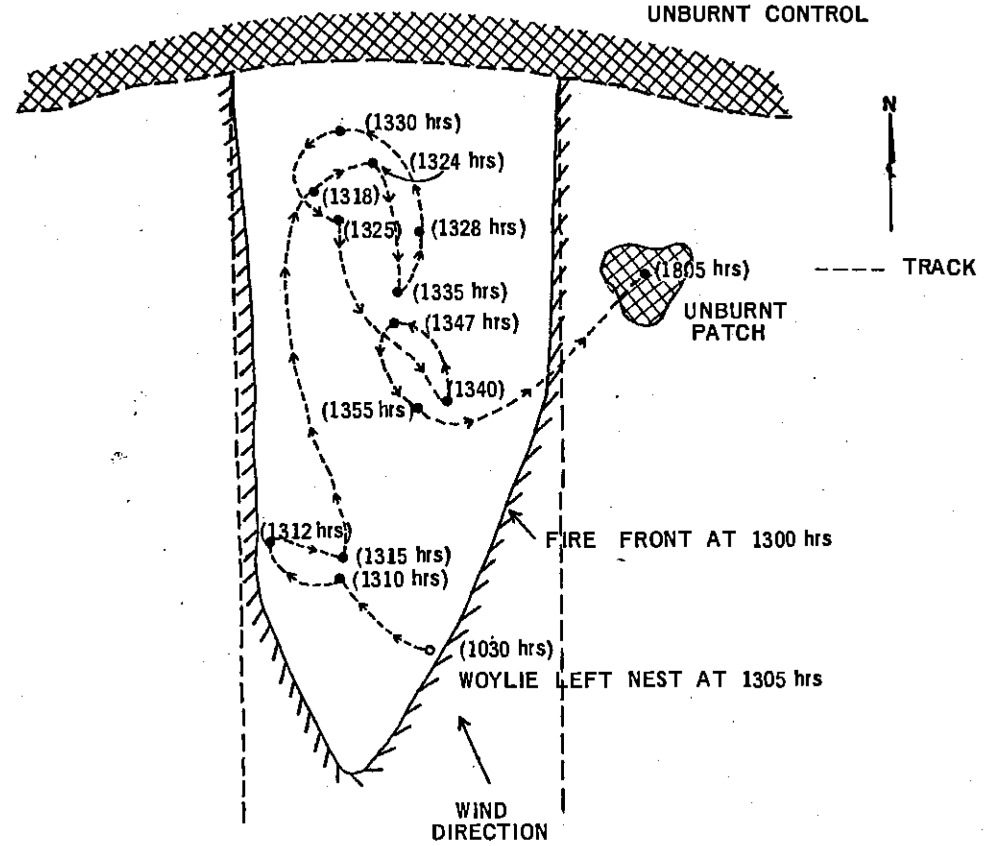
The woylie - fate of animals with transmitters

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

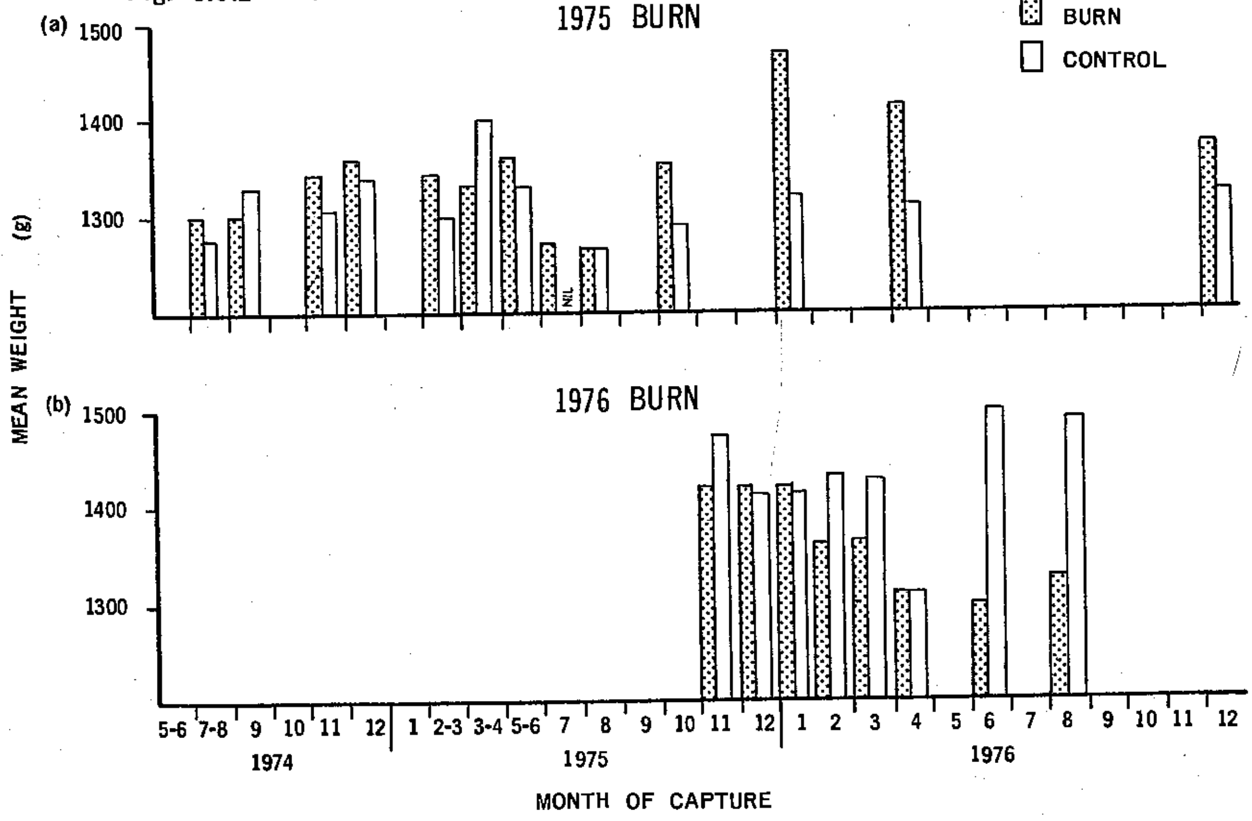
* one of each of these deaths is a control animal.

Fig. 3.6.1 WOYLIE CHANNEL 6.15 MOVEMENTS DURING THE 1976 BURN



THE FIRE WAS LIT ALONG THE TWO TRACKS BETWEEN 12.30 p.m. AND 13.00 p.m. AND BURNT OUT THE AREA BETWEEN THE TRACKS BY 14.30 p.m.

Fig. 3.6.2 THE WOYLIE - MEAN WEIGHT PER TRAP SESSION



3.6.3 Population analysis

(a) Population structure

Immediately after the 1975 fire, in March-June, there was a decrease in total captures on the burn area (Figs. 3.4.1 and 3.4.2). This appears to be due to a complete absence of captures of new non-adults during this period (Figs. 3.4.3 and 3.4.4). No such decrease is evident after the 1976 burn.

There is no significant decrease in the overall percentage capture after the 1975 burn (Table 3.4.2). But there is a general decrease in overall percentage captures after the 1976 burn (Table 3.4.2). This decrease is greatest in the control block, but the burn area also shows a considerable decline. Since this decline has its origins in February, following the removals, and is particularly pronounced in the unburnt control area, it is reasonable to assume that it is a result of these removals rather than an effect of the fire.

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

After the 1975 burn there was a marginal increase in the number of male captures relative to female captures (Fig. 3.4.1 (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 3.6.2). A slightly increased proportion of the post-fire capture in the control plot was also male (Table 3.6.2); inspection of the data showed this to be an edge effect.

No changes in the relative proportion of males to females were observed in the 1976 burn. However, the last trap session appears 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 is the increasing proportion of non-adult captures relative to adult captures (Fig. 3.4.2). Again, this difference is 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 is only just significant. Amongst the new untagged animals the ratio changes from significantly more adults before the burn to significantly more non-adults after the burn

TABLE 3.6.2

Totals of animals caught per session, comparison of sexes

			Total no. 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

TABLE 3.6.3

The woylie -
Totals of animals caught per session, comparison of adults and non-adults

			Total no. 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	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

(Table 3.6.3). Some of this difference is undoubtedly due 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 is much smaller it seems that there has been a significant increase in the proportion of non-adults on the burn.

Exactly the same pattern may be observed after the 1976 burn (Fig. 3.4.2(c) and (d), and Table 3.6.3). Note that the pattern in the control, where re-population is taking place after removals, is 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 3.6.4). The numbers of non-adults increased three times more than the numbers of adult females increased on the burn over the three-year period of the study. No increase is evident in the control area.

Re-population of both burns and the 1976 removal (control) area is achieved almost exclusively by new untagged non-adults. This is similar to the 'normal' pattern of replacement in the unburnt control (Fig. 3.4.3). After all trappable animals in the area have been captured, any new untagged woylies must all be non-adults (Fig. 3.4.3).

The pattern of re-population in the 1976 burn removal area was similar to that on the burnt areas. Re-population was 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 (Fig. 3.4.4 (d)).

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

(b) 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 be victims of predators soon after the fire (Table 3.6.6). Animals on the edge of the burn may survive by moving onto the unburnt edge and a few may survive on the burn itself. Survival of adults and non-adults in the unburnt control area

TABLE 3.6.4

The woylie -
non-adults as a percentage of the
total female population, 1975 burn

No. of animals captured	1974	
	Burn/edge	Control
Non-adults	9	10
Adult females	22	18
Non-adults as percentage of females	40.9	55.6

No. of animals captured	1975	
	Burn/edge	Control
Non-adults	20	14
Adult females	24	25
Non-adults as percentage of females	83.3	56.0

No. of animals captured	1976	
	Burn/edge	Control
Non-adults	25	10
Adult females	18	24
Non-adults as percentage of females	138.8**	41.7

** Sig (0.01 level) higher than control (Chi-square test).

does not differ significantly during the period of the study (Table 3.4.3). However, on the burn and the edge of the burn, survival of non-adults is significantly lower than adult survival (t test 0.05 and 0.01 levels respectively). Survival of the remaining adults had increased whilst the survival of non-adults had decreased.

The capture data confirm that there is a higher mortality amongst these new non-adult immigrants to the burn. In the burn area the number of single captures increases after the fire; in the control block the number of single captures decreases over the same period (Table 3.6.5).

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

(c) Reproduction

No effects of fire on reproduction were observed.

(d) 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, t test) than those on the control area between October and April (Fig. 3.6.2 (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. 3.6.2 (b)).

Weights of animals on the control area appear to increase relative to those on the burn area following removals in February. They are significantly higher over the February, March, June and August trapping sessions. Although significant, the figures are based on the weights of a few individuals, and these results should be treated with some 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.

3.6.4 Movements

The detailed movements after the burn of animals with radio transmitters are plotted in Figures 3.4.7, 3.4.8 and 3.6.3.

TABLE 3.6.5

The woylie - percentage of animals per capture class during three periods of four trap sessions each, 1975 burn

Trap period	Percentage of animals per capture class			
	CONTROL			
	1 capture	2 captures	3 captures	4 captures
<u>Pre-burn</u>				
Sept. 1974 to March 1975	75.0 (24)	18.7 (6)	6.3 (2)	-
<u>Post-burn</u>				
March 1975 to August 1975	71.0 (22)	25.0 (8)	4.0 (1)	
<u>Post-burn</u>				
Oct. 1975 to Dec. 1976	41.7 (15)	41.7 (15)	13.9 (5)	2.7 (1)

Trap period	Percentage of animals per capture class			
	BURN			
	1 capture	2 captures	3 captures	4 captures
<u>Pre-burn</u> Sept. 1974 to March 1975	40.7 (24)	35.6 (21)	16.9 (10)	6.8 (4)
<u>Post-burn</u> March 1975 to August 1975	66.7 (24)	19.4 (7)	11.1 (4)	2.8 (1)
<u>Post-burn</u> October 1975 to December 1976	60.0 (30)	20 (10)	14 (7)	6 (3)

( ) Actual numbers of animals

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 whilst 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 (Figs. 3.6.3 (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 (Fig. 3.6.3).

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 (Fig. 3.4.7). Radio transmitter animal Channel 9.55, a male, survived with its nesting area centred on an unburnt patch of approximately 3 ha. The range of this animal was further documented in 1976, when it was given another radio transmitter, Channel 12.25 (Figs. 3.4.8 and 3.6.3). This animal was still alive at the end of the study in December 1976.

One individual, radio transmitter 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 (Fig. 3.6.3), 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 Channel 4.35, 6.3 and 12.25, made no shifts in their home range areas during the period of study (Figs. 3.4.8 and 3.6.3). Results are summarized in Table 3.4.6.

Trapping results generally confirm the results obtained using radio telemetry. Table 3.4.6 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 block.

Of the 13 that moved from the burn area, 10 were successful, whereas only one 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 are therefore most successful but a good proportion of the animals that stay also survive.

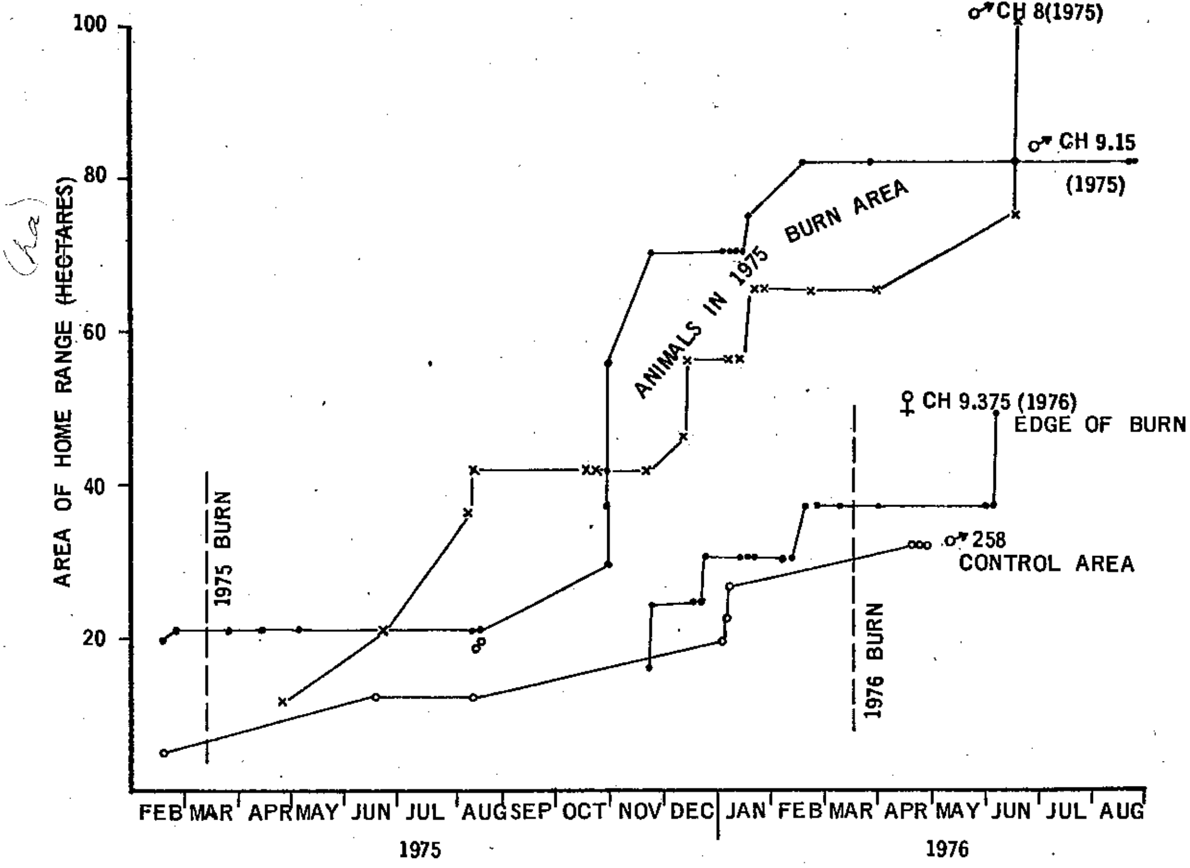
There were no significant differences between pre- and post-burn home range sizes calculated using either radio points or trapping data (Table 3.4.5). Some error may have been introduced by the different numbers of radio points for each animal, but in most cases many points were available and the error is considered minimal. Areas of male post-burn home ranges calculated from trapping data appear to be larger than pre-burn areas, but the difference is not significant as individual variation is very high.

