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FIRE AND MAMMALIAN SECONDARY SUCCESSION IN AN AUSTRALIAN COASTAL HEATH¹

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Abstract. A species-rich small-mammal community on 7 ha of diverse coastal heath in Myall Lakes National Park, New South Wales, Australia, was studied for 7 mo before the area burned in a wildfire (August 1974) and has subsequently been monitored for 5 yr since the fire. Species regularly trapped were the dasyurids *Antechinus stuartii* and *Sminthopsis murina*, the peramelid *Isoodon macrourus*, and the native murids *Pseudomys novaehollandiae* and *P. gracilicaudatus*, together with the introduced *Mus musculus*. *Pseudomys* species, *M. musculus*, and *S. murina* reached greater abundance on early seral stages, while the abundance there of both *Rattus fuscipes* and *R. lutreolus* was much reduced. Species reach peak abundance in an orderly replacement sequence exhibiting a mammalian secondary succession. A habitat accommodation model is proposed with species entering the succession and reaching peak abundance as externally controlled changes in the vegetation fulfil the habitat requirements of each species. Species leave the succession or are greatly reduced in abundance when these local physical conditions move out of the optimal range for the species.

This study shows that a major perturbation of a small-mammal community can produce a variety of responses among species, suggesting that regeneration time may represent a resource axis subdivided by community members in this secondary succession. The rapid recovery illustrated by the total number of individuals, as a measure of community response, supports the suggestion that fire and fire frequency have been major factors in producing a fire-adapted, species-rich small-mammal community on this heathland.

Key words: Australia; community; fire; habitat accommodation; heath; resource utilization; small mammal; succession.

INTRODUCTION

In this paper I analyze responses of mammalian populations and communities to a major perturbation. The data set was obtained from a community of small mammals occupying a mosaic of habitats in Australian coastal heathland that was perturbed by fire. The variety of responses exhibited by species suggests that the ability of a species to respond to fire, or more correctly, to the postfire environment, is part of a response continuum. Regeneration time then becomes a resource axis with each species exhibiting a different resource utilization curve. High response ability or lack of it then forms part of a species "regeneration niche," an extension of the concept envisaged by Grubb (1977). The result is a species replacement sequence or succession that may facilitate coexistence, increase species richness, and determine species composition and community structure. I compare a number of alternative mechanisms by which fire may affect community structure and assess these against models of succession proposed by Connell and Slatyer (1977); then describe a habitat accommodation model to explain the observed mammalian secondary succession.

Gill (1975), in a comprehensive review of fire and the Australian flora, puts forward the idea that plant species are adapted to a particular fire regime, incor-

porating fire intensity, frequency, and season, rather than the occurrence of fire itself. This seems likely for small-mammal species as well, given that small-mammal habitat selection relates to both structural and floristic components of the vegetation (Fox and Fox 1981). I consider here the idea that changes in small-mammal abundance following fire might be thought of as a response to vegetation change, itself responding to a specific fire regime, rather than a response to the phenomenon of fire. A review dealing specifically with the response of heathlands to fire has been completed recently by Specht (1981). Fire, either as wildfires or as repeated controlled burns, is an important factor on ecological as well as evolutionary time scales, particularly with respect to its ability to effect substantial habitat change. Such changes can drastically alter the composition of the mammal community (Beck and Vogl 1972).

Some of the possible mechanisms by which fire may alter the structure of mammalian communities and influence species richness are:

- 1) Frequent fires can create new habitats equally available to all species present in the community and to which they can immigrate;
- 2) Fire creates a sequence of microhabitats that are a function of time since fire (plant secondary succession), and these are selected preferentially by different mammalian species;
- 3) Frequent fires can create underutilized habitats to be occupied by fugitive species that are then replaced by later mammal species;

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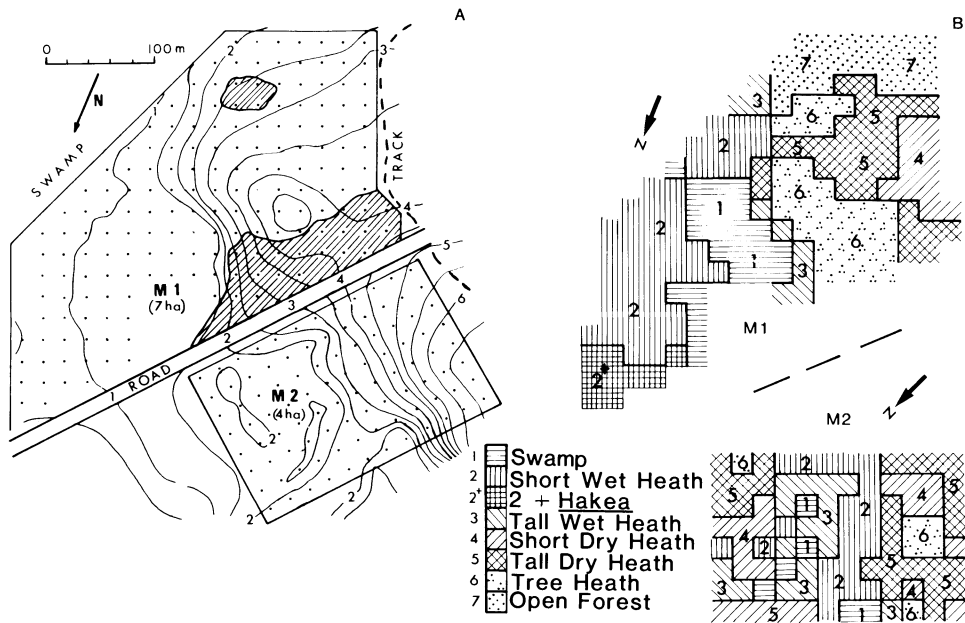


