

# Small Mammals, Habitat Components, and Fire in Southeastern Australia<sup>1</sup>

P. C. Carling, A. E. Newsome, and G. Dudzinski<sup>2</sup>

Although the study of the effects of fire on the Australian vertebrate fauna is still at an early stage, sufficient data exist for general evolutionary concepts to have emerged (Kikkawa and others 1979, Dwyer and others 1979, Catling and Newsome 1981). Kikkawa and others (1979) concluded that specialization for heathland living must have arisen many times and with differing chronologies for the different major vertebrate taxa. As heathlands contracted over evolutionary time, widespread extinction of some forms is envisaged with radiation away from heathlands for some groups. Significant adaptations of the vertebrate fauna to fire, as for the flora, have also been examined (Catling and Newsome 1981) with eight a priori propositions being erected:

1. Archaic forms would survive in the least fire-prone habitats;
2. Species diversity overall would be low;
3. There would be fire specialists;
4. The seral response would be truncated;
5. Species diversity would be highest in the least fire-prone habitats;
6. Reproductive patterns would be modified;
7. There would be a prevalence of ecological generalists;
8. There would be few forms in the lowest strata of vegetation.

Supportive evidence was found for all of them except Proposition 5. It was the wet sclerophyll forest (Eucalyptus dominated) which held the highest diversity of mammals and birds and not

<sup>1</sup>Presented at the Symposium on Dynamics and Management of Mediterranean-type Ecosystems: An International Symposium, June 22-26, 1981, San Diego, California.

<sup>2</sup>Division of Wildlife Research, CSIRO, P.O. Box 84, Lyneham, A.C.T. 2602, Australia.

Abstract: In Australia, eucalypt forests are the major vegetation form. They are highly fire-prone, but also the major repository of the vertebrate fauna. Recent studies have demonstrated that the fauna, like the flora, may be adapted to fire. Simple divisions of environments into habitats satisfactorily predicted the abundance and diversity of small mammals. The habitat preferences of four species of small mammal were examined in relation to various components of the habitat using principal component analysis. The environmental components scored were the abundance of litter, brush and boulders, of ground vegetation, and of shrubs, and of trees and their canopies. The patterns which emerged are examined for projected effects of fires of high or low intensity upon the habitat components and hence upon the small mammal fauna.

the rainforest (non-Eucalyptus) as at first thought. Eucalypt forests provide the habitats for the great majority of birds and mammals (Tyndale-Biscoe and Calaby 1975). One pre-eminent feature of the Australian Eucalypt forest is the frequency of intense wildfire. Southeastern Australia has a summer fire season which can be very severe and major fires can be expected every 3-10 years or so (Cheney 1979, Walker 1979) (fig. 1.). Managers in Forest Departments and National Parks utilize "cool control" fires to reduce the chance of those fierce uncontrollable wildfires. Yet it seems that the eucalypts themselves ensure such fires with their oils (hutch 1970).

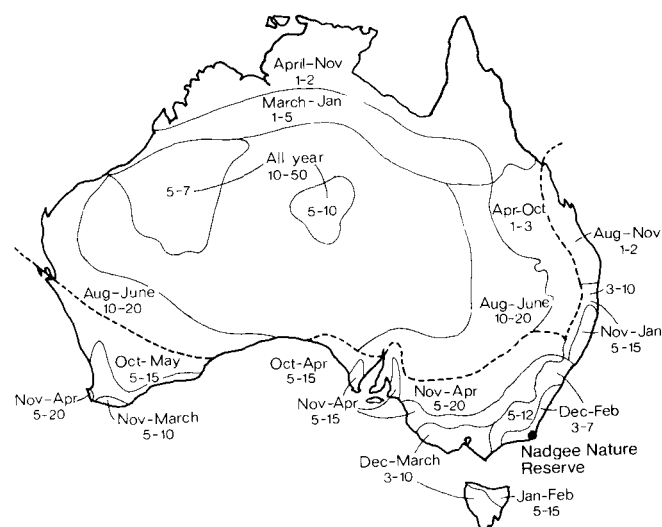


Figure 1--Fire frequency (range in years) for the fire season regions (range in months) in Australia. Area below dotted line is summer fire season only (after Walker 1979).

Models of successional vegetative responses exist in Australia (Specht and others 1958, Jackson 1968, Noble and Slatyer 1981), although little is known similarly for the fauna. However, some general points can be made from the study of the vegetative changes in a heathland in a mediterranean climate burnt at various times over 25 years and 50 years prior to the study (Specht and others 1958). Four groups of plants burgeoned sequentially: The grasses and forbs, the understorey, the undershrubs and the trees (*Banksia ornata*). If burnt every 5 years then only the grass and herb layer would remain, so that we could expect animals utilizing that habitat to be present. If burnt every 10-15 years we would expect fauna that frequent healthy shrubs to be present. Animals exploiting the tree layer would do best if fire was avoided for 20-30 years, unless they nest in holes, when only old senescent trees might suffice.