There is some indication from well documented individual cases that the home range area may be increased after burning (Fig. 3.6.4). This increase in range appears to take place over the summer after the burn.

3.6.5 Movement - the 1976 burn

Post-fire radio tracking results (Fig. 3.6.3) 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, Channels 1.12 and 9.375, moved into the empty area. The latter's nest area was already largely within the empty area

Fig. 3.6.4. THE WOYLIE - HOME RANGE AREAS CALCULATED FOR SUCCESSIVE CAPTURES.



AREA CALCULATED USING THE EXCLUSIVE BOUNDARY STRIP METHOD (SEE TEXT).
GRAPHS COMMENCE AT THIRD CAPTURE.

before the burn. One animal, 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 locations (nests) gradually shifts further eastwards into the empty area through time (Fig. 3.6.3 (a)). This behaviour typifies the general pattern of movement observed after the burn, viz. there is no immediate exodus from the burn but rather a gradual change brought about by 'probing' moves into new and unfamiliar areas.

3.7 Fire effects - the tammar

3.7.1 Population analysis

(a) Population structure

Despite considerable trap interference by brushtailed possums (*Trichosurus vulpecula*) and a bird, the squeaker (*Strepera versicolor*), trapped in numbers after the fire, the capture rate of tammars increased dramatically (Fig. 3.5.1). The highest capture rate recorded during the study, 42%, was recorded immediately after the 1975 fire. A general weight loss at this time (see 3.7·1 (d), although not significant, suggests that the high capture percentage might be 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 is attributed to the animals' being attracted to the new green grass on the burn area after autumn rain.

The structure of the population caught in the burnt area also changed. During the 4 trapping sessions between October 1975 and December 1976, 19 adults and no non-adults were captured on the burn (difference significant @ 0.01 level). During the same period 21 adults and 7 non-adults were captured on the control area (difference N.S.). Eleven of 19 animals on the burn were tagged animals coming in from the unburnt surrounds, 3 having previously lived in the burnt area. The remaining 8 were all new untagged adults.

Unlike the woylie, there was no increase after the fire in the number of animals trapped only once (Table 3.6.7). This suggests that there was no increase in mortality on the burn area after the fire. This is because there has been no re-colonization by young tammars on the burn as yet. The animals caught there were adult animals from the surrounding unburnt areas.

(b) Survival

Survival of female compared with male and non-adult compared with adult tammars appears to be considerably lower on the burn area than on the edge and control areas (Table 3.5.1). The differences are, however, not significant.

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

(c) Reproduction

No effects due to fire were observed.

(d) 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 (Fig. 3.5.3). The differences are not significant. During June and August the weights of tammars caught on the burn were significantly higher (0.05 level) than those of animals on the control. This may be a reflection of the abundant feed available on the new grassy areas of the burn.

3.7.2 Movements

(s) All 4 tammars fitted with radio transmitters behaved in a similar manner following the burn (Fig. 3.5.4). For the first few days they stayed on the burn using small unburnt patches of heartleaf thicket for cover. Later, 2 animals shifted to an unburnt patch on the edge of the thickets, where they remained for some days. During this period, one animal, Channel 5, died in a funnel trap as a result of self-inflicted injury. Its collar was attached to another animal known to live in the same area.

The tammar with radio transmitter Channel 3 disappeared, presumed the victim of a predator. The remaining 3 animals moved to neighbouring thickets. One large male, 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

TABLE 3.6.7

The tammar -
percentage of animals per capture class during two
periods of six trapping sessions each

Trap period	Percentage of animals per capture class			
	CONTROL			
	1 capture	2 captures	3 captures	More than 3 captures
Pre-burn May 1974 to March 1975	100 (3)			
Post-burn April 1975 to December 1976	61.3 (19)	9.7 (3)	19.4 (6)	9.6 (3)

	Percentage of animals per capture class			
	BURN			
	1 capture	2 captures	3 captures	More than 3 captures
Pre-burn May 1974 to March 1975	68.4 (39)	17.5 (10)	12.3 (7)	1.8 (1)
Post-burn April 1975 to Dec. 1976	69.4 (43)	17.7 (11)	6.5 (4)	6.4 (4)

( ) Actual number of animals

groups and was thus already familiar with tammars in the new area. The remaining 2 animals, 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-optimal habitat.

Hand-monitoring and records using the Rustrak recorder indicate that animals with transmitters returned to feed on the burn at night (Appendix 4). The remains of the tammar with Channel 5, almost certainly killed and eaten by a fox, were discovered in September. It was found at a point between its new daytime refuge and its feeding area on the burn.

(b) Table 3.5.3 shows that all 11 animals that remained on the burn disappeared, presumed the victims of predators. Ten of the 16 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 3 animals which stayed were successful.

3.8 Mortality factors

(a) The woylie

During the course of the study some information on the cause of mortality in both species was obtained (Table 3.8.1). The main predator of the woylie in the study area appears 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 appear to be due to some form of psychological 'shock' brought on by the effects of the fire. After fire, some animals appear dazed and in a state of shock and allow close human approach before they hop away slowly. They may also have been affected by smoke, but some never recover; they appear to lose the will to live and make little attempt to survive. A number 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.

TABLE 3.8.1

Mortalities recorded during the study

(a) The woylie

	Probable cause of death							
	European fox	Native cat	Wedgetailed eagle	Fire 'shock'	Starva-tion	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'	Starva-tion	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

(b) The tammar

The European fox again appears 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 due to trap mortality, usually by a condition attributable to shock. When caught in the funnel traps, animals would normally leap about wildly on 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.

It is felt that the condition might be a form of the so-called 'overstraining disease' (Harthoorn and Van Der Walt, 1974) or 'fear shock' (Guthrie et al., 1967).

Recent research (Oliver et al., 1977) indicates that many species 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.

3.9 Discussion

3.9.1 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% 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 recolonization 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 largely due to the loss of non-adult animals within the area. This loss appears to be mainly due to 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% (n = 20) in 1975 and 38.6% (n = 25) in 1976 reached the non-adult stage (Table 3.6.4).

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 year to 18 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 5.1). Recovery of the understorey may be expected to take 3 to 5 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 were, 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-colonizers 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 due to an increase in food density: the animals' diet may comprise a higher proportion of dry fungi.

3.9.2 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 three-year-period 34 late juveniles and non-adults were recorded in a total population of 51 adult females. This represents a survival rate of 66.7% compared with the 11.4 -15% 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-optimal 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 recolonization 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.

4. FOOD STUDIES

4.1 Introduction

Detailed work on food seemed beyond the scope of this study in the time available. Sampson (1971) was unable to recognize 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 recognizable in the gut; the contents appeared to be an unrecognizable amorphous mass as reported by Sampson (1971). However, detailed microscopic examination revealed vast numbers of fungus spores. Six distinct spore types were recognized, 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 were discovered. Further sifting of soil in the area yielded a collection of 26 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 W.A.) 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 (Photo 4.1.1). Pieces of the outer peridium of specimens of this genus have since been found frequently in association with fresh diggings in burnt areas (Photo 4.1.2).

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 on the potoroo (Potorous tridactylus), an animal similar to the woylie in very many ways, indicated that its diet contained a very

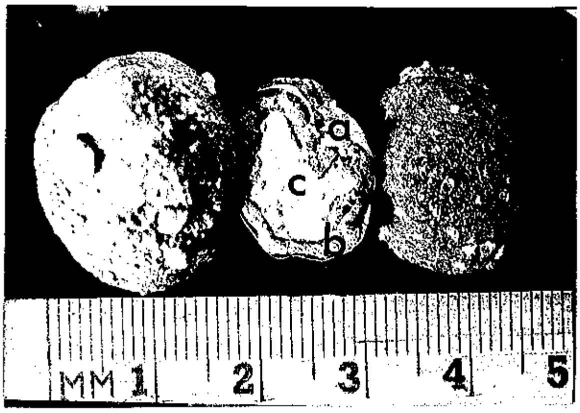


Photo 4.1.1. Sporocarps of Mesophellia sp. The T.S. shows a = outer peridium
b = spore-bearing layer(hymenium)
c = central edible sterile columella.

Photo 4.1.2. Digging on recently burnt ground. Pieces of outer peridium can be seen discarded on the freshly dug soil.

Photo 4.1.3. Spores in prepared scat sample as seen under light microscope 600mag.
a = Mesophellia sp.
b = Martellia sp.
c = Australasia chlorospora

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:

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

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

Fungus spores pass through the gut of the woylie unharmed, losing none of their identifiable characteristics (Photo 4.1.3), so that it is comparatively simple to obtain data on this diet by means of scat analysis.

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.

4.2 Scat and stomach content analysis - the woylie

4.2.1 Methods

Scat samples were collected from traps during normal routine trapping in Boyicup; a total of 163 samples, representing 10 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 10 months available. From these subdivisions, three samples were selected at random, where available, for processing. A total of 67 samples were used. Samples from Tutanning (coll. J. Sampson) were obtained from the Zoology Department, and 11 of these, representing 6 months of the year, were used for comparison with samples from the Boyicup woylies. Nine short-nosed bandicoot scat samples representing 6 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 were 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 onto a Hawksley haemocytometer. Twenty fields, 1 mm apart, on 2 transects across the slide were examined. Each field represented 25 squares of a gridded optical eye piece under 15 x 40 magnification. This is equivalent to 0.00156 mm^3 of solution per field.

The following categories were recognized in the sampling:

(a) Spore types - spores were classified into types according to morphological characteristics (Appendix 6). A reference collection of line drawings and photographs was kept to aid identification (photos 4.2.1, 4.2.2 and 4.2.3). The total number of spores of each type per field was recorded.

(b) Fungal matter - hyphal tissues and sterile columella.

(c) Cellular matter - cellular plant tissues, non-wheat.

(d) Wheat - wheat grain tissue.

(e) Sand grain.

Categories (b) to (e) 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 error per slide, @ 95% confidence limit expressed as percentage variation of the mean were: 18.24% (range 11.4 to 28) for fungus spores (based on the most frequent type, <u>Mesophellia</u> species); and 51.7% (range 31.2 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 4.2.1).

The stomachs of 11 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

Photo 4.2.1. Spores of
Mesophellia sp.
(Electron micrograph, 2500 mag.)
(Photo Nick Malajczuk)

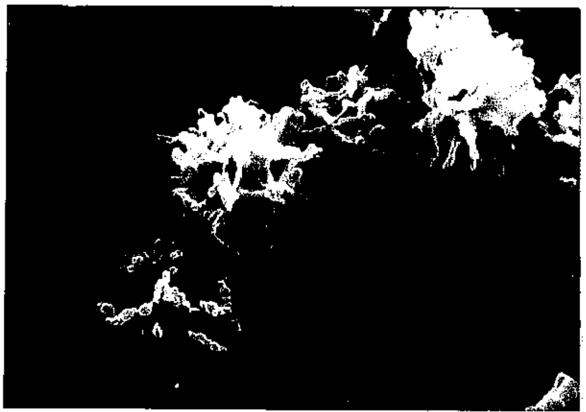


Photo 4.2.2. Spores of
Martellia sp. Nov.
(Electron micrograph, 2500 mag.)
(Photo Nick Malajczuk)

Photo 4.2.3. Spores of
Australasia chlorospora
(Electron micrograph, 5000 mag.)
(Photo Nick Malajczuk)

TABLE 4.2.1

Stomach content analysis - the woylie

History of animal	Non-spore material (% of total)				Fungus spore types													
	Fungal	Cellular	Wheat	Insect	Mesophellia	4	1	16	15	40	45	28	14	44	33	12	41	32
Killed by eagle in trap 11.2.75 B2/6	60	1.9	37.3	0.7	2													
W284 died heat exhaustion G4/14 5.3.75	5		95		1													
W51 killed by tammar in trap G/6.5 6.3.75	37	2.4	55.7	4.8	5	2												
Ch 9.15 died after fire 9.4.76	89		11		4	3												
W123 killed by tammar in trap 18.6.75	70		19.1	10.8	4	3												
W327 paralysis sample B2/4 19.6.75	75.5		24.5		4	2											4	1
W133 died paralysis 18.6.75	5		95		2	1												
Killed by native cat in trap G/22 1.7.74	60		40		5		3		1						1	2		
Road casualty Landgraft Rd 13.9.74	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	1						
Ch 8.3 asphyxiated during fire 19.3.76	96.7	3.3			5	1												

Fungal spores are estimated on a 5-point scale (see 4.2.1) petri dish of water and examine it under the microscope at 12 x 4 or 12 x 8 magnification. Twenty fields were examined in each of two separate samples using 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, 1975a) since the samples were non-quantitative.

4.2.2 Results

The Boyicup woylies' diet appears to be composed largely of fungi throughout the year (Fig. 4.2.1). Dependence on fungi is 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 shows a definite increase during this period (Fig. 4.2.2). Some of the starch grain appears 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.

The Tutanning woylie and the Boyicup bandicoot both have a much higher cellular component in their diet than the Boyicup woylie (Fig. 4.2.3 and 4.2.4): there is a more pronounced increase in the proportion of cellular matter over the spring period in the case of the Tutanning woylie and Boyicup bandicoot.

Results of stomach content analysis (Table 4.2.1) support the scat sampling results. With the exception of those stomachs contaminated with wheat, the major item in all stomachs is fungal matter. The lack of cellular material in the one stomach from Tutanning is interesting. Unfortunately it was undated and little is known about it.

There is a seasonal variation in the number of spore types (species?) recorded in scat samples (Fig. 4.2.5).

The number of spore types reaches a peak during spring with a smaller peak in autumn. Least variety exists 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 (e.g. Australasia chlorospora (Fig. 4.2.6)) or more rarely in spring alone (e.g. spore type 15 (Fig. 4.2.7)). A bimodal fruiting pattern is common in fungi where sporocarp production is controlled by environmental factors (Fogel, 1976).

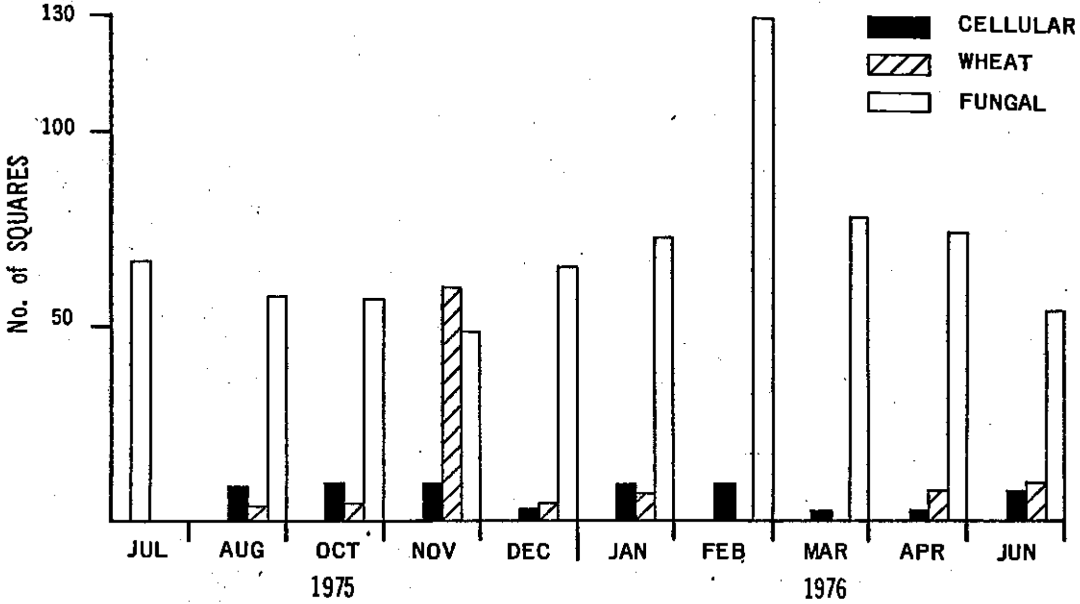


FIG.4.2.1 Boyicup - Seasonal variation in the quantity of cellular, wheat and fungal matter from woylie scats