FIG. 1. A: topographic map of the study area with a 0.5-m contour interval (arbitrary datum). Trapsites are marked on each plot. The hatched area on M1 remained unburned. B: the major habitat types in the study area (redrawn from Fox[1981]).

- 4) Frequent fires can lead to the evolution (or co-evolution) of “fire specialists” suited to the exploitation of early seral stages;
- 5) Later species can enter the succession by displacing species already present;
- 6) Early successional species may be able to alter plant pyric succession (e.g., by grazing pressure) to delay habitat changes favoring later successional species, thus prolonging the mammalian succession.

Mechanism 1 would lead to either the tolerance or inhibition models of Connell and Slatyer (1977), but would exclude their facilitation model. Mechanisms 2, 3, and 4 would all represent modifications of the facilitation model. In these cases, the conditions necessary for later mammalian species are facilitated not by previous mammal species but by vegetation changes concomitant with plant secondary succession. Thus, the cause of the successional change is external to the mammalian community (Whittaker 1975: 171). I have called these “habitat facilitation” models. Mechanism 5 represents a similar modification of the tolerance model, with the mammalian succession responding to the external stimulus of vegetation change, and I refer to this as the “habitat tolerance” model. Individuals of later successional species enter the succession in spite of the continued presence of established populations of early successional species. Changes in the vegetational succession could make the habitat less suitable for early species, but might have little effect on later species. Mechanism 6, although mediated by vegetational change, is initiated within the community, so that it represents a less drastic

change to the inhibition model as stated by Connell and Slatyer (1977). Still-present individuals of early successional species are able to suppress or exclude subsequent colonists of all species. Early occupants modify the environment to be less suitable for both early and late-succession species.

This study cannot hope to test these mechanisms completely, given that it is a single descriptive study dealing with the effects of fire after the event, without the benefit of replication and experimental treatments. However, I have erected this framework of possible mechanisms in an effort to understand this mammalian succession as a basis for comparison, and perhaps to stimulate testing of these ideas against other mammalian secondary successions. By introducing the device of response to externally induced changes in vegetation, I have tried to extend Connell and Slatyer’s models to cover this mammalian succession. The mammalian succession observed in open forest within 10 km of this study showed close agreement with these models based on 16 study plots from five different fire regeneration ages (Fox and McKay 1981), and this observation encouraged me to attempt this analysis.

The study area

The study site was located in coastal heathland in Myall Lakes National Park (latitude 32°28’S, longitude 152°24’E) north of Sydney, New South Wales, Australia. The heath supports nine species of small mammals, and is diverse when compared to other habitats in the park and to other heathlands on the eastern Australian coast (cf. Posamentier 1976). The outer

TABLE 1. Trappability data for each species calculated as (A) Population trappability (Krebs 1966) using (1) proportion of marked individuals of each species captured during each 4-day trapping session and averaging over the total number of sessions that the species was present; (2) average proportion of marked individuals of each species captured each day over an intensively sampled trapping period. (B) Individual trappability (Hilborn et al. 1976) using the number of days that an individual was captured divided by the number of days that the individual was exposed to capture (excluding first and last captures) averaged over all individuals with three or more captures.

		<i>Antechinus stuartii</i>	<i>Sminthopsis murina</i>	<i>Mus musculus</i>	<i>Pseudomys novaehollandiae</i>	<i>Pseudomys gracilicaudatus</i>	<i>Rattus fuscipes</i>	<i>Rattus lutreolus</i>
(A) Population trappability								
Sessions/session (Total)	Mean	0.81	0.69	0.98	0.82	0.83	0.85	0.80
	Variance	0.13	0.21	0.003	0.09	0.08	0.05	0.02
	N	16	18	13	18	31	11	6
Days/day (Intensive sampling)	Mean	0.61	0.54	0.90	0.66	0.56	0.89	0.74
	Variance	0.15	0.11	0.04	0.08	0.22	0.06	0.08
	N	21	17	23	25	24	24	29
(B) Individual trappability								
Days/day (Total)	Mean	0.52	0.43	0.81	0.56	0.67	0.72	0.66
	Variance	0.12	0.07	0.06	0.07	0.05	0.10	0.11
	N	7	8	36	38	39	11	15

barrier high dunes are forested, while the low relief inner barrier dunes support heath. The 4–5 m of relief provided by these low dunes permit gradation from swamp to tall dry heath (Osborne and Robertson 1939, Carolin 1970). Such a gradation occurs on the study site. Part of a former lagoon, the study site has a low transverse dune supporting a patch of eucalypt woodland with a dense, tall, dry heath understorey, thus including the full range of habitats available. These are shown in Fig. 1B and are described in Fox (1980).