In Australian forests the small mammal fauna is never as diverse or abundant as in North America. Moreover, they never irrupt like their North American counterparts, nor their Australian desert counterparts (Carstairs 1974, Newsome and Corbett 1975). Some species of small mammal have specific habitat requirements and so are limited in their distribution (Keith and Calaby 1968, Posamentier 1976, Cockburn 1978, Braithwaite and Gullan 1978, Barnett and others 1978, Newsome and Catling 1979, Fox, in press). Other studies have been more general and the association between small mammals and the vegetation has often been described in relation to broad vegetation types (Golley 1962, Tyndale-Biscoe and Calaby 1975). For example, dry sclerophyll forest includes both forest with a thick heathy understorey and one with a grass and herb understorey with few shrubs. Newsome and Catling (1979) concluded that the simple grouping of environments into "habitats" was more satisfactory in predicting small mammal species abundance and diversity than broad structural formations. The reason was that other components of the environment such as litter and brush, creeks, swamps, boulders, shrubs etc. were considered part of the habitat.

The paper is based on data collected for seven years following the severe wildfire which swept through Nadgee Nature Reserve in south-eastern Australia in December 1972 (fig. 1). From this study, patterns of population responses have been documented (Newsome and others 1975, Catling and Newsome 1981), habitat preferences and particular components of those habitats identified (Newsome and Catling 1979) and models erected of possible responses to changes in supplies of food and shelter and in numbers of predators (Newsome and Catling, in press). This paper examines the effects of individual habitat components on four small mammal species in south-eastern Australia and the projected effect of fire on those components, and hence on the small mammals. The predictions are also examined relative to known responses.

## MATERIALS AND METHODS

### (a) Trapping Grids

In April 1972 five trapping grids were established in different habitats in Nadgee Nature Reserve as part of the study of the diet of dingoes (Newsome and Catling unpublished). The five habitats were lowland and upland open sclerophyll forest, closed scrub, closed and open graminoid heathland. Twenty traps were set on each grid in two parallel lines 10 metres apart. There were 10 traps per line set 7 metres apart. Each trap was set in the same location for three consecutive nights every three months. The traps were baited with peanut butter and rolled oats, cleared in the morning and reset. In 1979 when small mammal populations were at their highest (P. Catling and A. Newsome unpubl. fig. 2) vegetational data (see below) were collected around each trap site in the grids and related to the captures of each species of small mammal there for 1978 and 1979.

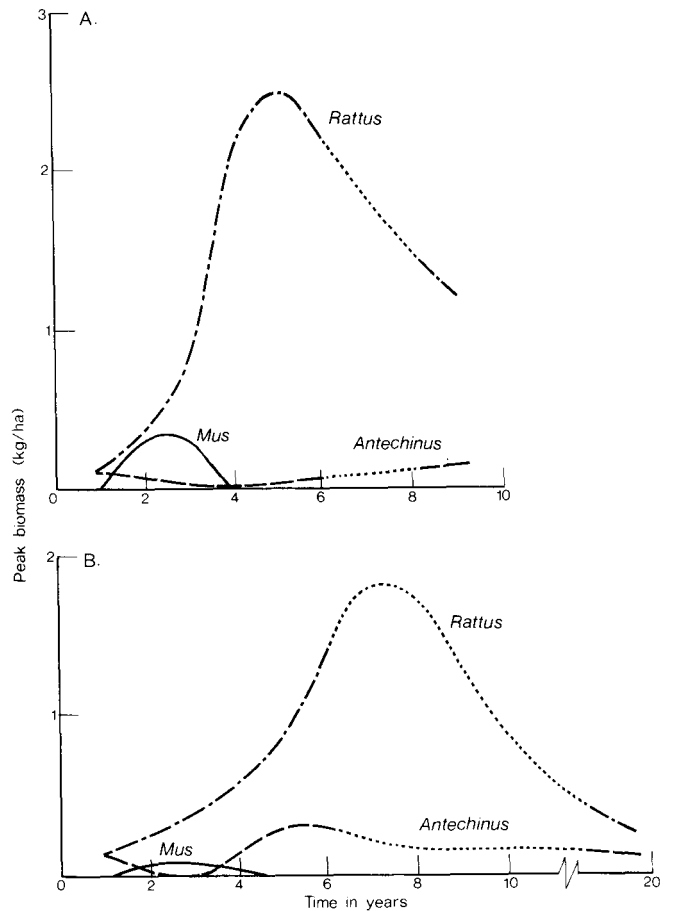


Figure 2--Peak biomass (kg/ha) per year after fire. The end points represent values immediately before the fire transposed to time since previous fires (from Catling and Newsome 1981).

- A. Wet habitats - closed scrub and closed graminoid heath.
- B. Open sclerophyll forest.

(b) The Animals

The small mammals studied were the two small dasyurid marsupials, Brown Antechinus (Antechinus stuartii Macleay) (20-40 g) and Dusky Antechinus (Antechinus swainsonii (Waterhouse)) (40-120 g), and two native rodents, Bush rat (Rattus fuscipes (Waterhouse)) (90-180 g) and Swamp rat (Rattus lutreolus (Gray)) (90-180 g). The introduced House mouse (Mus musculus Linnaeus) was also trapped, but numbers were too low in 1978/1979 for inclusion in the analysis. The animals were weighed, toe-clipped, and released. Other biological data were obtained but are not used here.