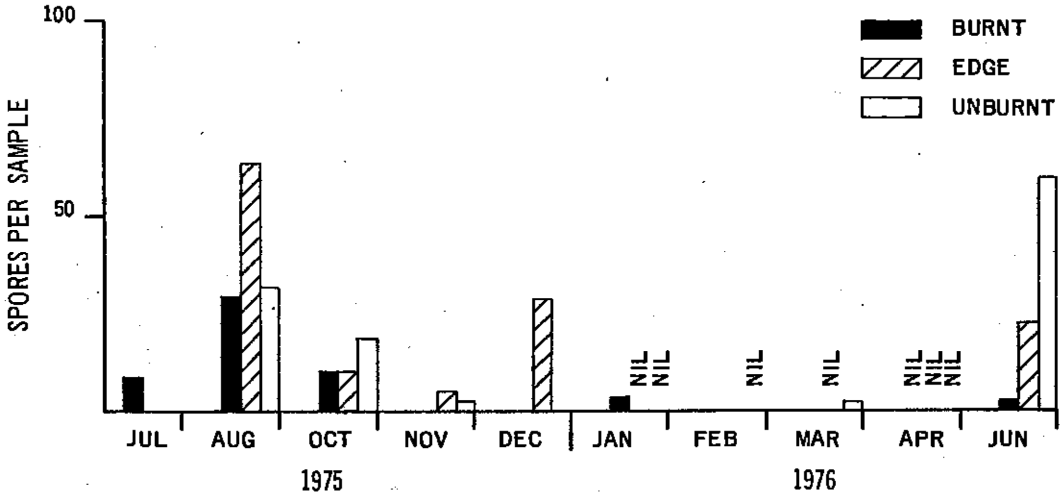


FIG. 4.2.2. Boyicup - Seasonal variation in the number of starch grains in samples from woylie scats

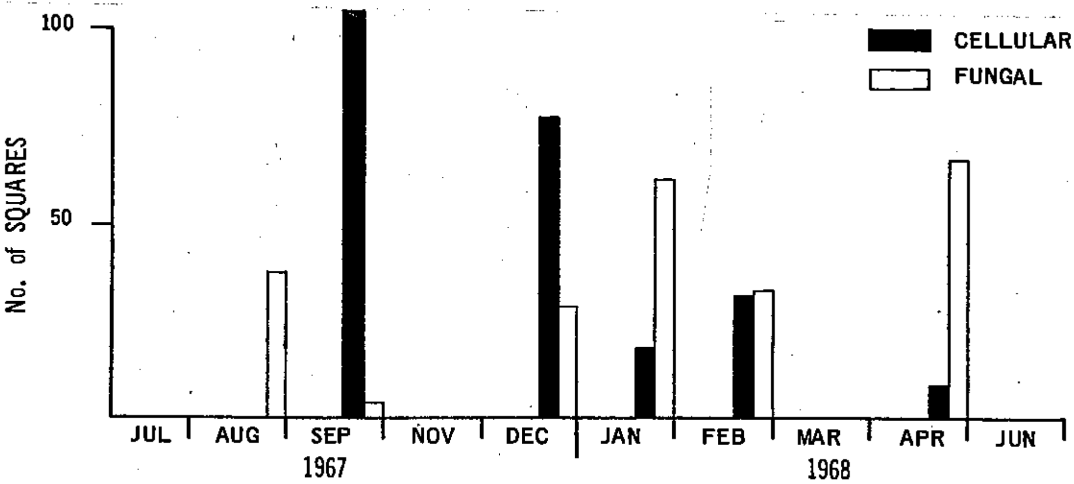


FIG.4.2.3 Tuttaning - Seasonal variation in the quantity of cellular and fungal matter in samples from woylie scats

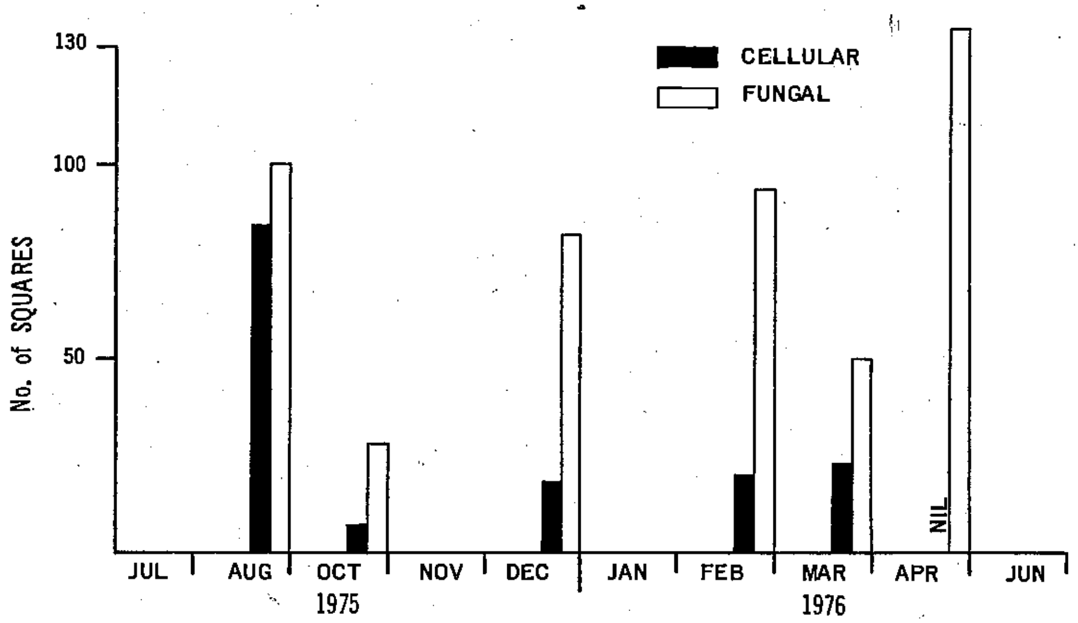


FIG. 4.2.4 Boyicup - Seasonal variation in the quantity of cellular and fungal matter in samples from bandicoot scats

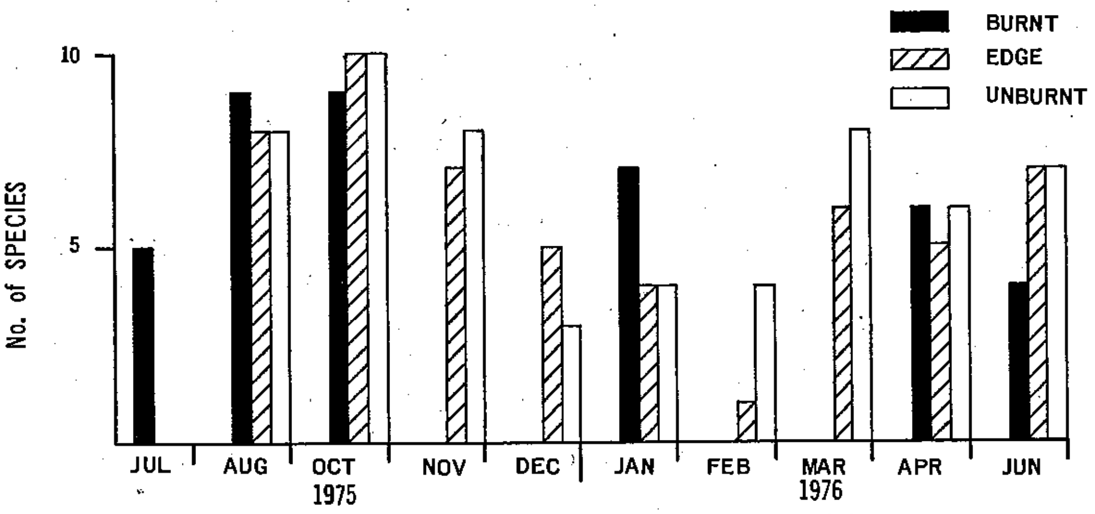


FIG. 4.2.5 Boyicup - Seasonal variation in the number of fungus species recorded in samples from woylie scats

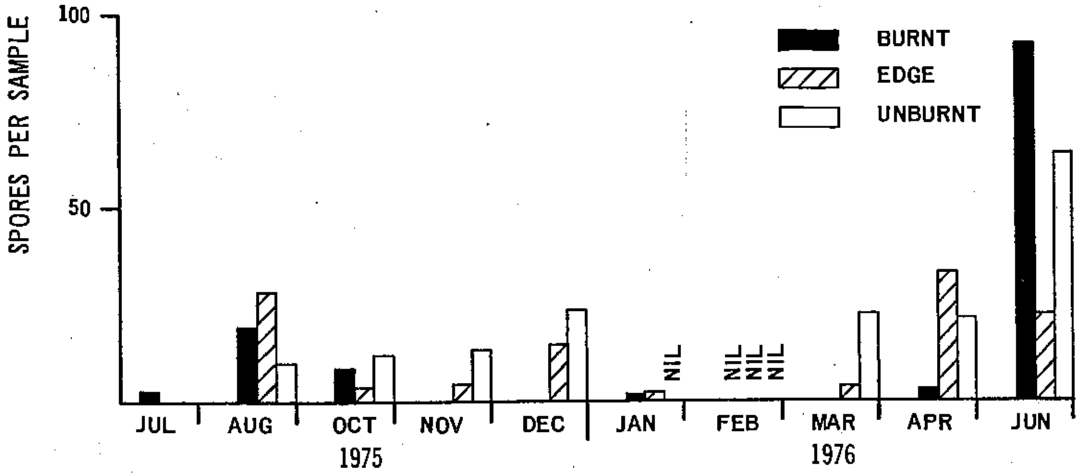


FIG. 4.2.6 Boyicup - Seasonal variation in the number Australasia chlorospora type spores in samples from woylie scats

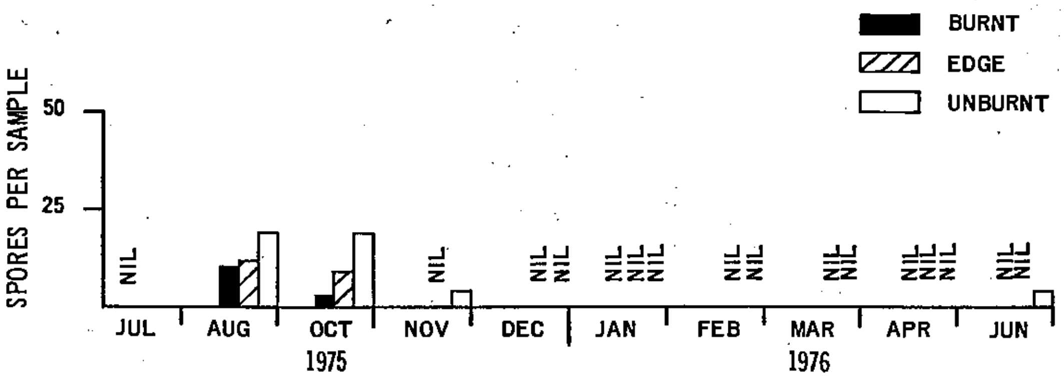


FIG. 4.2.7 Boyicup - Seasonal variation in the number of "Spore Type 15" spores in samples from woylie scats

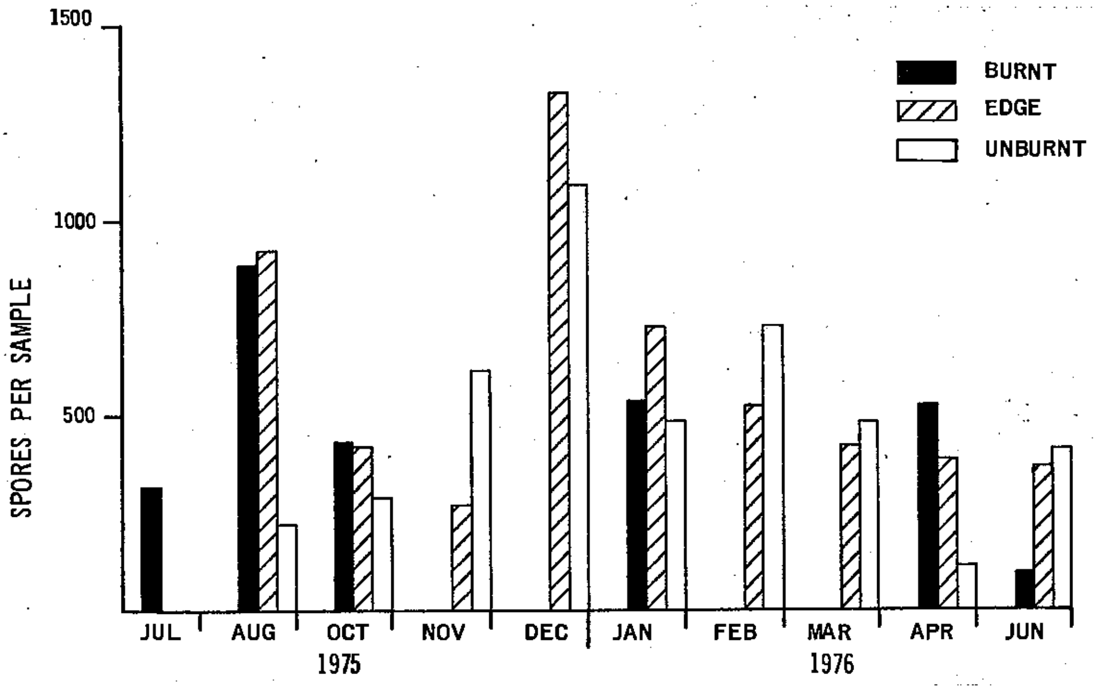


FIG. 4.2.8 Boyicup - Seasonal variation in the number of Mesophellia spores recorded in samples from woylie scats

The outstanding exception to this pattern of occurrence is the most frequently encountered spore type Mesophellia (Fig. 4.2.8). This spore type occurs more frequently during the summer months: it is 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.

4.3 Digging activity

4.3.1 Methods

The woylie makes characteristic small diggings when searching for fungi and other foods (Photo 4.1.2). Some confusion may arise since other animals, notably bandicoots, also dig holes. However, this species is not very common in the study area (Table 3.4.1), and furthermore, it is often possible to recognize its diggings by the characteristic 'v notch' shape and steep sides.

There is seldom anything left to indicate what a woylie was digging for. The remains of the outer coverings of the orange bulbs of Drosera bulbosa, orchid leaves and tops of certain unidentified small liliaceous plants are occasionally found.

To record digging activity on a seasonal basis, 36 plots each 15 x 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.

4.3.2 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. 4.3.1). 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. 4.3.1(a)). Significant differences were also recorded between individual unburnt plots on the same site (Figs. 4.3.2 and 4.3.3). Both of the plots with higher digging activity were on the edge of heartleaf thickets.

It is at the head of the drainage lines, often close to or on the edge of heartleaf thickets, that most of the digging takes place. Diggings were recorded on 280 plots each 10 x 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 4.3.1).

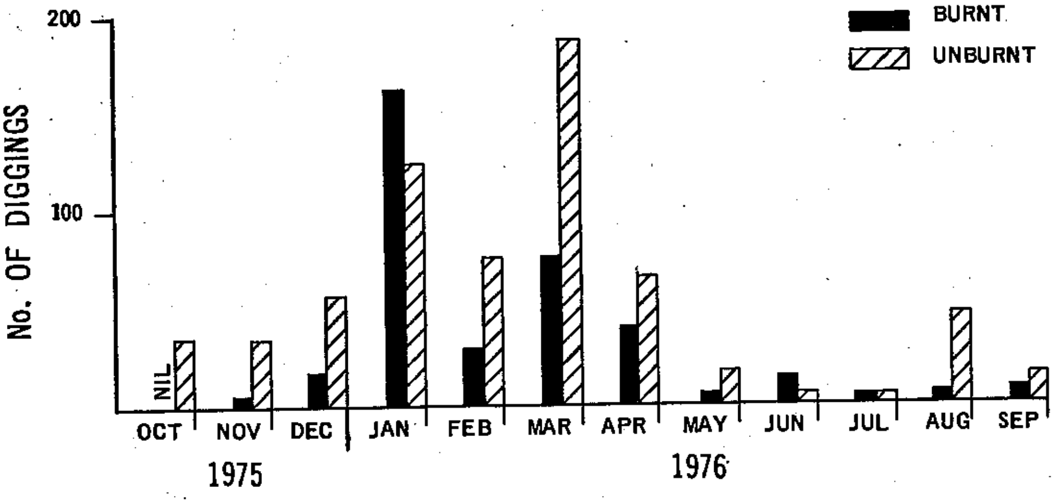
The most intense digging activity was recorded on the sandy loams associated with the heartleaf areas. On the lower slopes on the edge of the heartleaf thickets the number of diggings recorded was significantly higher than on either of the ridge sites.