A wildfire in August 1974 swept over the heathland from the open forest in the north, burning >2000 ha. The fire was very hot at ground level, leaving only sand and ash, and burned the canopy of the malleeform eucalypts. Much of the adjacent open forest on the high dunes was burned as well, both understorey and canopy. The area has experienced a high fire frequency for at least the last 100 yr. Over the last 10 yr, some sections of the nearby open forest have burned in each of 1979, 1978, 1977, 1976, 1975, 1974, 1971, and 1968 (Fox and McKay 1981: fire map). The result has been a mosaic of forest patches with different regeneration ages and histories. The existence of a high fire frequency was reinforced when the study site (M1 and part of M2) burned, as part of another extensive wildfire, in August 1980.

METHODS

In May 1974, a trapping grid with 20-m trap spacing was established and trapped. The main study plot (M1) was 7 ha, with a second 4-ha plot (M2) adjacent to it but separated by a gravel road. M2 was survey trapped in May 1974 and functioned as an unburned reference plot after M1 burned in August 1974. The purpose of M2 was to monitor seasonal changes and help distinguish them from changes on M1 occurring as part of

the regeneration process. Both plots are shown on the topographic map in Fig. 1A.

M1 was trapped at \approx 2-mo intervals (1974–1978) with additional trapping sessions, sometimes at 2-wk intervals, during breeding seasons. For each trapping session the minimum number of animals known to be alive on the study plot during the session (MNA) was taken to be the simplest measure of abundance (Krebs 1966). M2 was monitored at \approx 3-mo intervals for 16 trapping sessions comprising 5590 trap nights, while M1 was monitored for 34 trapping sessions comprising 16 350 trap nights.

Collapsible aluminum small-mammal traps ($33 \times 10 \times 9$ cm) were set, one at each trapping station, and baited with a mixture of rolled oats and peanut butter. Traps were checked in the early morning, except during winter when traps were also checked at night to minimize trap mortality. In each session, trapping was carried out for four successive nights with no prebaiting period. At the time of first capture, all animals were identified and given an individual toe clip, and a numbered metal ear-tag was attached. At the first capture in a trapping session, body measurements were taken (head and body, tail, and hind foot). For every capture the mass of the animal was determined to the nearest 0.5 g, and the animal was identified to species and individual. The sex and reproductive condition were noted and the trap station recorded for all captures.

RESULTS AND INTERPRETATIONS

To justify the use of the measure "minimum number alive" (MNA), I have presented trappability data for all species (Table 1), calculated on both population and individual bases using the methods of Krebs (1966) and Hilborn et al. (1976). The only entry in the table

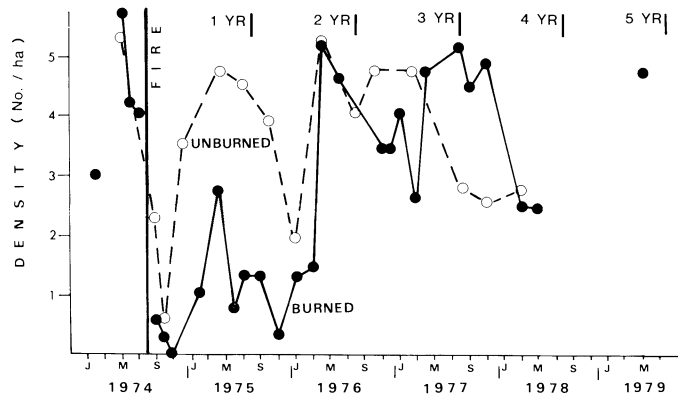


FIG. 2. Changes with time in the density of animals known to be alive (MNA) at each trapping session. ●—● indicates the burned plot (M1); ○—○ the unburned plot (M2). January, May, and September are marked on the time scale.

below the 0.50 trappability recommended by Hilborn et al. (1976) is for *Sminthopsis murina* when calculated for individuals on a day by day basis. However, when calculated on the same 4-d sessional basis used to determine MNA values, the appropriate trappability is 0.69.

A minimum estimate (MNA) for the total number of animals on each study plot is used to calculate densities on each study plot for comparison (Fig. 2). Of 74 animals marked in the 3-mo period before the fire, only 4 were recorded in the first trapping session 1 mo after the fire. Chew et al. (1959) reported finding large numbers of carcasses immediately after a wildfire in chaparral. Animals were probably killed in this fire too, although no carcasses were found at the first post-fire trapping session.