(c) Habitat Components

A 36 m<sup>2</sup> area around each trap site was visually estimated for ground vegetation cover (pct); cover of litter, brush, logs and rocks (pct); tree cover (pct) and shrub cover (pct). The tree height (m) directly above the trap site was measured with an inclinometer and the sedge and grass height (cm) and shrub height (cm) were measured at four points (the major points of the compass) 1.5 metres from the trap site and then averaged.

(d) Analysis

The grids were divided into treed and treeless groups. No animals were trapped on the open graminoid heathland, so it was not included in the analysis (see below for further comment).

The dependent variables Y<sub>1</sub> ... Y<sub>4</sub> were captures of Y<sub>1</sub> - Antechinus stuartii, Y<sub>2</sub> - Antechinus swainsonii, Y<sub>3</sub> - Rattus fuscipes, Y<sub>4</sub> - Rattus lutreolus. These were examined relative to the independent variables X<sub>1</sub>...X<sub>7</sub>, X<sub>1</sub> - ground vegetation height (cm), X<sub>2</sub> - shrub height (cm), X<sub>3</sub> - tree height (m), X<sub>4</sub> - cover of litter, brush, rocks and logs (pct), X<sub>5</sub> - ground vegetation cover (pct), X<sub>6</sub> - shrub cover (pct), X<sub>7</sub> - tree cover (pct). Tough captures on quadrats within any grid may not be independent, we decided to investigate the data assuming no bias, seeking insights into the effects of different habitat components upon the catch. To aid the interpretation of the relationship between the catch (Y<sub>1</sub> ... Y<sub>4</sub>) to the intercorrelated environmental measurements (X<sub>1</sub> ... X<sub>7</sub>), the X<sub>1</sub> ... X<sub>7</sub> measurements were transformed by Principal Component Analysis into orthogonal (uncorrelated) variables (Z<sub>1</sub> ... Z<sub>7</sub>). For detailed description of the use of Principal Component Analysis in multiple regression see Dudzinski (1975).

RESULTS

(a) Captures

The five habitats were trapped 8 times generating a total of 2,400 trap nights. Total

captures for each species were A. stuartii (112), A. swainsonii (44), R. fuscipes (184) and R. lutreolus (168).

(c) Correlation of Vegetation Components

The correlation between the vegetation components are presented in Table 1. In general, in the treeless sites the higher the shrubs and the cover of litter etc. the lower the cover and height of the ground vegetation. In the treed sites the higher the trees and shrubs the lower the ground vegetation height and cover and cover of shrubs.

Table 1--Correlation between the original habitat variables.

(i) Treed sites

	X1	X2	X3	X4	X5	X6
X2	.11					
X3	-.41	-.01				
X4	.31	.10	.31			
X5	.47	.17	-.71	-.06		
X6	.40	-.40	-.19	.18	.61	
X7	-.22	-.08	.37	.15	-.27	-.19

(ii) Treeless sites

	X1	X2	X4	X5
X2	-.43			
X4	-.62	.71		
X5	.86	-.48	-.71	
X6	.25	.08	-.03	.19

Values > 0.31 are significant at .05.

(b) Principal Component Analysis

The Principal Component loadings for each habitat variable and the percent of the overall variation accounted for by each component are presented in Table 2.

Table 2--Solution of Principal Component Analysis.

(i) Treed sites.

	Components						
	Z1	Z2	Z3	Z4	Z5	Z6	Z7
	37.5*	20.5	18.3	10.0	6.7	5.1	1.7
X1	-.43+	-.31	.13	.54	.15	.62	.08
X2	-.13	-.25	-.74	-.10	.56	-.13	.17
X3	.47	-.39	-.07	-.29	-.29	.39	.54
X4	.01	-.75	.12	.25	-.22	-.55	-.11
X5	-.54	.11	.29	-.18	-.01	-.31	.70
X6	-.42	-.31	.10	-.71	-.05	.21	-.41
X7	.34	-.14	.57	-.12	.73	-.03	.02

(ii) Treeless sites.

Components					
	Z1	Z2	Z3	Z4	Z5
	58.7*	22.5	11.3	5.0	2.5
X1	.51+	.22	-.43	-.37	.61
X2	-.43	.41	-.60	.53	.11
X4	-.51	.20	-.21	-.76	-.26
X5	.53	.14	-.38	.04	-.74
X6	.10	.85	.51	.02	-.03

+ Values <.29 are assumed not to contribute significantly to the interpretation of the Z variable.

\* Percent variability accounted for.

(d) Interpretation of Principal Components

The components in Table 2 are interpreted in terms of the interrelationships of the vegetation as follows:

(i) Treed sites - upland and lowland open forest.