4.4 Seed-burying habits

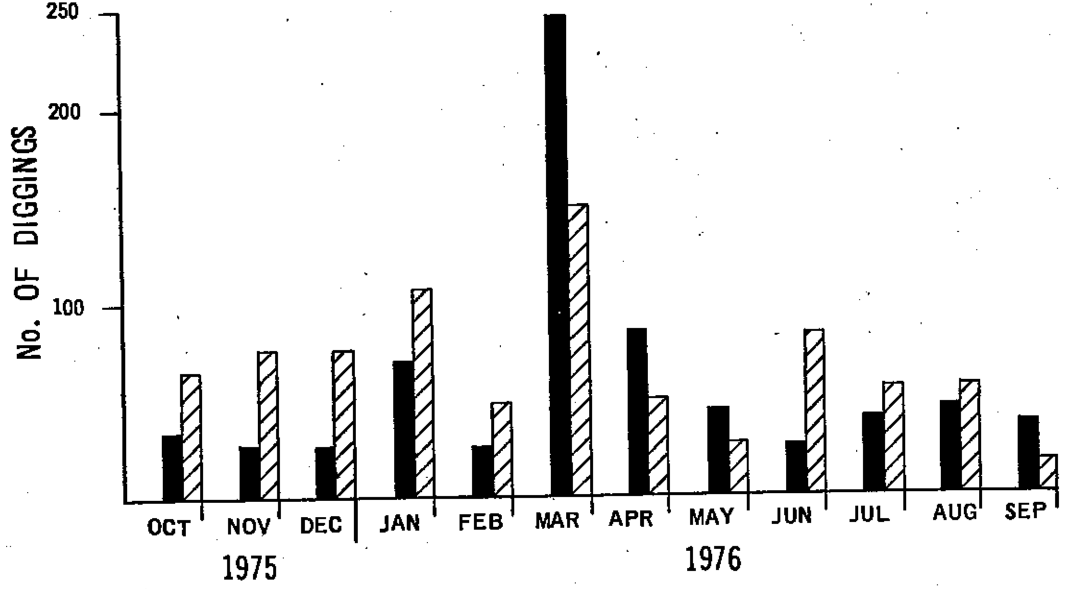
The woylie has a peculiar habit of burying small quantities of seed, seemingly at random, in places close to the source of origin. The habit has been commented on by a number of observers (Sampson, 1971). During this study it was first noticed after the 1975 fire when small clumps of green wheat plants 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 4.4.1). Approximately 40 to 50 grains are buried in any one hole.

WOYLIE DIGGING PLOTS

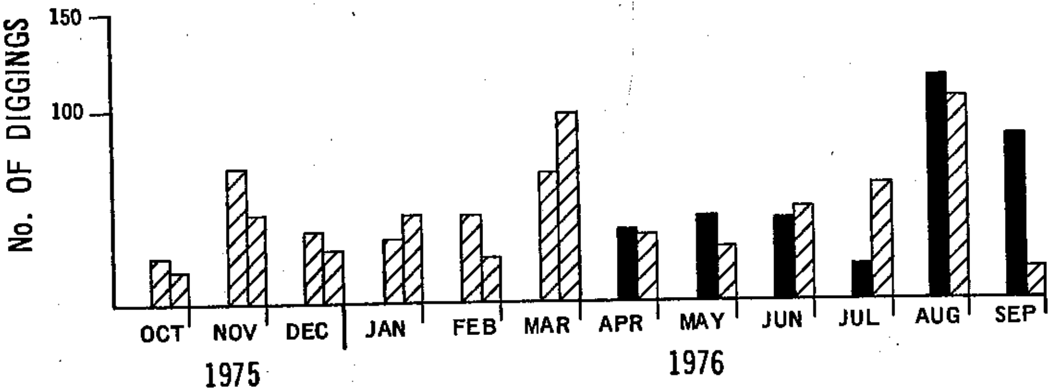
Fig.4.3.1(a) SITE 1: HEARTLEAF GULLY - 1976 BURN.



(b) SITE 2: B.ORNATA RIDGE - 1975 BURN.



(c) SITE 3: B.ORNATA RIDGE - 1976 BURN



Mean number of diggings per month in six, 225 m^2 plots in burnt and unburnt areas on three sites.

WOYLIE DIGGING PLOTS

Fig. 4.3.2(a)

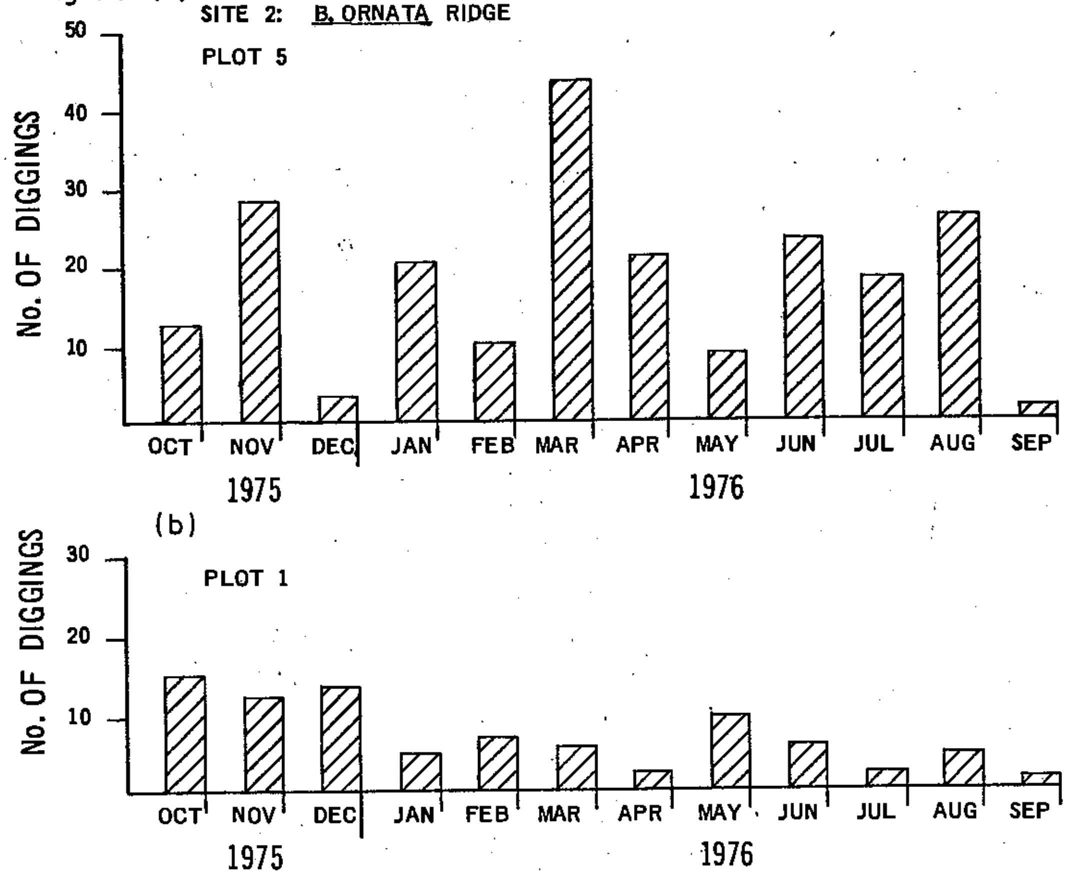
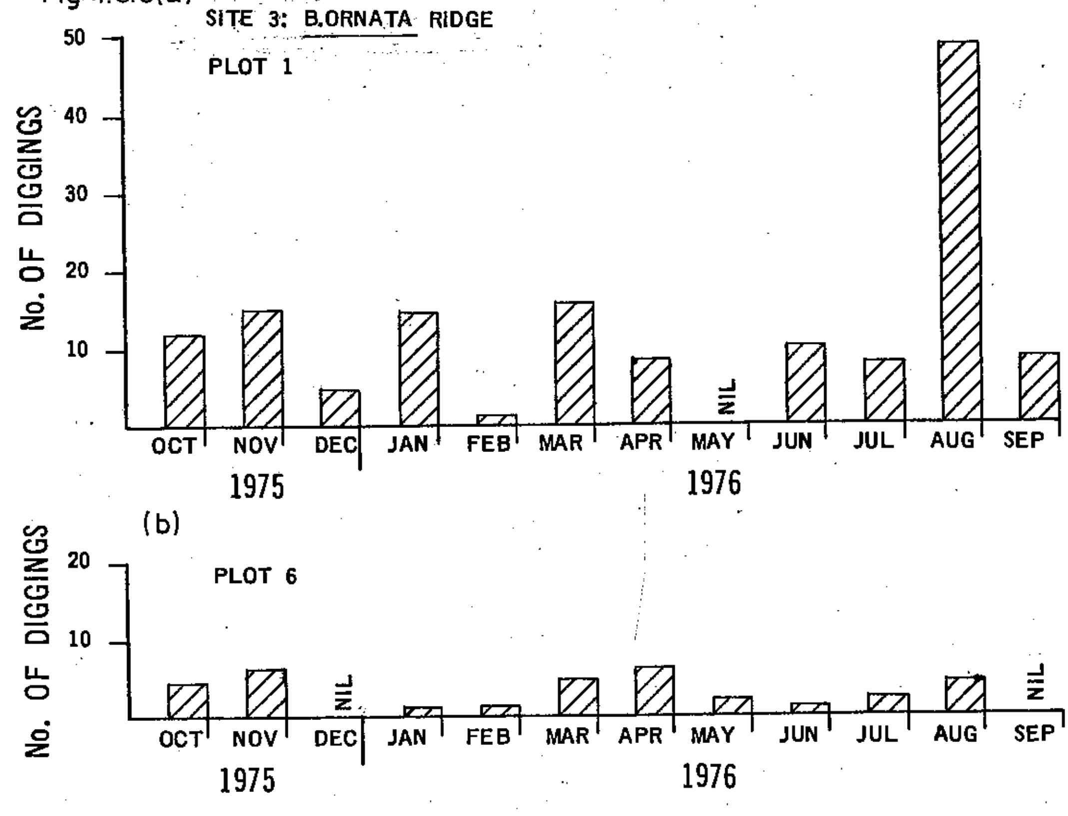


Fig. 4.3.3(a)



Monthly digging activity on pairs of unburnt plots from each of the ridge sites. The plots show a significant difference in the number of diggings over a one year period. Significant at 0.01 level.

TABLE 4.3.1

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)

( ) Total no. of 10 x 8 m plots sampled within each site type

TABLE 4.5.1

Tammar stomach contents

History of animal	% Monocot material (grass)	% Dicot material	Comments
Died in trap 27.11.74	95	-	A little fungal matter present
Fox kill 21.4.75	-	95	No monocot material, a little fungal matter
Died in trap 10.7.75	50	50	
Died in trap 26.11.75	90	10	

TABLE 4.4.1

Distance from funnel traps to clumps of wheat germinated from seed buried by woylies

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

Heartleaf seed was observed germinating in similar small clumps after the fire (Photo 4.4.1). 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_ (Oliver, personal communication).*

4.5 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) concludes that it is a very adaptive feeder. Tammars browse predominantly on 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 4.5.1). 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 indicate that the tammar rarely leaves the heartleaf areas, spending the nights feeding within or close to these thickets. The major understorey is composed almost entirely of grasses and annual herbs. Five species of grass have been identified in the area, viz. _Danthonia pilosa_, _Stipa semibarbata_, _Airia carvophylla_, _Bromus hordaceus_ and _Vulpes bromoides_. The last three species are introduced. Observations before the fire indicated that there was very heavy grazing pressure on these grasses.

4.6 Fire effects on food resources

4.6.1 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

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* T. Oliver, Agriculture Protection Board, Perth.

months (July, August and October) in the 1975 burn, Mesophellia species increased in the scats (Fig. 4.2.8).

Fire had remarkably little effect on digging activity as evidenced from the permanent plots. Neither was there any significant difference in the number of diggings recorded on the edge and 300 m inside the burn.

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 (Fig. 4.3.1 (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 (Fig. 4.3.1 (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 4 years previously compared with those that had been burnt 9 years previously (Table 4.3.1).

The decrease in digging activity during spring after the fire coincides with the increase in Mesophellia spores in scats from burnt areas and occurs at a time when consumption of Mesophellia is at its lowest on the unburnt areas (Fig. 4.2.8). There is also a marked increase in peridial remains, mainly Mesophellia species, found associated with diggings after the fire (Table 4.6.1).

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 recognized in the scats and these were separated as types two, three, five, seven and thirteen. 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 is 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 4.6.2).

On the other hand, Mesophellia-type sporocarps formed the vast majority of the fungus collection made during May 1975 on an unburnt area. Also, the fact that peridial remains are found next to diggings so soon after fire (Table 4.6.1(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 10 days after fire a large white mushroom appears, which is followed 3 to 4 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 81 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, 14 weeks after the fire, few fungi were to be found.

4.6.2 The tammar

There is direct evidence that fire intensity can influence the grasses that are the tammar's main food source in the Boyicup area (Table 2.6.2). In those places where fire is hot enough to cause

TABLE 4.6.1

(a) No. of diggings with hypogean fungal remains - 1975 burn, 6 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

TABLE 4.6.1

(b) No. of diggings with hypogean fungal remains - 1976 burn, 3 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 4.6.2

The distribution of <u>Mesophellia</u> species peridial remains on the digging plots

	Burnt plots			Unburnt plots		
	Ridge plots		Heart-leaf gully	Ridge plots		Heart-leaf gully
	18.3.75	18.3.7~~5~~6	18.3.75	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 <u>Mesophellia</u> remains on six 15 m x 15 m plots. Burns were carried out on 18 March 1975 and 18 March 1976 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 (Photo 4.6.1). 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 2.6.2).

4.7 Discussion

4.7.1 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 by 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 due to variations 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 7).

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 K, Ca, Mg and Mn, but higher in N and P. 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% (MEOH/CH_3Cl extraction) and 37.5% (petroleum ether extraction) (Kinnear, personal communication). *

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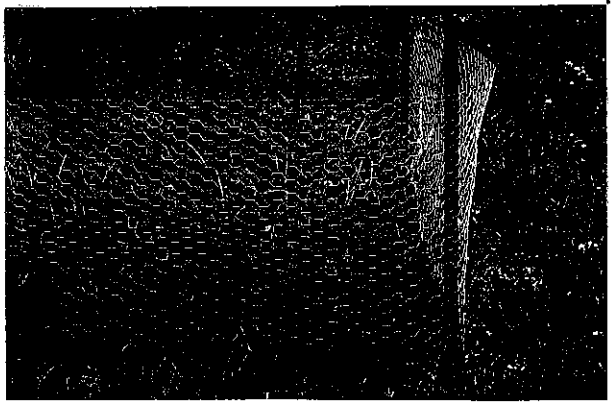
*J. Kinnear, Zoology Department, University of W.A.

Photo 4.4.1. Clump of heartleaf seedlings germinated after a hot fire from seed buried by a woylie.

Photo 4.6.1. Exclusion plot in burnt heartleaf 8 months after burning. Note growth of grasses within enclosure in comparison with that outside.



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 (Photo 4.1.1). Most of the spores in woylie scats appear to be morphologically mature and pass through the gut apparently unharmed (Photo 4.1.3). 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 of importance with regard to fire effects, is that many 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 N 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 N 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 9 years old was significantly less than on sites 4 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 fire.

The concept of N 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 N 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.

4.7.2 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 2.5.2). The rarity of grasses in south-western ecosystems has already been mentioned (see 2.5.2), and it is considered that the role of heartleaf in N 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.

5. GENERAL DISCUSSION

5.1 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 (1975a), who found indication 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 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 inhabitat 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 suppotred by evidence of the disappearing of the woylie from certain areas of State forest some time after 1930 (D. 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 the fire. Re-population of the area will be effected by young animals from the unburnt surrounds and large unburnt patches.

Results were in general agreement 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-organization 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-colonization 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 of importance for two reasons. Firstly, the range of responses, viz.staying and dying, partial re-organization 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 very high order of fidelity to home range was observed by 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-organization 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 in 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. Whilst 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 woylie's 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 of importance and in a large fire situation there may well be less movement out of the burnt area.

5.2 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 of importance 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.

How 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 mozaic 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 a 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?

5.3 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 fires 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 in 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 colonizers for the burn. Similarly, the tammar is well adapted to re-colonize 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.