Both plots undergo a seasonal variation in total abundance (MNA), peaking in early to midwinter and reaching a low point in early to midsummer. Seasonal changes in abundance are most marked in *Pseudomys novaehollandiae*, *Sminthopsis murina*, and *Antechinus stuartii*, and apparent local extinctions occur for parts of the year. The extent to which this may be a behavioral response, producing reduced trappability, should not be overlooked. Kemper (1977) reported a decrease in the number of males in her trappable population during early summer, but she trapped males later in the summer that were old enough to have been in the population earlier. Fletcher (1977) has shown seasonal changes in trappability for *A. stuartii* in rain forest, with up to 18% of the population avoiding traps completely.

M1 shows a marked depression in MNA until mid-1976, which is superimposed on the seasonal variation observed in M2 (Fig. 2). I have interpreted the overall population increase on M1 from late 1974 as a part of the regeneration process, numbers peaking at the end of 1977, then decreasing again. The very marked decline in MNA on M2 during September and October 1974 may have resulted from the influx of predators,

particularly accipiters, observed following the fire on M1. Temporal changes in abundance (MNA) of all species on both plots are presented in Fig. 3.

Postfire recolonization

Four stages can be recognized in the process of recolonization by a species. First, dispersal from other areas results in the presence of transient individuals on burned areas. Later, dispersers are able to establish residence on burned areas, thus becoming colonists. A third stage is reached when colonists successfully reproduce, and the final stage is the increase in abundance associated with the recruitment of resident juveniles in addition to dispersers. Different species excel in different stages, so that they exhibit different and independent rates of recolonization.

Rattus lutreolus (Fig. 3D), a specialist herbivore, showed the most dramatic decline in MNA. Of 18 individuals caught on M1 in the 3 mo before the fire, only 1 was recaptured in the 1st mo postfire. No individuals were caught in the next 3.5 yr, despite the presence of potential colonists in nearby unburned vegetation. Furthermore, there was no successful breeding until almost 5 yr after the fire. This species, then, exhibits both poor dispersal and poor colonization ability.

Rattus fuscipes (Fig. 3C), an omnivore, differed from *R. lutreolus* in that individuals were able to colonize for short periods. Successful breeding on M1 did not occur until 4 yr after the fire, even though breeding on M2 was successful in each year. This species, then, shows good dispersal and colonizing ability, but is limited by its failure to reproduce successfully until later seral stages.

Antechinus stuartii (Fig. 3B), an insectivorous marsupial, although present within 6 mo of the fire, remained at a low level, only reaching 57% of its prefire abundance after 3 yr and 70% after 5 yr. Juvenile recruitment was successful in 1977 and again in 1978. This species achieves the first three stages of recolo-

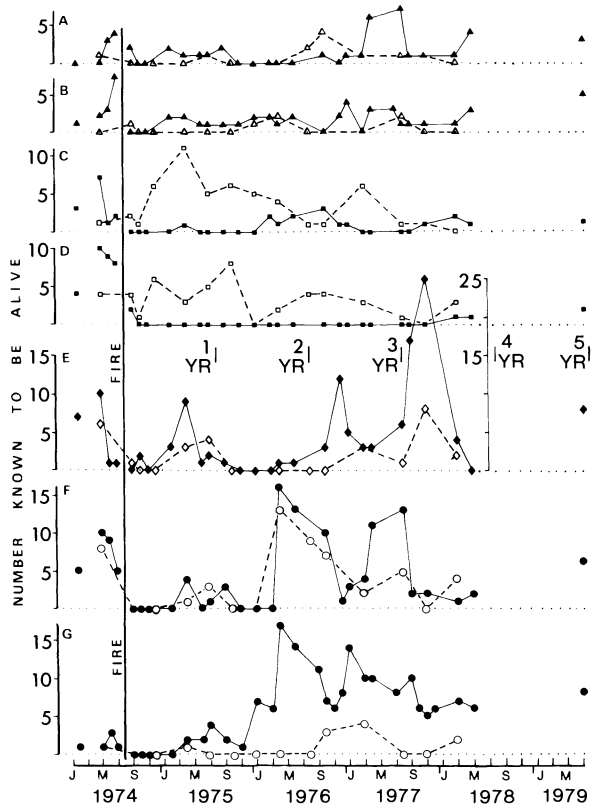


FIG. 3. Changes with time in numbers (MNA) for each species on each plot at each trapping session. As M1 is 7 ha and M2 is 4 ha, comparisons should be for relative changes rather than absolute numbers. (A) *Sminthopsis murina*, (B) *Antechinus stuartii*, (C) *Rattus fuscipes*, (D) *R. lutreolus*, (E) *Mus musculus*, (F) *Pseudomys novaehollandiae*, (G) *P. gracilicaudatus*. Different symbol shapes indicate different taxonomic groups; open vs. closed symbols as in Fig. 2.

nization but is now limited by a slow increase in abundance.