- Z1 Height and cover of ground vegetation plus shrub cover contrasts with height and cover of trees.
- Z2 Abundance of litter etc., and shrubs and height of trees and ground vegetation.
- Z3 Shrub height contrasts with tree cover.
- Z4 Shrub cover and tree height contrasts with height of ground vegetation.
- Z5 Tree cover and shrub height contrasts with tree height and litter.
- Z6 Height of trees and ground vegetation contrasts with cover of litter etc. and height of ground vegetation.
- Z7 Cover of ground vegetation and tree height contrasts with shrub cover.

(ii) Treeless sites - closed scrub, open and closed graminoid heath.

- Z1 Cover and height of ground vegetation contrasts with shrub height and litter and brush cover.
- Z2 Shrub cover and height.
- Z3 Shrub cover contrasts with shrub and ground vegetation height and ground vegetation cover.
- Z4 Ground vegetation height and cover of litter etc. contrasts with shrub height.
- Z5 Ground vegetation cover contrasts with height of ground vegetation.

(e) Regression of Catch on Habitat Components

The following equations resulted from regressions of captures on significant components:-

(i) Treed sites

Antechinus stuartii

$$Y_1 = 2.15 + 0.92 Z_5 + 1.48 Z_7 + 0.36 Z_2$$

(P < 0.001; percent variance accounted for : Z<sub>5</sub> 14.8, Z<sub>7</sub> 9.5, Z<sub>2</sub> 6.8; Total = 31.1)

Antechinus swainsonii

$$Y_2 = 1.07 - 0.59 Z_1$$

(P < 0.001; percent variance accounted for: Z<sub>1</sub> 34.8; Total = 34.8)

Rattus fuscipes

$$Y_3 = 1.95 - 0.71 Z_2 - 0.61 Z_3$$

(P < 0.02; percent variance accounted for: Z<sub>2</sub> 10.5, Z<sub>3</sub> 6.7; Total = 17.2)

Rattus lutreolus

$$Y_4 = 0.40 - 0.28 Z_1 - 0.58 Z_6$$

(P < 0.001; percent variance accounted for: Z<sub>1</sub> 13.1, Z<sub>6</sub> 7.3; Total = 20.4)

(ii) Treeless sites

Antechinus stuartii

Y<sub>1</sub> - no relationship.

Antechinus swainsonii

Y<sub>2</sub> - no relationship.

Rattus fuscipes

$$Y_3 = 2.65 + 1.32 Z_2 + 0.71 Z_3$$

(P < 0.001; percent variance accounted for: Z<sub>2</sub> 40.8, Z<sub>3</sub> 4.9; Total 45.7).

Rattus lutreolus

$$Y_4 = 3.8 + 1.92 Z_2 + 2.41 Z_5 + 1.00 Z_3$$

(P < 0.001; percent variance accounted for: Z<sub>2</sub> 37.0, Z<sub>5</sub> 5.3, Z<sub>3</sub> 4.0; Total 46.3).

(f) Interpretation of Regression

The interpretations of the above equations in terms of habitat components for each species are as follows (see Table 2 for detail):

(i) Treed sites

Antechinus stuartii

The greater the tree cover and height, shrub height, and ground vegetation cover, the higher should be the catch. The cover of litter, brush, and logs is also contributing (Z<sub>2</sub>...6.8%). Generally, the improvement of alt habitat components should improve the catch. A. stuartii should be favoured by a maturing forest.

Antechinus swainsonii

The better the ground vegetation cover and height and the shrub cover, (i.e. the lower vegetation strata), the better should be the catch. Those strata are suppressed in tall closed forest. A. swainsonii should not be as successful as A. stuartii in maturing forests, but should be favoured by low open forests with a thick understorey.

Rattus fuscipes

The supply of litter, logs, and brush is a major habitat component, but the height of all vegetation strata and shrub cover contribute importantly. All these items infer preference for maturing stands of relatively open forest

producing much litter. Like A. stuartii, Rattus fuscipes should be favoured by maturing forests.

#### Rattus lutreolus

The shrubs and ground vegetation are again important together with the litter, logs and brush, but the cover and height of trees reduces the favourability of habitat. Forests should not favour these rats.

#### (ii) Treeless sites

#### Rattus fuscipes

Shrubs are all important in treeless habitats, both their height and cover. The catch should be best on older heaths. Young heaths would not have adequate shrub cover or height.

#### Rattus lutreolus

Again shrub cover and height are important, but ground vegetation height is more important than for Rattus fuscipes. The catch should be best on maturing heaths; however, R. lutreolus could be expected on young heaths providing the ground vegetation height was adequate.

### DISCUSSION

Before discussing the results in general, one particular aspect of them is addressed. The low capture rates in this study highlight the statement earlier that small mammal populations are characteristically sparse in Australian forests. We had followed population changes for 7 years post-fire, and populations were maximal at the time of this study (fig. 2).