5.4 The significance of fire dependence in relation to the woylie and the tammar

Fire dependence may be expected to mainfest 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.

5.4.1 The structural component of the habitat

(a) 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 *Gastrolobium 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. Fertilizer 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 woylie's 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.

(b) 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 25 to 30 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.

5.4.2 (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 hypogean fungus sporocarps and also the grasses that constitute the food of the tammar.

There is increasing evidence that native legumes play an important rōle 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 association 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 distrubution and numbers.

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APPENDIX 1

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 ht. 16-18 m, low open understorey, typical sp. *Leucopogon pulchellus*; others *Hakea lissocarpha*, *Astroloma pallidum* and *Pimelia suaveolens*. Light-coloured stony soil.
B Camelar	10	•+•	Ridge site, jarrah-wandoo forest, canopy ht. 17-21 m. Low open understorey, typical sp. *Hypocalymma angustifolia*, *L. pulchellus*, *Dryandra nivea*, *Acacia pulchella*. Clayey soil.
C Dudijup	10	*	Ridge-top site, jarrah forest, canopy ht. 25-30 m. Low fairly dense understorey, typical sp. *Bossiaea ornata*, *Xanthorrhoea gracilis*, *L. capitellatus*, *Persoonia longifolia*. Gravelly sandy loam.
D Eastern Rd.	15	* *	Lower slopes, jarrah-wandoo forest, canopy ht. 19-24 m. Low to medium understorey, typical sp. *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 ht. 20-30 m. Low understorey, typical species *B. ornata*, *H. lissocarpha*, *Thomasia grandiflora*, *A. pallidum*. Light coloured clayey soil.
F Boyicup	32	* *	Ridge sites, jarrah forest, canopy ht. 18-25 m. Low fairly dense understorey, typical sp. *B. ornata* *H. lissocarpha*, *L. capitellatus*, *Macrozamia riedlei*. Gravelly sandy loam.
G Mordalup Rd.	10	+	Ridge site. High quality jarrah forest, canopy ht. 25-30 m. Low dense understorey, typical sp. *B. ornata*, *H. lissocarpha*, *L. capitellatus*, *P. longifolia*. Gravelly clayey loam.

Appendix 1 (cont.)

Site and location	Plots sampled	Woylies	General description
H Moopinup	15	'+'	Largely ridge sites. Dry eastern jarrah forest, canopy ht. 16-25 m. Low open understorey, typical sp. *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 species *Acacia cyanophylla*, *Hakea prostrata*, *Hypocalymma angustifolia*, *Drosera bulbosa*. Very shallow clayey soils.
J Nyamup	15	+	Ridge-top site, high quality western jarrah-marri forest, canopy ht. 35-40 m. Medium ht. dense understorey, typical sp. *Hovea elliptica*, *B. linophylla*, *Pteridium esculentum*, *Clematis pubescens*. Clayey soils.
K Granite outcrop	10	'+'	Ridge-top granite outcrop, few trees, dense low understorey. Typical sp. *Dryandra ornata*, *Hakea undulata*, *Gastrolobium bilobum*, *Baeckea camphorosmae*. Shallow coarse sandy soil.
L Northern Rd. South	15	'+'	Low lying marri-jarrah forest, canopy ht. 25-30 m. Low open understorey largely composed of monocot sp., also present are *B. linophylla*, *Hibbertia glabberrima*, *L. australis*. Grey sand.
M Northern Rd. Wandoo	12	'+'	Low ridges, Wandoo forest, canopy ht. 18-20 m. Very open understorey, typical sp. *H. angustifolia*, *A. pulchella*, *L. pulchellus*, *D. nivea*. Clayey soil.
N Warrup	15	'+'	Ridge, high quality jarrah forest, canopy ht. 26-32 m. Low open understorey, typical sp. *L. propinquus* *C. aristata*, *Macrozamia riedlei*, *Banksia grandis*. Sandy loam.
O Melaleuca thicket	7	'+'	Eastern jarrah-wandoo forest. Dense medium ht. 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.

Appendix 1 (cont.)

Site and location	Plots sampled	Woylies	General description
P Melaleuca flat	7	+	Eastern jarrah-wandoo forest. Dense medium ht. 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 ht. M. viminea thicket on grey sandy soil along drainage lines, seasonally wet, understorey of small monocots.

NB. These sites are not equivalent to the site-vegetation types of Havel (1975).

Woylies + = Not present
·+· = Transitory
* = Low to medium density populations
⁑ = High density population

APPENDIX 2

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 - 0-60 cm)
5. Scrub density - 60-120 cm) density estimated*
6. Scrub density - 120-240 cm)
7. Scrub density - 240 cm+)
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 x 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)(ppm); N, C (%); pH

    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 methodof MacArthur (1961). The eye of the observer standing in the middle of the plot was kept at a certain height above the ground whilst 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%. 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.

Appendix 2 cont

** 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 W.A. Forests Department.

APPENDIX 3

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 posterointernal talon, (Wood-Jones, 1923-25) 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).

Age curves based on head length data (Appendix 3(a)) and tooth eruption (Appendix 3(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 whilst 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

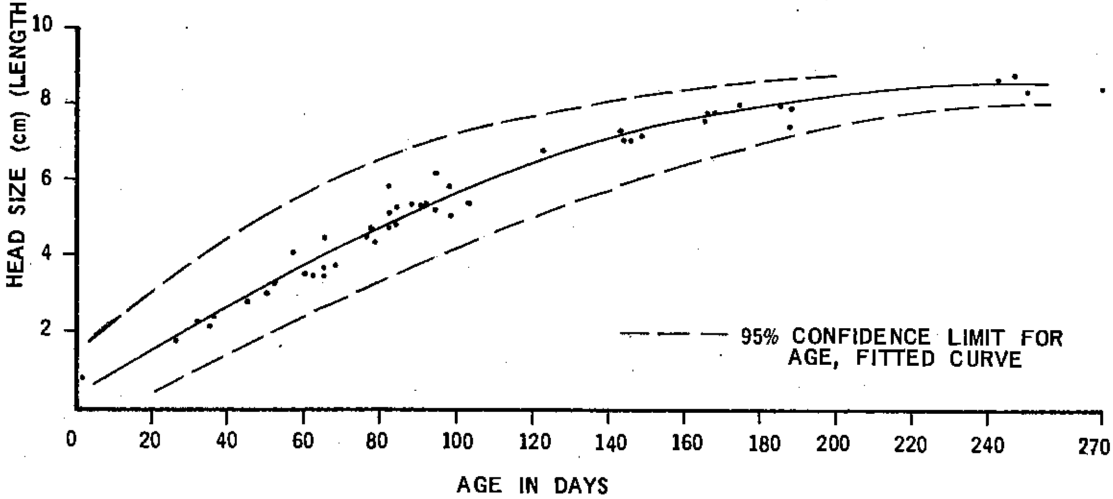
Graphs for ageing the tammar were constructed initially with the pes, tail and weight data of Jones et al., (1966) to age joeys. These data were used to start curves which were built on with further data from Boyicup animals (Appendixes 3(c) and (d)).

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 Appendix 3(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.

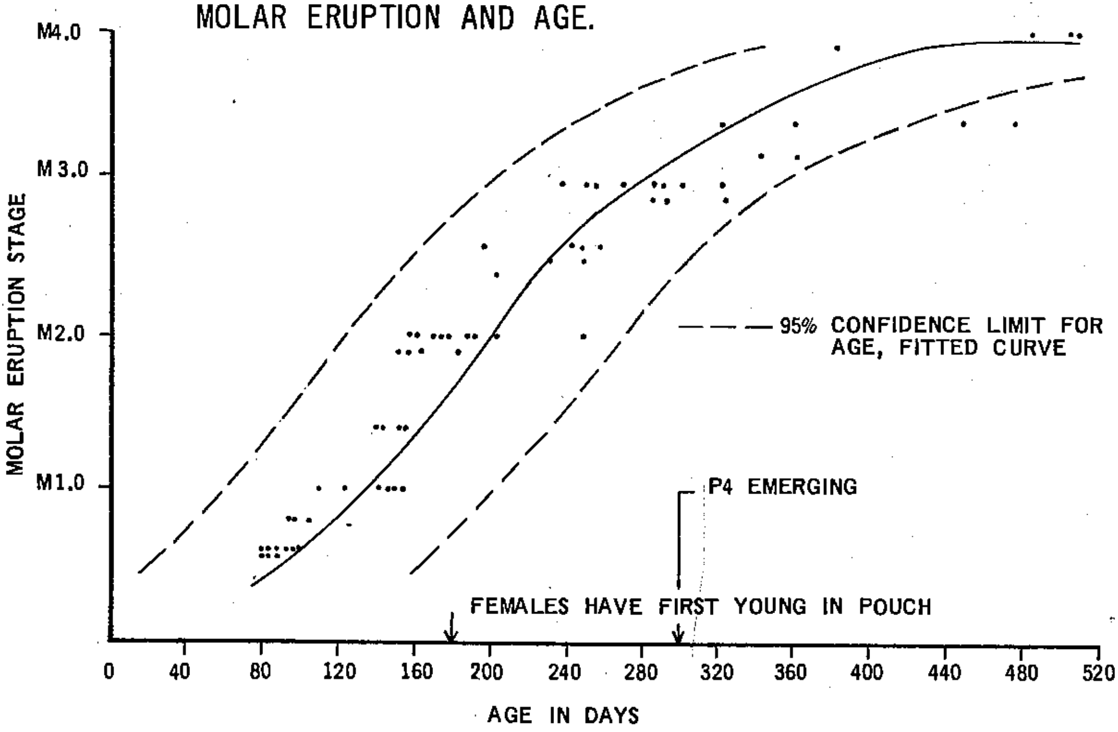
Appendix 3(a)

THE WOYLIE - GRAPH SHOWING THE RELATIONSHIP BETWEEN HEAD SIZE AND AGE.



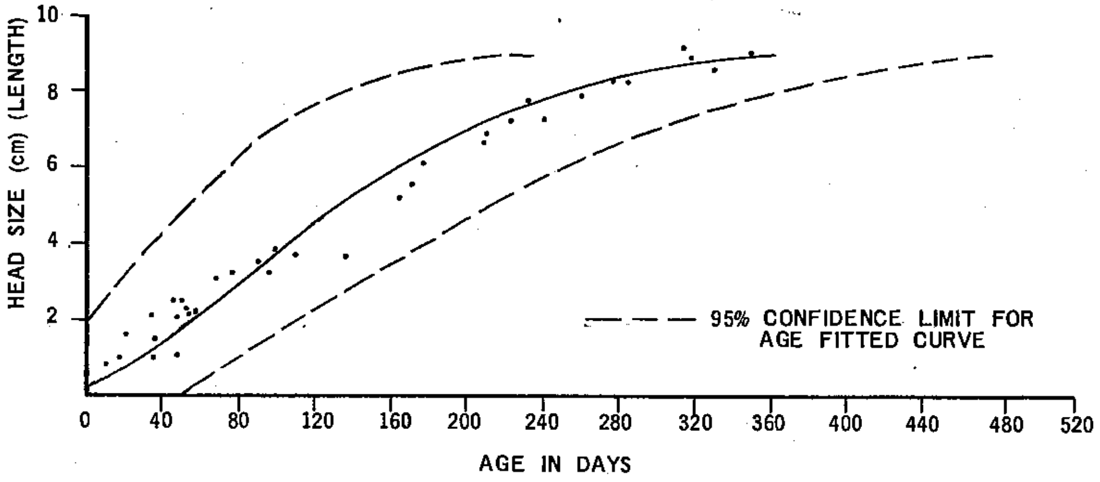
Appendix 3(b)

THE WOYLIE - GRAPH SHOWING THE RELATIONSHIP BETWEEN MOLAR ERUPTION AND AGE.



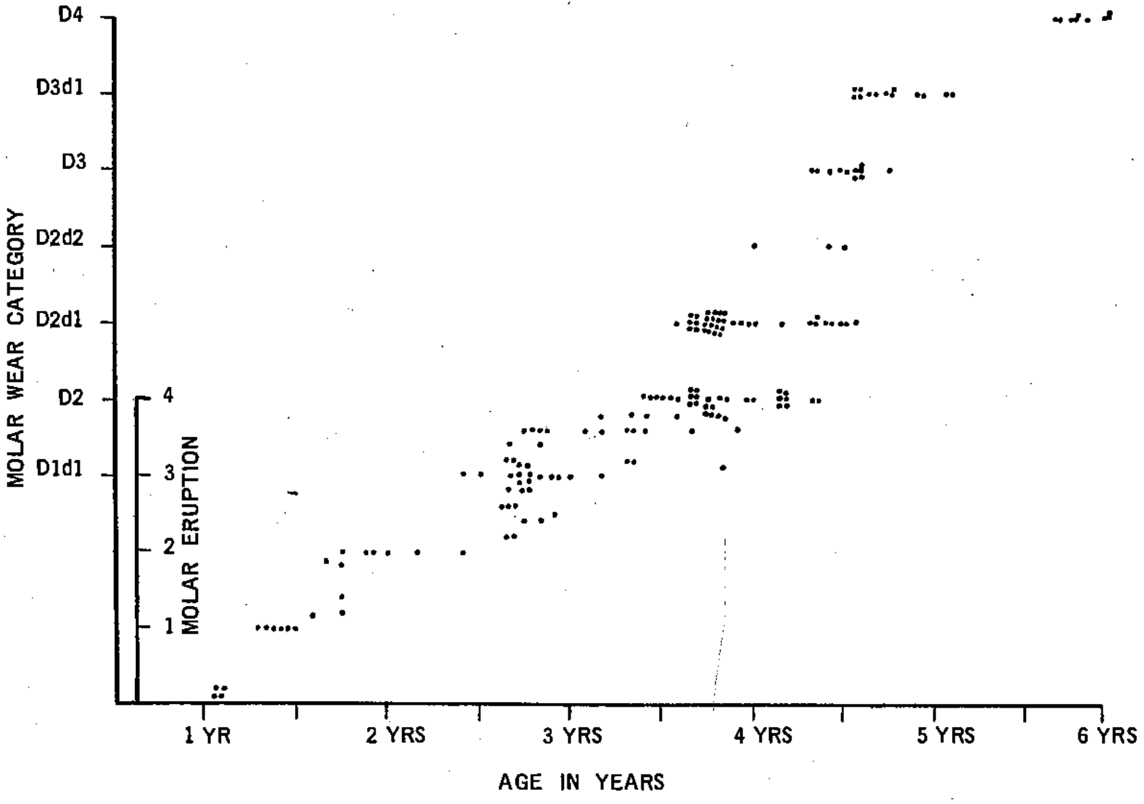
Appendix 3(c)

THE TAMMAR - GRAPH SHOWING THE RELATIONSHIP BETWEEN HEAD SIZE AND AGE.



Appendix 3(d)

THE TAMMAR - GRAPH SHOWING THE RELATIONSHIP BETWEEN MOLAR ERUPTION, WEAR AND AGE.



APPENDIX 4

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. (Daytime 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 5

DATES REFERRING TO NUMBERS ON RADIO LOCATION MAPS

(FIGS. 3.4.7, 3.4.8, 3.5.4 and 3.6.3)

1975 Burn	
1	25/2/75
2	26/2
3	27/2
4	28/2
5	3/3
6	4/3
7	6/3
8	10/3
9	11/3
10	12/3
11	13/3
12	14/3
13	17/3
14	18/3
15	19/3
16	20/3
17	21/3
18	24/3
19	25/3
20	26/3
21	27/3
22	28/3
23	30/3
24	1/4
25	3/4
26	7/4
27	10/4
28	14/4
29	17/4
30	18/4
31	21/4
32	22/4
33	23/4
34	24/4
35	29/4
36	31/4
37	5/5
38	8/5
39	9/5
40	12/5
41	19/5
42	23/5
43	25/5
44	27/5
45	28/5
46	30/5
47	3/6
48	5/6
49	9/6
50	10/6
51	17/6
52	20/6
53	25/6
54	27/6
55	2/7

1976 Burn daytime location	
1	20/2/76
2	23/2
3	24/2
4	25/2
5	26/2
6	27/2
7	2/3
8	4/3
9	8/3
10	10/3
11	11/3
12	15/3
13	17/3
14	18/3
15	19/3
16	22/3
17	24/3
18	26/3
19	29/3
20	1/4
21	5/4
22	7/4
23	9/4
24	13/4
25	15/4
26	20/4
27	22/4
28	27/4
29	28/4
30	29/4
31	30/4
32	7/5
33	12/5
34	17/5
35	24/5
36	28/5
37	2/6
38	10/6
39	14/6
40	17/6
41	5/7
42	29/7
43	19/8
44	25/8
45	26/8
46	27/8

Nocturnal location	
1	26/2
2	8/3
3	11/3
4	18/3
5	30/3
6	1/4
7	14/4
8	27/4
9	7/5
10	17/5
11	28/5
12	16/6
13	5/7
14	29/7
15	23/8
16	26/8

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

APPENDIX 6

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 x 5 - hyaline and smooth
3	Yes						10 x 5 - hyaline and smooth
5	Yes						10 x 5 - hyaline and slightly knobbly in appearance
7	Yes						12 to 13 x 5 - hyaline, oval, scar of attachment
13	Yes						12 to 14 x 5 - hyaline, oval and smooth
4	Yes	3	3	1			12 x 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 golf ball
18	Yes	1			1		6 to 8 diameter - hyaline, spherical, knobbly
11	Yes				1		12 x 5 - hyaline, oval, looks like a spindle
12	Yes	3	1				8 x 5 - hyaline, lemon shaped
14	Yes	2	2		2		15 x 30 - dark, oval with pointed ends
15	Yes	3	1			1	4 x 5 - greenish brown, oval, knobbly
16	Yes						10 x 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

Appendix 6 (cont.)