Sminthopsis murina (Fig. 3A), another insectivorous marsupial, showed a marked increase in late 1976 after an unsuccessful initial attempt at recolonization on M1 in 1975. Breeding was successful in 1976. This species exhibits successful recolonization at each stage.

Mus musculus (Fig. 3E), an introduced omnivore, colonized M1 and began successful breeding in less than a year, increased sufficiently in abundance in mid-1975 to cause dispersal to M2 but disappeared from both M1 and M2 by the end of the year. Further recolonization occurred in late 1976, causing a population explosion in late 1977 followed by a precipitous decline in early 1978. This species has excellent dispersal (high numbers of transient individuals) and short-term colonizing ability combined with an equally high rate of reproduction and ability to increase. However, populations are not stable. A similar irruption in *Mus* numbers was noted during 1977 on recently

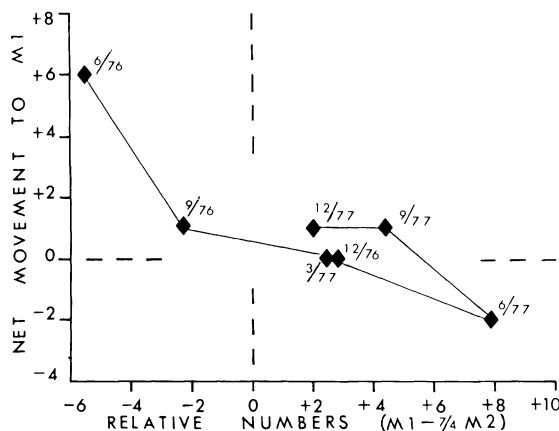


FIG. 4. For *Pseudomys novaehollandiae*, the relation between net migration into M1 in each quarter and the relative population numbers (M1 = 1.75 M2), with account taken of the smaller area of M2 (i.e., for equivalent populations, abscissa value is zero). Dates are midpoints of quarters when dispersal was recorded.

burned plots in nearby open forest (Fox and McKay 1981). The very large fluctuations in numbers of *Mus* perhaps indicate the behavior of a fugitive species responding to change, rather than that of a fire specialist. Laurie (1946) reports that *Mus* has the ability to breed all year round.

Pseudomys novaehollandiae (Fig. 3F), a generalist granivore, benefited from very high dispersal. M2 provided colonizers for M1 in early 1976, but in turn received animals in mid-1977 when animals were abundant on M1 but in low numbers on M2. This is illustrated by Fig. 4, which shows that not only the direction but also the magnitude of dispersal are functions of the relative populations on the two plots. This species exhibits good performance at all stages and shows longer occupation periods for individuals than does *M. musculus*.

Pseudomys gracilicaudatus (Fig. 3G), a generalist herbivore, had high juvenile survival producing good recruitment. Good colonizing ability made up for a lower dispersal rate. Abundance reached prefire levels in 1 yr and increased sixfold within 2 yr, largely due to high recruitment on M1. Numbers did not increase beyond the mid-1976 peak and slowly decreased during 1978 and 1979, even though successful breeding occurred. These factors support the characterization of *P. gracilicaudatus* as a fire specialist.

Spatial niche parameters calculated for species in this community show significant rejection of null hypotheses of noninteraction between species in relation to their use of space (Fox 1981). These results are consistent with circumstantial evidence for interaction between congeners and pairs of similar species in this community (Fox 1980). The strongest evidence of interaction was the relationship between native species and the introduced *Mus*. Newsome and Corbett (1975)

TABLE 2. Yearly population maxima for each species over a 5-yr period on the unburned plot tested against a null hypothesis of no significant difference between years. Kolmogorov-Smirnov tests (Siegel 1956) were used, and values for the statistic *D* and significance levels are included together with the total number of individuals for each species as the degrees of freedom.

	Yearly population maximum (unburned plot)					Σ	<i>D</i>	<i>P</i>
	1974	1975	1976	1977	1978			
<i>Pseudomys gracilicaudatus</i>	0	1	0	4	2	7	.46	.1 > <i>P</i> > .05
<i>Mus musculus</i>	6	4	0	3	8	21	.18	> .2
<i>Pseudomys novaehollandiae</i>	8	3	14	7	5	37	.10	> .2
<i>Sminthopsis murina</i>	1	1	2	4	1	9	.18	> .2
<i>Antechinus stuartii</i>	0	1	2	2	0	5	.20	> .2
<i>Rattus fuscipes</i>	1	11	5	7	1	25	.16	> .2
<i>Rattus lutreolus</i>	4	6	4	4	3	21	.08	> .2

report that for central Australia, *Mus* displaces native species. However, the observed pattern here is consistent with *Mus* reacting to changes in abundance of native species. The two dasyurids *A. stuartii* and *S. murina* also exhibit a marked ecological separation (Fox 1982).