The results of this study confirm the importance of cover to native small mammals as found in other Australian studies (Barnett and others 1978, Braithwaite and others 1978, Suckling and Heislars 1978, Braithwaite and Gullan 1978, Newsome and Catling 1979), and in North America (Gunderson 1959, Cook 1959, Birney and others 1976, Kirkland 1978, Quinn 1979). By identifying particularly relevant habitat components, however, our study can be extended to predict the effect of fire on small mammals due to changes in the vegetation. Known effects from our earlier study (Newsome and others 1975, Newsome and Catling 1979, Catling and Newsome 1981) and other studies are then compared.

#### (a) Rattus lutreolus and Rattus fuscipes

R. fuscipes is primarily a forest species (Catling and Newsome 1981); however, it is known to inhabit older stands of heath where the shrubs are tall and litter cover is good (Braithwaite and others 1978, Braithwaite and Gullan 1978; Fox in press; this paper). R. lutreolus is the converse being primarily a wet heath species (Braithwaite and others 1978, Braithwaite and Gullan 1978, this paper) and will inhabit shorter heaths than R. fuscipes.

Our results indicate that Rattus lutreolus might be expected in all habitats as ground vegetation regenerates from fire in the early stages of vegetation succession. R. fuscipes might be expected in later stages as shrubs predominate and trees regain their leafy canopy. We would expect few Rattus fuscipes after a fire on heathlands, low-medium densities as ground vegetation increases and maximum densities as shrubs become dominant and litter and brush increase.

In our study, Rattus lutreolus quickly disappeared from all burnt areas (fig. 3) and only returned once the ground vegetation thickened (fig. 2). However, in the first few years post-fire, Rattus lutreolus was the first to invade the forest, and persisted - presumably because of the dense, tall ground vegetation which contained a high percentage of sedges. Braithwaite and Gullan (1978) found R. lutreolus preferred wetter areas with a good sedge cover both for cover and food. After the fire there were several very wet years which may have aided the invasion of R. lutreolus into the forest. Pre-fire, R. lutreolus was not caught at all in the forest, which had not been burnt for about 20 years (A. Fox, pers. comm.). Understorey shrubs were sparse and grasses dominant. Moreover, Braithwaite and others (1978) considered R. lutreolus to be a riparian species and that forest habitat is marginal. The results obtained here provide an explanation.

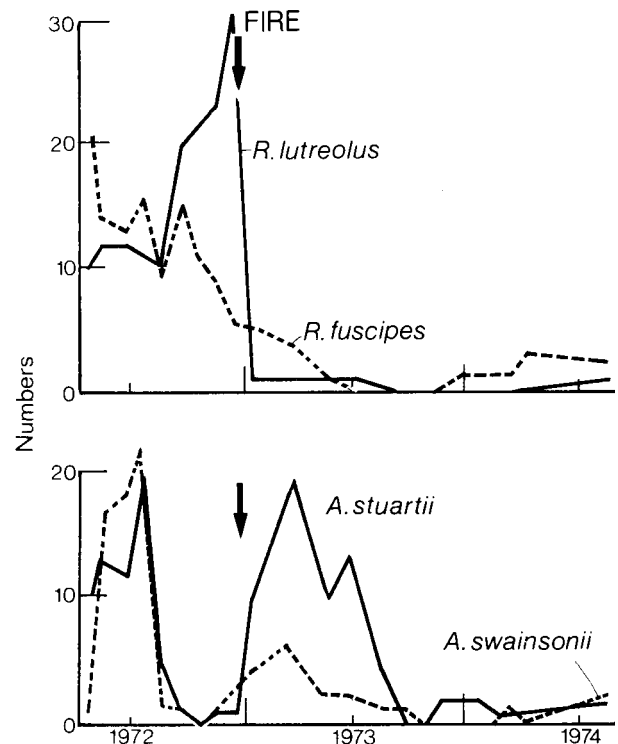


Figure 3--Detailed short-term fluctuations of small mammals after wildfire (from Newsome and others 1975).

Post-fire R. fuscipes survived for a few months before disappearing until the ground vegetation began to recover (fig. 3). Cowley and others (1969), Leonard (1972), Christensen and Kimber (1975), and Fox (in press) found similar results. Christensen and Kimber (1975) attributed the disappearance of R. fuscipes to the lack of ground cover and increased predation. In our study in the longer term (5-7 years post-fire) R. fuscipes reached levels well above that found pre-fire (fig. 2). This coincided with the shrub cover and height, and litter and brush cover reaching their maxima particularly in the forest. Bell and Koch (1980) report that the decline in plant diversity in jarrah forest in Western Australia after about 6 years was apparently due to senescing of "fireweed" species and reduction in number of smaller herb species. From our vegetation analysis shrubs were very important for R. fuscipes. It could be postulated that as the forests age and shrubs die out R. fuscipes abundance would decline as indicated in fig. 2.

(b) Antechinus stuartii and A. swainsonii

The vegetation analysis revealed Antechinus would not be expected on treeless habitats. In forests post-fire, Antechinus may be expected to survive where the tree canopy had not been severely damaged and in particular A. stuartii, as they are known to be scansorial (Wakefield and Warneke 1967). However, as the important shrubs and ground cover are removed by fire, Antechinus would not be expected to persist, and recovery not to begin, until the vegetation recovered.