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	
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 x 5 - yellow brown, banana shape, thick walled, stalk
17	Yes	2					12 x 7 - hyaline, slightly opaque, rounded oval with bumpy surface
41	No	3	2		2		3 x 1 - hyaline, oval
42	No	1					7 x 5 - dark, irregular pear shape
43	No			1			20 x 10 - brownish yellow, oval, with stalk, thick walled
45	No					1	
44	No		1				16 diameter - dark, spherical, with very long numerous spines
28	No					1	15 x 8 - dark, oval, with stalk, smooth thick wall
29	No				2		15 x 5 - dark, oval, thick wall with septa
46	No				2		18 x 8 - yellow brown, oval, scar of attachment knobbly
37	No	2					7 x 7 - brownish yellow spherical thick wall

Scale of increasing frequency 0-5 (see 4.2.1)

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 7

Concentrations of elements in selected green and senescent leaves and fungi

Species	Element													
	% N	% P	% K	% Ca	% Mg	% Na	% Si	% Al	% S	Mn ppm	Zn ppm	Cu ppm	Cl ppm	Ni ppm	Fe ppm
Jarrah Eucalyptus marginata leaves (green)	0.84	.041	.57	.58	.43	.29	-	-	.103	117	5.6	2.9	-	-	-
Jarrah E. marginata Leaves senescent	0.30	.009	.26	.74	.40	.29	-	-	.085	192	3.0	2.5	-	-	-
Acacia pulchella leaves (green)	2.15	.039	..86	1.19	.24	.03	-	-	.209	47	8.0	4.5	-	-	-
Mesophellia sp. central core. Spores*	1.64 *3.52	.085	.26	.042	.060	.047	.088	.105	.30	9.4	35.8	14.3	.029	2.0	127
Agaricales sp.	2.8	.34	2.6	.028	.09	.13	-	-	.283	21	47	24	-	-	-

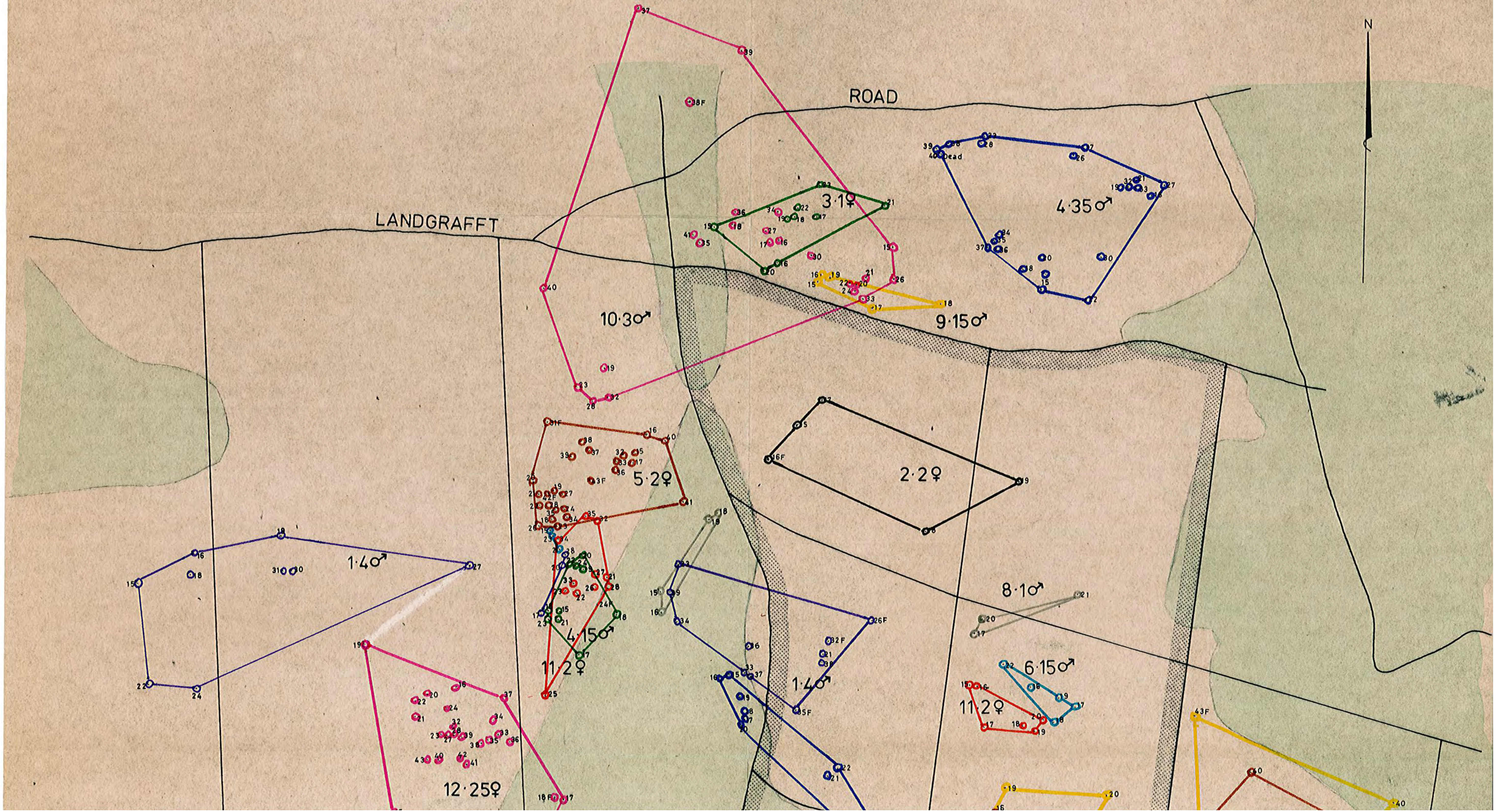
N. concentration of Mesophellia sp. supplied by J. Kinnear Zoology Dept. Uni of W.A. (personal communication)

Other data supplied by Dr. N. Malajczuk, CSIRO Perth (personal communication)

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

FIG. 3.6.3a

1976 BURN
DAYTIME RADIO LOCATIONS OF WOYLIES - AFTER BURN



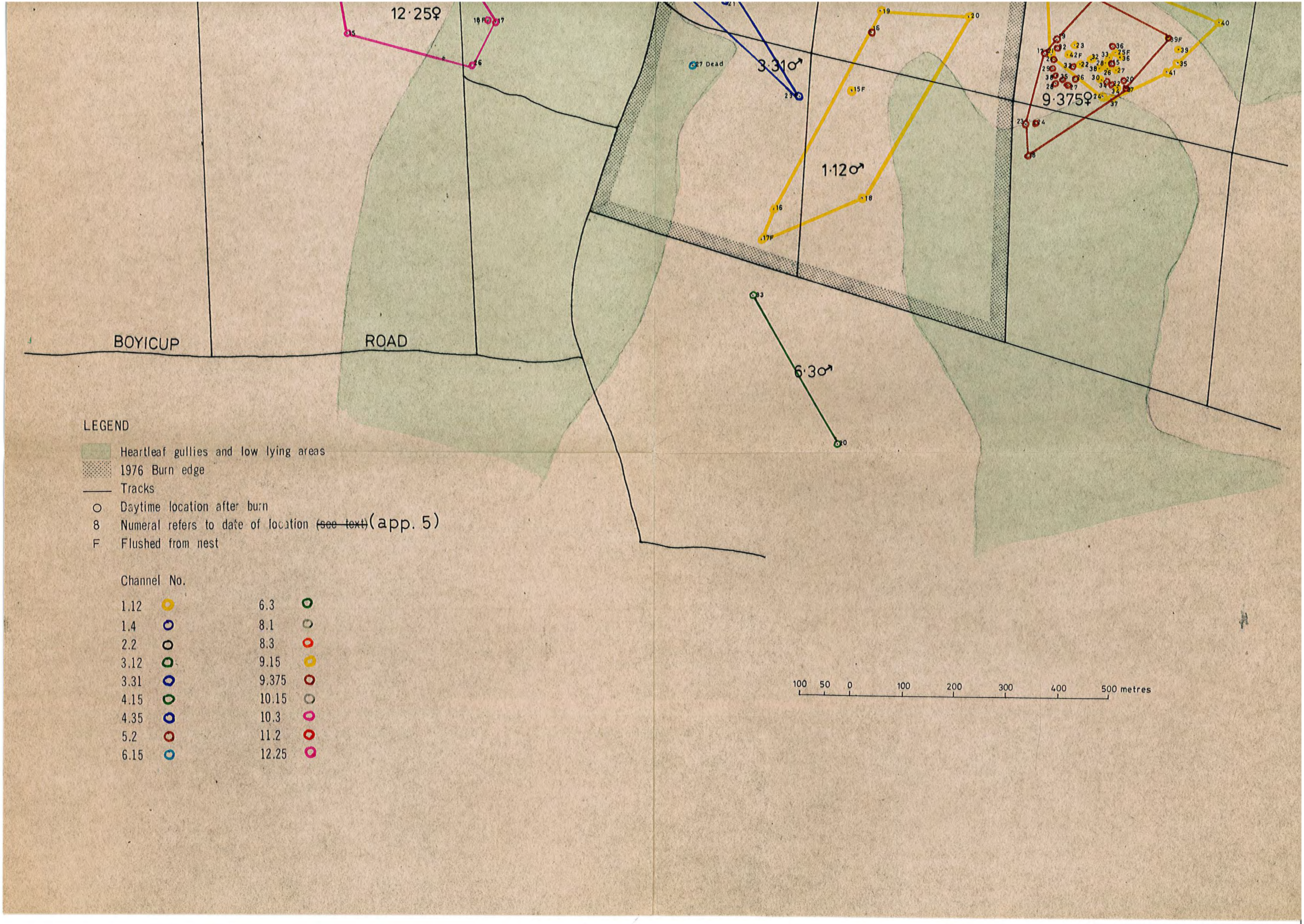
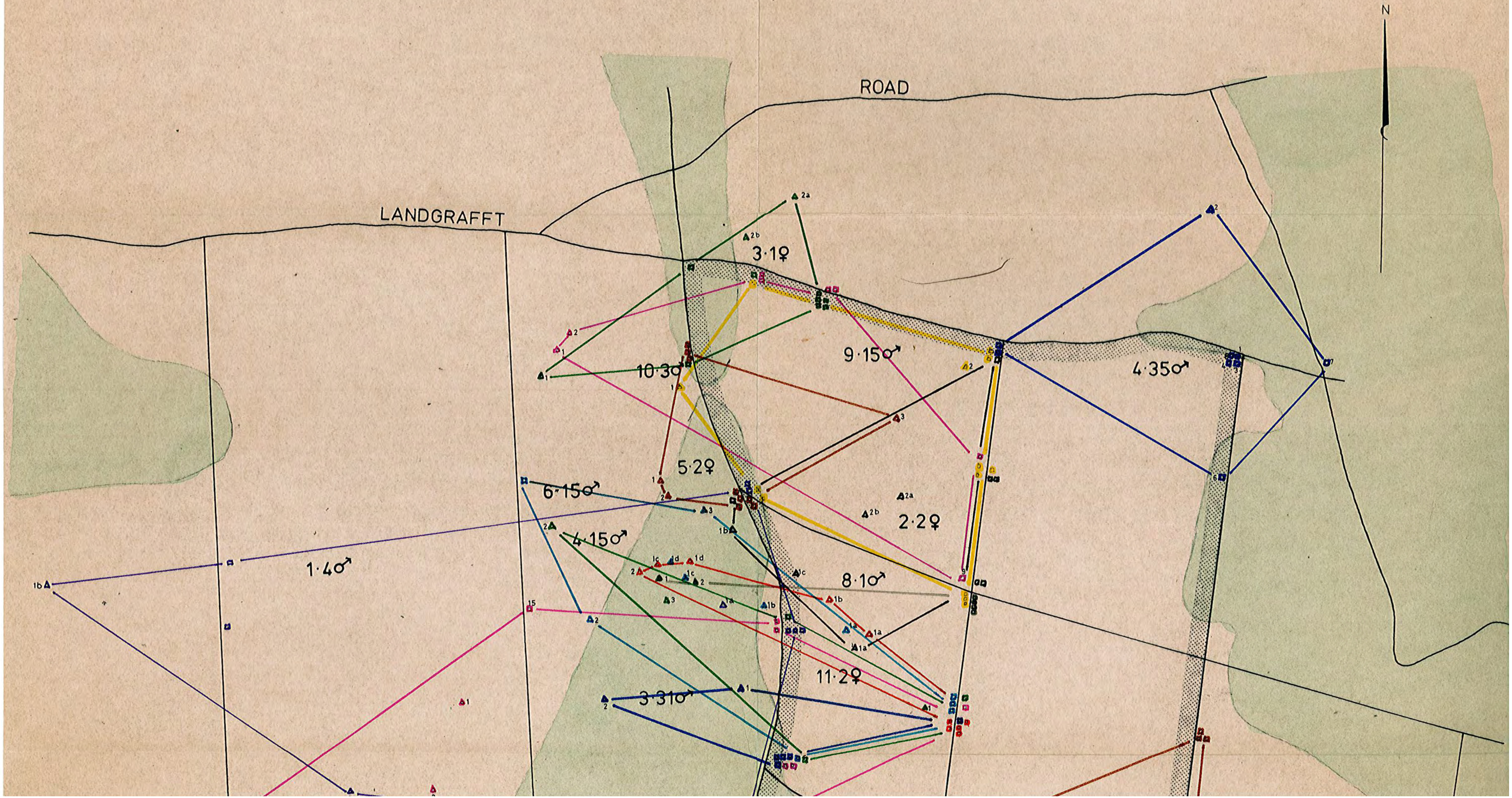

12·25♀
18F
17
5
6
21
27 Dead
3·31♂
23
19
20
16
15F
1·12♂
18
16
17F
40
19
9F
39
35
41
9·375♀
23
24
8
33
6·3♂
30
BOYICUP
ROAD
LEGEND
Heartleaf gullies and low lying areas
1976 Burn edge
Tracks
Daytime location after burn
8 Numeral refers to date of location ~~(see text)~~ (app. 5)
F Flushed from nest
Channel No.
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
100
50
0
100
200
300
400
500 metres