Significance of changes in abundance

I use the criterion that the peak abundance for each species (MNA) during prefire trapping sessions represents the best estimate of peak abundance for that species in any year, had the fire not occurred. To test the appropriateness of this as an expected value, I tested the unburned plot (M2) against the null hypothesis of no significant differences in abundance between years (i.e., a uniform cumulative frequency distribution with five classes: 0.2, 0.4, 0.6, 0.8, 1.0), using the Kolmogorov-Smirnov test for goodness of fit (Siegel 1956:47, Sokal and Rohlf 1969:571). Yearly maxima (1974–1978) for each species on M2 are shown in Table 2, together with the test statistic (*D*) and its probability of occurrence by chance alone. The null hypotheses were accepted (*P* > .05): a uniform distribution is an appropriate method for determining expected values. Yearly maxima for the burned plot (M1) as shown in Table 3 were then tested over the same period (1974–1978). The zero values for *R. lutreolus* meant that population data for that species had to be tested with the Kolmogorov-Smirnov test also, but the more sensitive

G-test (log likelihood ratio; Sokal and Rohlf 1969:559) was used for all other species (Table 3). All species show significant changes from their 1974 maxima, so that differences represent real changes in abundance.

Response indices

To quantify these differences for each species, I calculated a fire response index for each year as the logarithm of the ratio of the maximum value of MNA in each year since the fire, to the maximum MNA before the fire. The behavior of this index for each species is shown in Fig. 5. Positive values represent increases on prefire levels, and negative values decreases. A total index was calculated from the logarithm of the ratio of the sum of the five postfire years to five times the prefire value. This overall fire response index was used to evaluate the effect of fire on each species.

The classification of species using a fire response index is in agreement with much of what limited information is available in the literature. Quantifying the response allows comparisons between species in this study, and, I hope, between studies. The community subdivides into four groups: one badly affected by the fire (< -0.4, both *Rattus* species); one less badly affected (-0.4 to -0.2, *A. stuartii*); a third group able to maintain populations in fire-perturbed areas (-0.2 to 0.2, *P. novaehollandiae*, *S. murina*, and *M. musculus*); and the last showing a positive overall response to the perturbation (> 0.2, *P. gracilicaudatus*). The

TABLE 3. Yearly population maxima for each species over a 5-yr period on the burned plot with results of a log likelihood ratio test (Sokal and Rohlf 1969) for departure from a uniform distribution equal to the prefire (1974) value. For *R. lutreolus* a Kolmogorov-Smirnov test (see Table 2) was used.

	Yearly population maximum (burned plot)					<i>G</i>	<i>P</i>
	1974	1975	1976	1977	1978		
<i>Pseudomys gracilicaudatus</i>	3	4	17	14	18	+169	≤ .001
<i>Mus musculus</i>	10	9	1	12	25	+44	< .001
<i>Pseudomys novaehollandiae</i>	10	4	16	11	13	+16.6	< .001
<i>Sminthopsis murina</i>	4	2	3	6	7	+8.2	< .05
<i>Antechinus stuartii</i>	7	2	2	4	3	-19.6	< .001
<i>Rattus fuscipes</i>	7	1	2	3	2	-19.0	< .001
<i>Rattus lutreolus</i>	11	2	0	0	1	<i>D</i> = 0.52	< .001

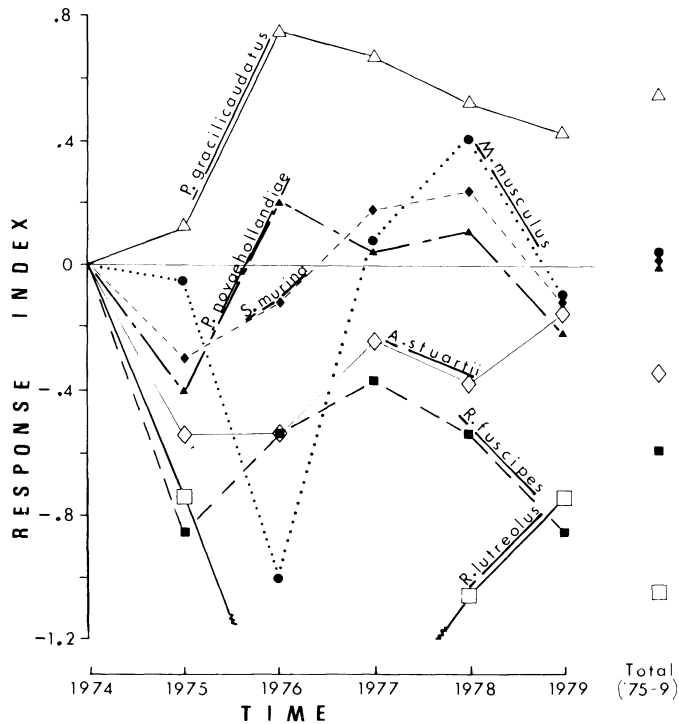


FIG. 5. Fire response index (logarithm of ratio of maximum value of MNA in each year to prefire [1974] maximum MNA) for each species as a function of time. Solid symbols show dry-habitat species, and open symbols show wet-habitat species.

division is based on each species' performance (see Fig. 5). *Antechinus stuartii* can also be separated from the two *Rattus* species because of its steady increase, as opposed to their delayed recovery.