Post-fire, Antechinus survived well, with A. stuartii doing the better (fig. 3). However, breeding appears to have failed in the second year with numbers falling dramatically to remain low or non-existent for several years (fig. 2). The reasons are unknown as there seems to have been an adequate supply of insects (Fox, A. 1978). Antechinus are insectivorous (Wakefield and Warneke 1963, 1967) and appear to be generalist and largely opportunistic (Hall 1980). Leonard (1972) found that the energy content of the leaf litter fauna fell 30% in the year post-fire, but he felt that it was unlikely that food for mammals was limiting. Similar results were obtained by Campbell and Tanton (1981). Predation is another possibility for the decline of Antechinus (Newsome and Catling in press). Leonard (1972) found that A. stuartii were not affected where some cover remained after fire. However, where dense cover was eliminated there was a significant decrease in the number of A. stuartii, (particularly females) although some individuals were able to persist. Leonard (1972) and Newsome and Catling (1979) found A. swainsonii mainly along gullies and creeks in dry sclerophyll forest, which are likely to survive fires of low intensity. Antechinus have been much slower to recover in the treeless habits (fig. 2). This is possibly because the heaths have not reached maximum height and cover,

whereas the density of shrubs etc. has reached its maximum in forest by year 6 or 7 post-fire.

(c) Other Species

Braithwaite and others (1978) suggest that although some species do have special structural requirements, resource partitioning appears to be primarily food orientated. They define five basic food niches in south-eastern Australian heath and forest communities, but only rarely are all five occupied. In this study R. fuscipes would be the common omnivore, R. lutreolus the specialist herbivore, A. stuartii the scansorial insectivore, A. swainsonii the soil fossicking insectivore. There was no generalist herbivore, which is usually filled by Pseudomys spp. in other studies (Braithwaite and others 1978), but no Pseudomys is present in Nadgee Nature Reserve though found both north and south of it. Cockburn (1978) found the Heath mouse (Pseudomys shortridgei (Thomas)) on heaths that had a maximum or near maximum diversity of woody plant species, an association which developed about 6-9 years post-fire in his study. Prior to 1965 farmers burnt the heaths in Nadgee every 3 or 4 years (A. Fox, pers. comm.). Perhaps the heaths have been burnt too frequently to allow them to reach maximum plant species diversity and so Pseudomys have disappeared. An example of such a heath is the open graminoid heath which was not used in our analyses. The ground vegetation and shrub height is low (< 30 cm) and the soils are very hard ground-water podzols. No native small mammal has been trapped there.

In most studies on fire and mammals in Australia there has been an invasion of Mus musculus into the burnt area within about 6 months post-fire (Christensen and Kimber 1975, Newsome and others 1975, Recher and others 1975, Fox in press) (fig. 2). Mus as well as being the immediate post-fire colonizer is considered to fill the food niches of A. stuartii and A. swainsonii in their absence (Braithwaite and others 1978).

No grid had more than three species present pre-fire. However, in the years 2-5 post-fire most grids at some stage had four species and the closed scrub had five species present 2 years post-fire. The number of food niches may therefore be increased by fire.

(d) Effect of Fires of Low and High Intensity

Fire itself, especially of low intensity, is unlikely to be a major mortality factor for small mammals (Leonard 1972, Cowley and others 1969). In fact most authors have found that fire-induced mortality only occurs under extreme conditions. In an experimental fire applied to fenced enclosures - reduced cover and seed availability and increased predation were the major factors for population declines (Crownor and Barrett 1979). Komerek (1969) observed cotton rats removing young from nests ahead of a fire of low

intensity and so surviving. However, a high intensity fire (wildfire) usually travels at considerable speed and consumes everything in its path including many birds and mammals. One exceptionally destructive situation arises when spot fires in Eucalypt forests coalesce. An enormous amount of energy is released in the form of flaming whirlwinds which can uproot and snap off trees with winds up to 100 km per hour (Cheney 1979).

In most cases fires and particularly those of low intensity leave a mosaic of unburnt patches as well as not burning all vegetation strata. This is most likely along creeks and drainage lines where the abundance and species diversity of small mammals could be expected to be greatest (Newsome and Catling 1979). The mosaic of unburnt vegetation is probably the most important factor in the survival and recolonization of small mammals.

Frequent, man-made "control" fires are, however, another matter. Vegetation analysis has revealed the importance of ground vegetation, shrubs, and litter for small mammals in south-eastern Australia. The vegetation correlations in Table 1(i) indicate that these components will increase if the canopy is opened up. There is no known fire which will selectively open up the tree canopy. There is evidence that repeated and frequent burning may convert open forest with a shrub understorey to open forest with a grassy understorey (Coaldrake 1961). With repeated fires Gilbert (1959) found the conversion of multi-layered understoreys to a single layer and Christensen and others (1981) found a 66 percent reduction in shrub density. Our vegetational analysis indicate that this will not favour small mammal abundance nor diversity. Therefore the small mammal fauna of south-eastern Australia seems advantaged and perhaps dependent in the longer term on the shrub regrowth which flourishes after severe fire, and disadvantaged by "cool control fires" lit to prevent severe wild fires.