FIG. 3.4.8.b

1976 BURN
NIGHT-TIME RADIO LOCATIONS
AND CAPTURES OF WOYLIES - BEFORE BURN



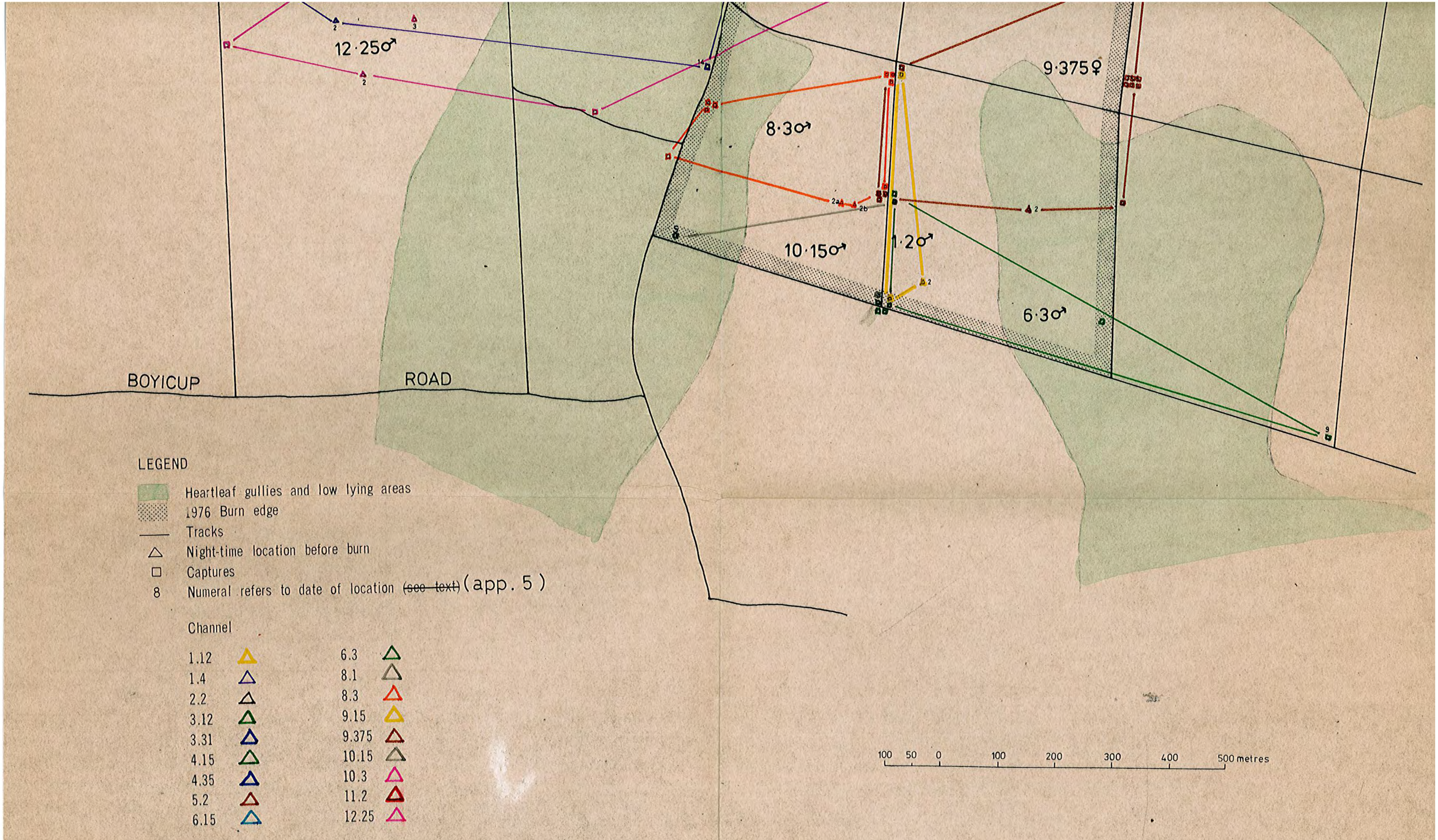
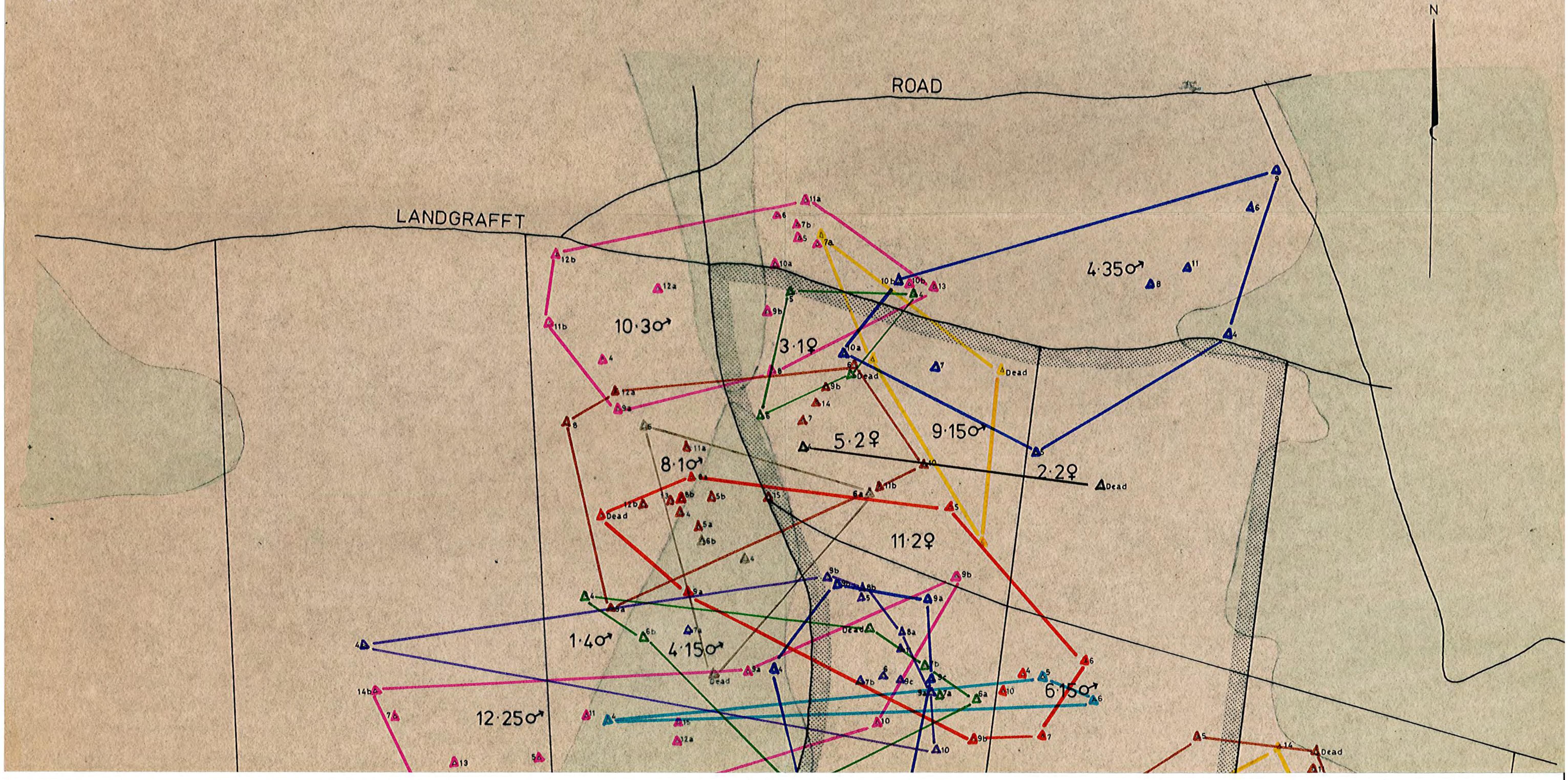

12·25♂
9·375♀
8·3♂
10·15♂
1·2♂
6·3♂
BOYICUP
ROAD
LEGEND
Heartleaf gullies and low lying areas
1976 Burn edge
Tracks
△ Night-time location before burn
☐ Captures
8 Numeral refers to date of location ~~(see text)~~ (app. 5)
Channel
1.12
1.4
2.2
3.12
3.31
4.15
4.35
5.2
6.15
6.3
8.1
8.3
9.15
9.375
10.15
10.3
11.2
12.25
100 50 0 100 200 300 400 500 metres

FIG. 3.6.3b

1976 BURN
NIGHT-TIME RADIO LOCATIONS OF WOYLIES - AFTER BURN



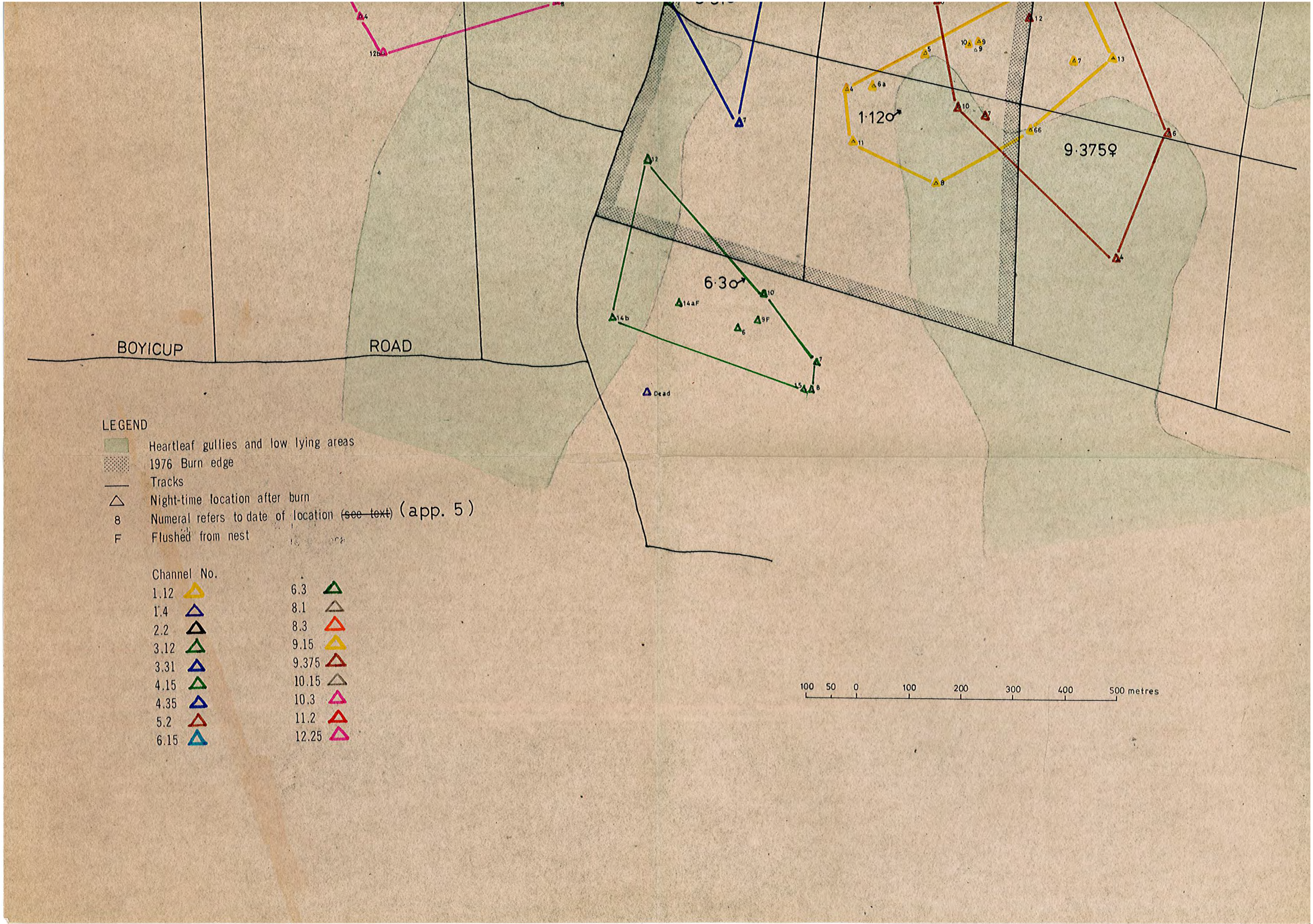
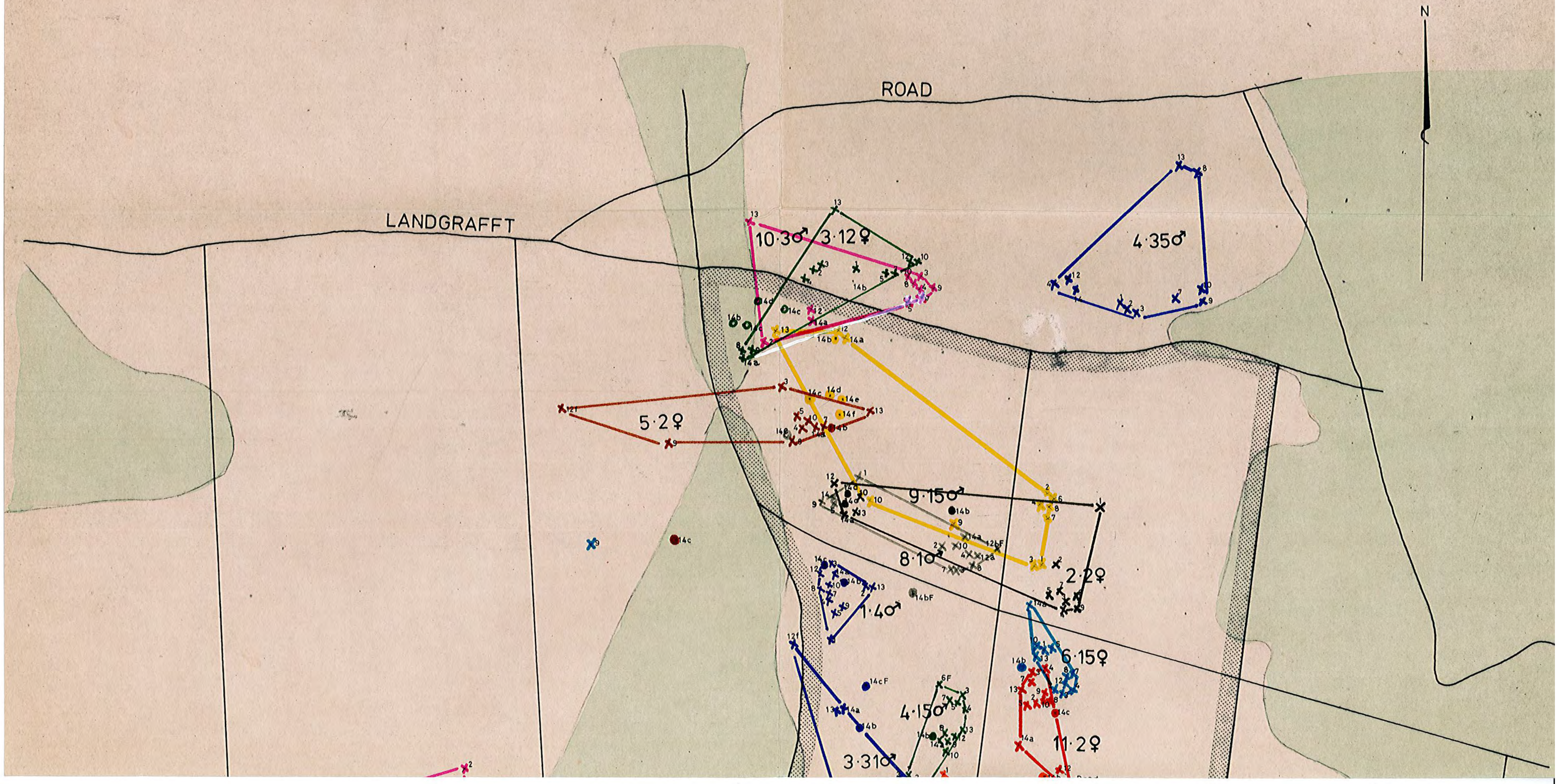

BOYICUP ROAD
1·12♂
9·375♀
6·3♂
Dead
14aF
14b
9F
LEGEND
Heartleaf gullies and low lying areas
1976 Burn edge
Tracks
△ Night-time location after burn
8 Numeral refers to date of location ~~(see text)~~ (app. 5)
F Flushed from nest
Channel No.
1.12
1.4
2.2
3.12
3.31
4.15
4.35
5.2
6.15
6.3
8.1
8.3
9.15
9.375
10.15
10.3
11.2
12.25
100 50 0 100 200 300 400 500 metres