Succession

A gradient in postfire responses of species is clearly demonstrated in Fig. 5. This is also reflected in the time required for each species to reach its peak abundance (Fig. 6). The sequences of species in wet heath and dry heath are shown separately. *Mus musculus* occurred predominantly in dry heath in 1975, but predominantly in wet heath in 1977–1978, and is shown in both habitats. *Pseudomys* occupies the early seral stages, and *Rattus* clearly occupies the later seral stages, with the dasyurids occupying mid- and late seral stages in this succession. Newsome et al. (1975) found that *A. stuartii* survived, with fluctuations, on open forest plots, but not on heath plots. Christensen and Kimber (1975) report a much longer period of 20 yr for a similar species, *A. flavipes*, to reach prefire levels in Western Australia. No information is available for *S. murina* apart from a study in a nearby forest by Fox and McKay (1981) which shows it to achieve maximum densities in forests whose understory was burnt 2–6 yr previously.

The order and timing of this replacement sequence is very similar to that observed on simultaneously trapped, replicated plots of different regeneration ages

in a nearby open forest (Fox and McKay 1981). Early and mid-seral stage species appear to increase and then decrease, peaking when their particular habitat requirements are best met. A significant body of information is now emerging that identifies four species of *Pseudomys* as fire- or disturbance-enhanced species: *P. novaehollandiae* (Posamentier and Recher 1974, Posamentier 1976, Kemper 1977, Braithwaite and Gullan 1978, Fox and Fox 1978, Fox and McKay 1981, and this study), *P. shorridgei* (Cockburn 1978), *P. albocinereus* (reported as a *personal communication* from C. R. Crouch in Cockburn 1978), and *P. gracilicaudatus* (this study).

The community composition changes drastically as a function of regeneration time. Beck and Vogl (1972) were able to convert an oak forest to brush-prairie savanna by increasing the fire frequency, and reported concomitant changes in small-mammal species composition. Cook (1959), however, shows changes in the abundance of species in brush and grassland habitats, rather than species replacement. Wetzel (1958) reports a mammalian succession following strip-mining on a Midwestern floodplain (USA), where a species replacement sequence was clearly demonstrated. Pearson (1959) has shown a similar mammal species replacement during old-field succession. Christian (1977) suggests that the rapid return of small mammals to a recently burned desert grassland is attributable to the fact that the normal ranges of the species encompass

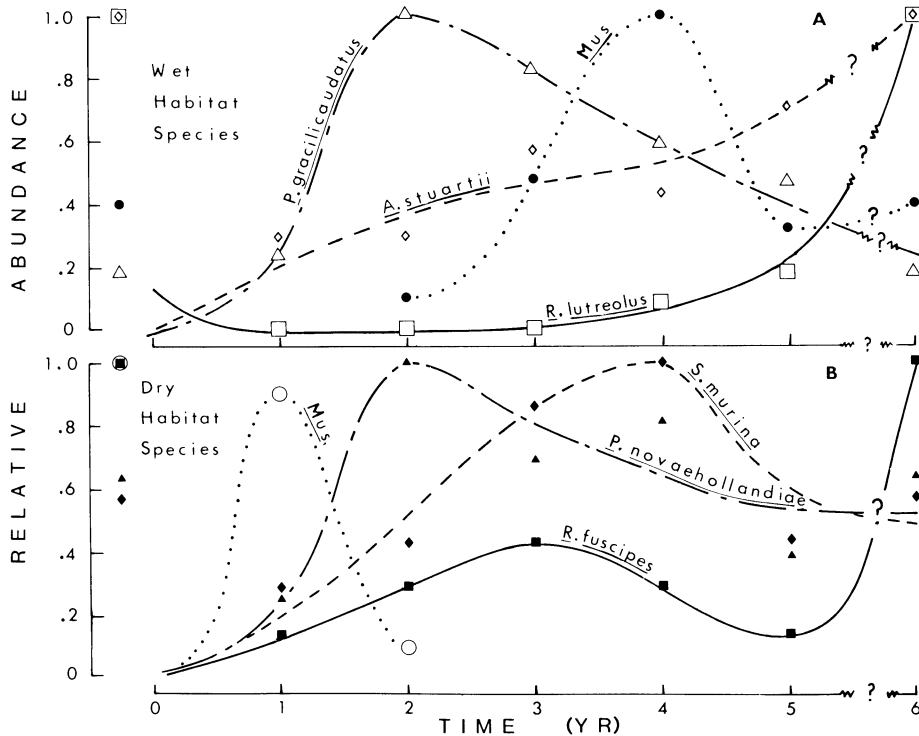


FIG. 6. The succession of mammal species responding to changes in vegetation regenerating after fire. A: wet-habitat species, B: dry-habitat species. Values for each species are shown as a proportion of that species' maximum abundance. Prefire abundances are shown to the left of the abscissa scale and again at 6 yr, the estimated age of the site since the last fire (hence the question mark).

natural areas equally as harsh. This is probably true for *Mus* and perhaps *Pseudomys* as well. Conversely, it may also be a reason why the two *Rattus* spp. appeared so late.