This study was conducted at years 6-7 post-fire, when shrubs averaged 1.8 metres with an average cover of 38% in the treed sites and 1.1 metres and 37% on the treeless sites. This is near their maximum, and yet conclusions have been drawn about earlier successional stages. It is encouraging that records of Rattus from those times, particularly soon after the fire, support these conclusions. Rattus lutreolus was the first native species into all habitats then, even the forest. Antechinus is a little more difficult to understand, however, mainly because it survived so well in the first year post-fire. It must be added, of course, that the precise resources required by the species have not been deduced, merely what appear to be preferred habitat associations.

#### ACKNOWLEDGMENTS

We thank the N.S.W. National Parks and Wildlife Service for permission to work in Nadgee Nature Reserve. We are grateful to Mr. R.J. Burt and Mr. H.L. Wakefield for field assistance. Mr. Frank Knight drew the figures and Mrs. Wendy Guy kindly typed the manuscript. The early part of the study to 1976 was part of Grant CS8S and CS17 from the Australian Meat Research Committee for the study of dingoes.

#### LITERATURE CITED

- Barnett, J.L., How, R.A.; Humphreys, W.F. The use of habitat components by small mammals in eastern Australia. *Aust. J. Ecol.* 3:277-285; 1978.
- Bell, D.T., Koch, J.M. Post-fire succession in the northern jarrah forest of Western Australia. *Aust. J. Ecol.* 5:9-14; 1980.
- Birney, E.C.; Grant, W.E.; Baird, D.D. Importance of vegetative cover to cycles of Microtus populations. *Ecology* 47:1043-1051; 1976.
- Braithwaite, R.W.; Cockburn, A.; Lee, A.K. Resource partitioning by small mammals in lowland heath communities of south-eastern Australia. *Aust. J. Ecol.* 3:423-445; 1978.
- Braithwaite, R.W.; Gullan, P. Habitat selection by small mammals in a Victorian heathland. *Aust. J. Ecol.* 3(1):109-127; 1978.
- Campbell, A.J.; Tanton, M.T. Effects of fire on the invertebrate fauna of soil and litter of a eucalypt forest. In: Gill, A.M.; Groves, R.H.; Noble, I.R., eds. Fire and the Australian Biota. Canberra: Australian Academy of Science; 215-242; 1981.
- Carstairs, J.L. The distribution of Rattus villosissimus (Waite) during plague and non-plague years. *Aust. Wildl. Res.* 1: 95-106; 1974.
- Catling, P.C.; Newsome, A.E. Responses of the Australian vertebrate fauna to fire: an evolutionary approach. In: Gill, A.M., Groves, R.H.; Noble, I.R., eds. Fire and the Australian Biota. Canberra: Australian Academy of Science; 273-310; 1981.
- Cheney, N.P. Our changing bushfire scene. *Rural Research* 105:8-13; 1979 December.
- Christensen, P.E.; Kimber, P.C. Effect of prescribed burning on the flora and fauna of south-west Australian forests. *Proc. Ecol. Soc. of Aust.* 9:85-106; 1975.
- Christensen, P.; Recher, H.; Hoare, J. Responses of open forests (dry sclerophyll forests) to fire regimes. In Gill, A.M.; Groves, R.H.; Noble, I.R., eds. Fire and the Australian biota. Canberra: Australian Academy of Science; 367-393; 1981.
- Coaldrake, J.E. Ecosystems of the coastal lowlands, southern Queensland. *CSIRO Aust. Bull. No.* 283; 1961.
- Cockburn, A. The distribution of Pseudomys