FIG. 3.4.8 a

1976 BURN
DAYTIME RADIO LOCATIONS OF WOYLIES BEFORE AND DURING BURN



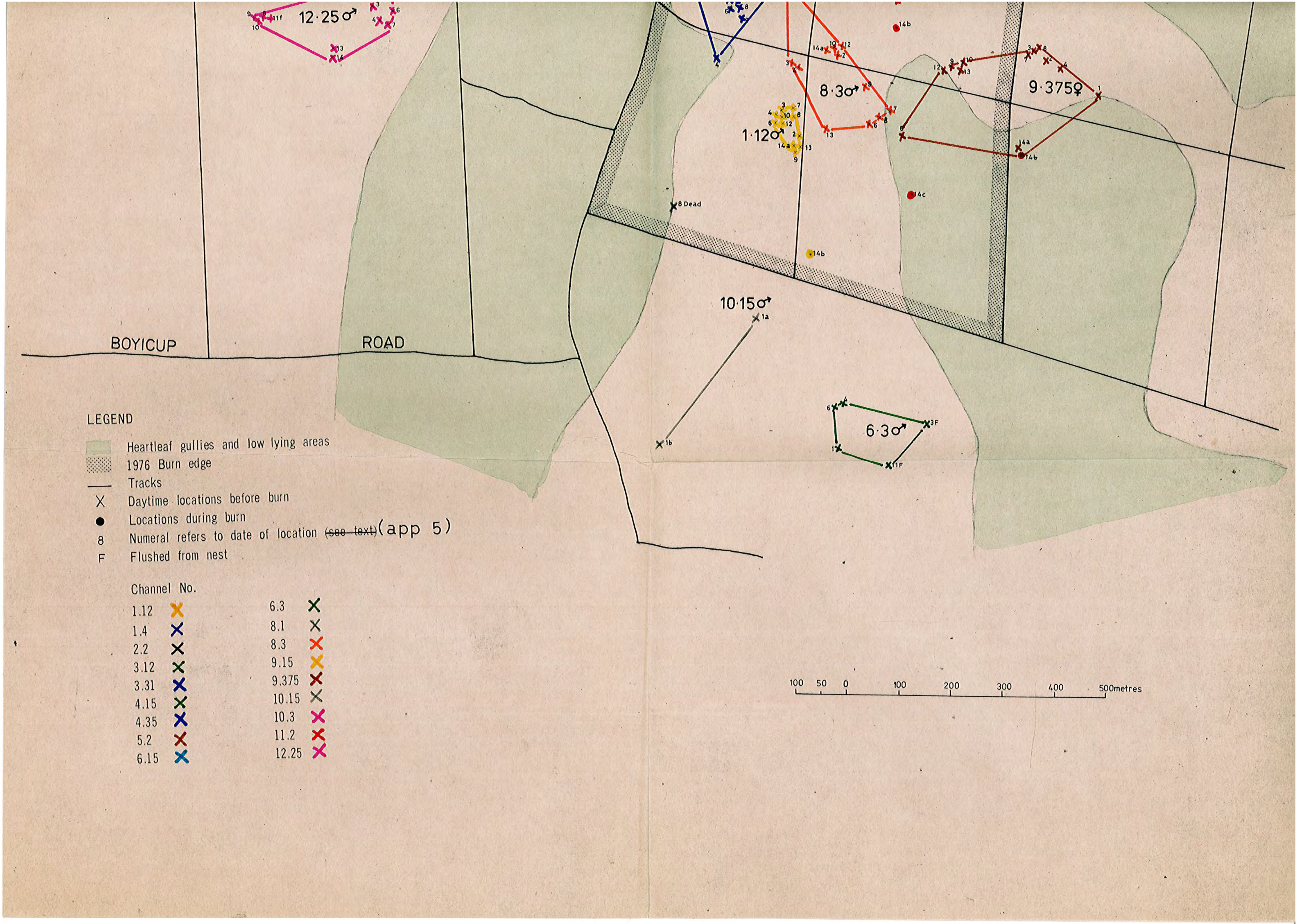
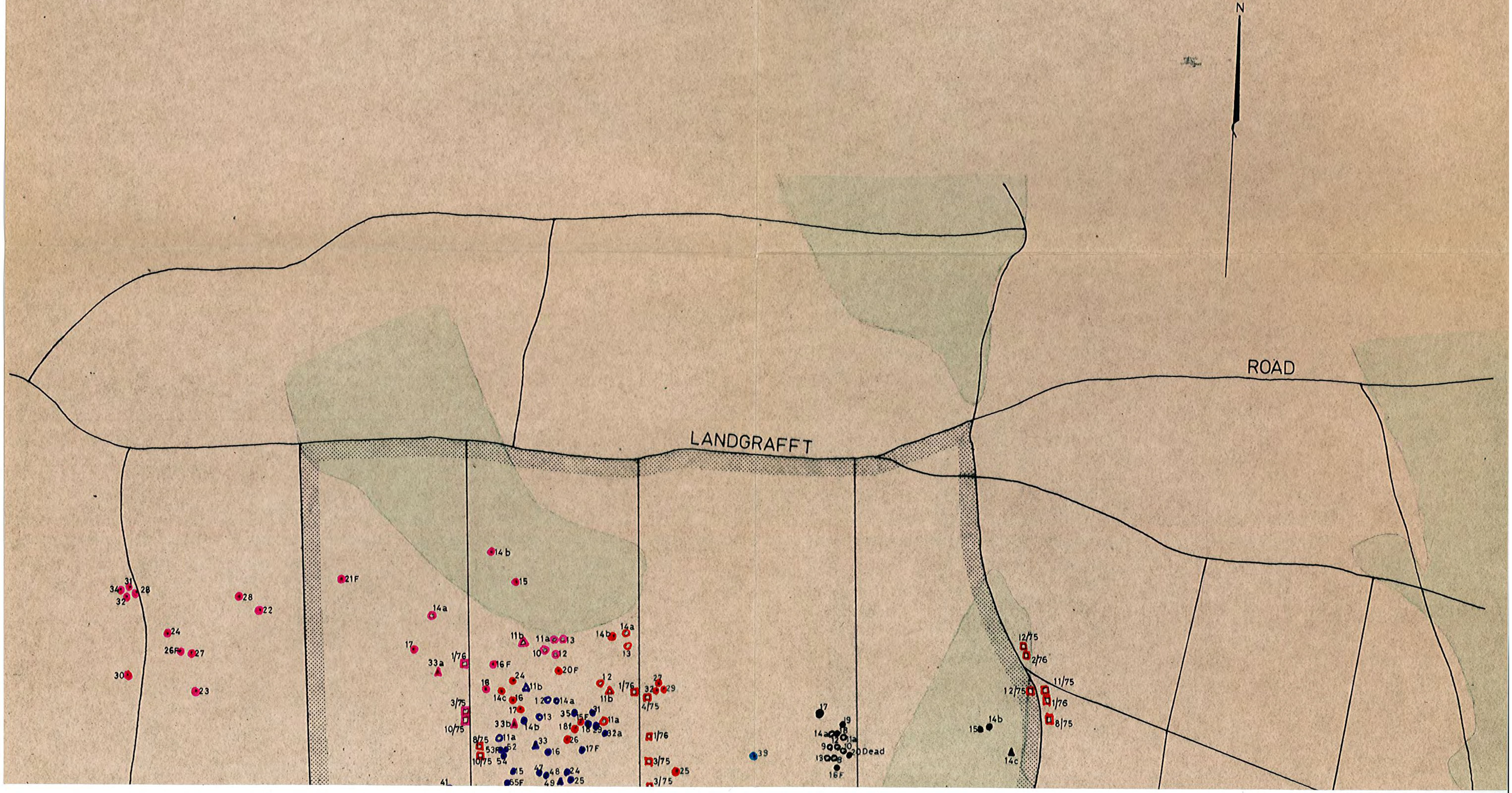

12·25♂
1·12♂
8·3♂
9·375♀
10·15♂
6·3♂
8 Dead
14a
14b
14c
1a
1b
3F
1F
BOYICUP
ROAD
LEGEND
Heartleaf gullies and low lying areas
1976 Burn edge
Tracks
X Daytime locations before burn
● Locations during burn
8 Numeral refers to date of location ~~(see text)~~ (app 5)
F Flushed from nest
Channel No.
1.12
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
100 50 0 100 200 300 400 500metres

FIG. 3.4.7.

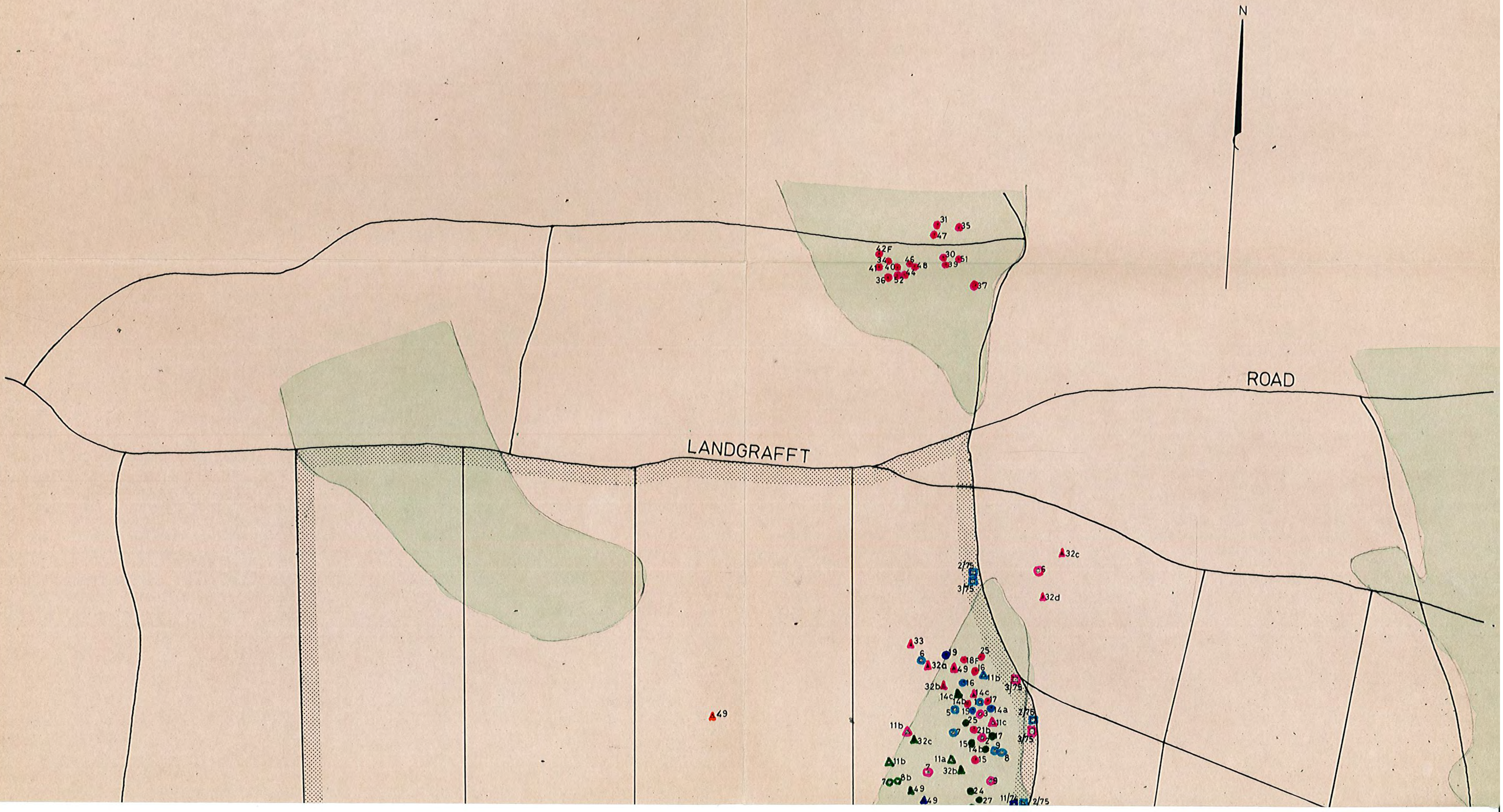
1975 BURN
WOYLIE RADIO TRACKING LOCATIONS

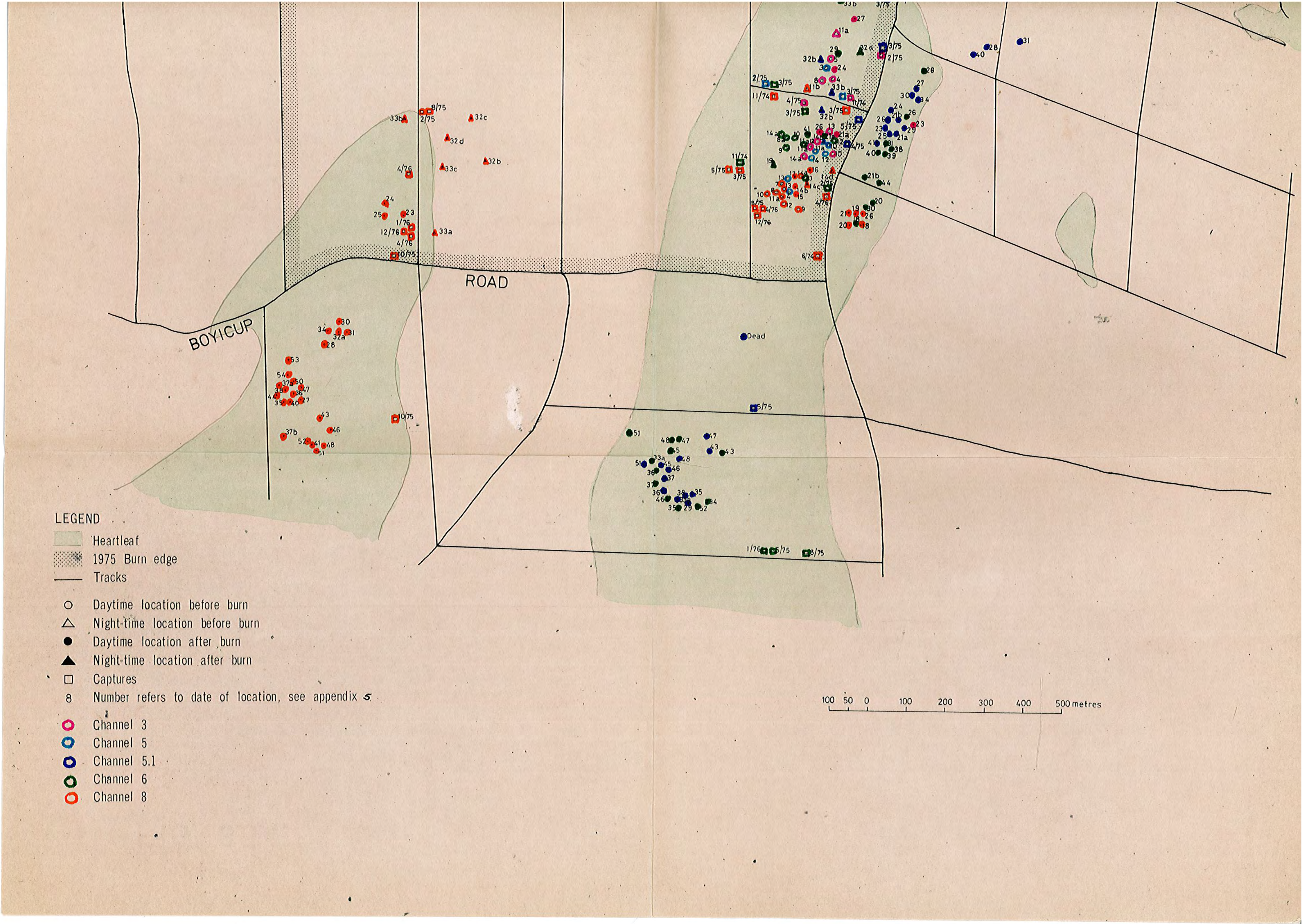



BOYICUP
ROAD
LEGEND
Heartleaf
1975 Burn edge
Tracks
○ Daytime location before burn
△ Night-time location before burn
● Daytime location after burn
▲ Night-time location after burn
□ Captures
8 Number refers to date of location, see appendix 5
Channel 2
Channel 4
Channel 6
Channel 7
Channel 8
Channel 9,15
Channel 9.55
Channel 10
100 50 0 100 200 300 400 500 metres
31 Dead
12/74
6/75
8/75
3/75
2/75
1/76

FIG. 3.5.4.

1975 BURN
TAMMAR RADIO TRACKING LOCATIONS




BOYICUP
ROAD
LEGEND
Heartleaf
1975 Burn edge
Tracks
Daytime location before burn
Night-time location before burn
Daytime location after burn
Night-time location after burn
Captures
8 Number refers to date of location, see appendix 5
Channel 3
Channel 5
Channel 5.1
Channel 6
Channel 8
Dead
100 50 0 100 200 300 400 500 metres