- shortridgei (Muridae: Rodentia) and its relevance to that of other heathland Pseudomys. Aust. Wild. Res. 5(2):213-219; 1978.
- Cook, S.F. Jr. The effects of fire on a population of small rodents. Ecology 40:102-108; 1959.
- Cowley, R.D.; Heislors, A.; Ealey, E.H.M. Effects of fire on wildlife: combination of papers. Vict. Resour. 11(3):18-22; 1969.
- Crowner, A.W.; Barrett, G.W. Effects of fire on the small mammal component of an experimental grassland community. J. Mamm. 60(4):803-813; 1979.
- Dudzinski, M.L. Principal Components Analysis and its use in Hypothesis Generation and Multiple Regression. In: Bofinger, V.J.; Wheeler, J.L., eds. Developments in field experiment design and analysis. Commonwealth Agricultural Bureaux; Alden Press, Oxford, 196.1975
- Dwyer, P.D.; Kikkawa, J.; Ingram, G.J. Habitat relations of vertebrates in subtropical heathlands of coastal southeastern Queensland. In: Specht, R.L., ed. Ecosystems of the World: Heathlands and Related Shrublands. Descriptive Studies; Vol 9A, 281-299; 1979.
- Fox, A. The '72 fire of Nadgee Nature Reserve. Parks and Wildlife 2(2):5-24; 1978.
- Fox, B.J. Small mammals and forest fire. Aust. J. Ecol. 5: in press.
- Gilbert, J.M. Forest succession in the Florentine Valley, Tasmania. Pap. Proc. Roy. Soc. Tas. 93: 129-51; 1959.
- Colley, F.B. Mammals of Georgia. University of Georgia Press, Athens. 1962.
- Gunderson, J.B. Red-backed voles habitat studies in central Minnesota. J. Mammal. 40:405-412; 1959.
- Hall, S. The diets of two co-existing species of Antechinus (Marsupialia:Dasyuridae). Aust. Wildl. Res. 7:365-78; 1980.
- Jackson, W.D. Fire, air, water and earth - an elemental ecology. Proc. Ecol. Soc. Aust. 3: 9-16; 1968.
- Keith, K.; Calaby, J.H. The New Holland mouse Pseudomys novaehollandiae (Waterhouse) in the Port Stephens district, New South Wales. CSIRO Wildl Res. 13:45-58; 1968.
- Kikkawa, J.; Ingram, G.J.; Dwyer, P.D. The vertebrate fauna of Australian heathlands - an evolutionary perspective. In: Specht, R.L., ed. Ecosystems of the World: Heathlands and Related Shrublands. Descriptive Studies. Vol 9A, 231-275; 1979.
- Kirkland, G.L. Jr. Population and community responses of small mammals to 2,4,5-T. USDA. Forest Service Res. Note, PNW-314, 6 pp; 1978.
- Komerek, E.V. Fire and animal behaviour. Proc. Tall Timbers Conf. No. 9. Tallahassee, Florida; 161-207; 1969.
- Leonard, B.V. The effect of fire upon selected small mammals and leaf litter fauna in sclerophyll forest in southern Australia. M.Sc. Thesis, Monash University; 1972.
- Mutch, R.W. Wildland fires and ecosystems - a hypothesis. Ecology 51: 1046-1051; 1970.
- Newsome, A.E., Corbett, L.K. Outbreaks of rodents in central Australia: origins, declines, and evolutionary considerations. In: Prakash, I., Ghosh, P., eds. Rodents in desert environments. Monographiae Biologicae. Dr. W. Junk: Den Haag. 1975.
- Newsome, A.E.; McIlroy, J.C.; Catling, P.C. The effects of an extensive wildfire on populations of twenty ground vertebrates in south-east Australia. Proc. Ecol. Soc. Aust. 9:107-123; 1975.
- Newsome, A.E.; Catling, P.C. Habitat preferences of vertebrates inhabiting heathlands of coastal, montane and alpine regions of south-east Australia. In: Specht, R.L., ed. Ecosystems of the World. Heathlands and Related Shrublands. 301-315; 1979.
- Newsome, A.E.; Catling, P.C. Animal demography in relation to fire and shortage of food: some indicative models. In: Mediterranean Type Ecosystems. The Role of Nutrients. Kruger, F.J., Mitchell, D.T., Jarvis, J.U.M., eds. Springer-Verlag (Ecological Studies) In press.
- Noble, I.R., Slatyer, R.O. Concepts and models of succession in vascular plant communities subject to recurrent fire. In: Gill, A.M., Groves, R.H., Noble, I.R., eds. Fire and the Australian biota. Canberra, Australian Academy of Science, 311-338. 1981.
- Posamentier, H. Habitat requirements of small mammals in coastal heathlands of New South Wales. M.Sc. Thesis, Sydney University; 1976.
- Quinn, R.D. Effects of fire on small mammals in the Chaparral. In: Koch, D.L., ed. Proceedings of Cal-Neva Wildlife Transactions (Long Beach, California. 125-133; 1979.
- Recher, H.F.; Lunney, D.; Posamentier, H. Effects of wildfire on small mammals at Nadgee Nature Reserve N.S.W. Third Fire Ecology Symposium, Monash Univ. Forestry Commission of Victoria; 30-36; 1975.
- Specht, R.L.; Rayson, P.; Jackman, M.F. Dark Island Heath (Ninety-mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight, and mineral nutrient status. Aust. J. Botany 6(1):59-88; 1958.
- Suckling, G.C.; Heislors, A. Populations of four small mammals in radiata pine plantations and eucalypt forests of north-eastern Victoria. Aust. Wildl. Res. 5:305-16, 1978.
- Tyndale-Biscoe, C.H.; Calaby, J.H. Eucalypt forests as refuge for wildlife. Aust. Forestry. 38: 117-133; 1975.
- Wakefield, N.A.; Warneke, R.M. Some revision of Antechinus (Marsupialia) - 1. Vict. Nat 80: 194-219; 1963.
- Wakefield, N.A.; Warneke, R.M. Some revision of Antechinus (Marsupialia) - 2. Vict. Nat. 84: 69-99; 1967.
- Walker, J. Aspects of fuel dynamics in Australia. CSIRO Div. of Land Use Res., Canberra. Tech. Mem. 79/7; 1979.