The ground cover may not have been thick enough to support *R. lutreolus* recolonization; Posamentier (1976) has shown that *R. lutreolus* requires a dense ground cover. Layne (1974) found that the reappearance of harvest mice and cotton rats after fire in a Florida flatwoods was correlated with the redevelopment of ground cover. For *R. fuscipes*, Christensen and Kimber (1975) report similar results up to 3 yr after fire on their shrub-understory plot. Although they had better colonization by males on their sword-grass plot, females were largely transient, thereby precluding successful breeding.

Newsome et al. (1975) indicate similar results on small grids, but on their larger grids in open forest, *R. fuscipes* survived and then increased in the 2nd yr after fire. They commented on the patchy nature of the forest which probably accounted for the *R. fuscipes* survival after the fire. Cowley et al. (1969) and Leonard (1970) report high *R. fuscipes* survival after control burns which left 30% and 50%, respectively, of the area unburnt. Leonard (1970) shows *R. fuscipes* to have overwhelming preference for dense unburnt areas on his plot. Fox and McKay (1981) found no *R.*

fuscipes colonists until 3 yr postfire. A period of increase in *R. fuscipes* biomass followed until 5 yr postfire when it began to plateau.

Comparison of succession models

In comparing the mechanisms by which fire may affect community composition, I draw upon the information from this study, together with relevant published work to which I have referred. Mechanism 1 does not describe the situation observed, which suggests that the vegetation present early in the succession is entirely unsuitable for the late seral stage *Rattus*. The presence of *Rattus* in nearby unburnt vegetation throughout the study supports rejection of this mechanism. Rejection of mechanism 1 implies that the tolerance and inhibition models of Connell and Slatyer (1977) cannot be considered as suitable descriptions. Mechanism 2 does appear to operate in general and is exemplified by the orderly way in which species reach their peak abundance (Fig. 6). Mechanism 3 is more specific and would appear to describe the response of the fugitive *M. musculus* that is then displaced by the native *P. novaehollandiae*, whose response is better described by mechanism 5. The response of the fire specialist *P. gracilicaudatus* is best described by mechanism 4. There is no evidence that any species has sufficient effect on the vegetation to

satisfy mechanism 6. For both *Rattus* species information is not complete, but they would appear to be best described by mechanism 5.

Mechanism 2 is consistent with the habitat facilitation model. However, the appropriateness of mechanisms 3, 4, and 5 for different species contravenes part of this model. A new model is needed, one able to encompass all small-mammal species in this secondary succession. The one I propose incorporates elements of both the habitat facilitation and tolerance models, and I have termed it the habitat accommodation model.

Habitat accommodation model

In this model, species do not modify local physical conditions. These conditions are changing in response to external factors. Species are able to enter the succession when the changing local physical conditions (habitat) first meet their specific requirements (habitat facilitation model), but as these conditions move out of the optimal range for the species, the animals leave the succession or are reduced in numbers (habitat tolerance model). This may result from the species no longer being able to obtain an adequate share of resources as their competitive ability is reduced.

The habitat accommodation model accounts for all species in this succession and would also appear to describe the postfire mammalian secondary succession observed in physiognomically similar California chaparral (Wirtz 1977, R. D. Quinn, *personal communication*).

An example of another system that may be described by a habitat accommodation model is the succession observed on a salt marsh (Randerson 1979). Accretion of sediment is the external causal factor, and although plant presence may accelerate accretion, Randerson (1979) has shown that the plants do not themselves cause the environmental changes. Plant species enter the succession and reach peak abundance when conditions are optimal for them, then are greatly reduced in abundance as marsh development continues. A similar externally induced succession is observed in the appearance of the reproductive structures of coprophilous fungi growing on herbivore dung (Hudson 1972).

CONCLUSIONS

This study has shown that a major perturbation of a small-mammal community can produce a variety of responses among the species comprising the community. These responses can be represented by a response index that suggests a long-term resource axis (regeneration time) partitioned among species. The rapid recovery illustrated by total number of individuals indicates that fire and fire frequency have been important factors in the development of the heath small-mammal community. This has been supported

by the marked increase in importance of the native murid *Pseudomys gracilicaudatus* in the postfire community, where it increased sixfold during the 1st 3 yr. The habitat accommodation model, or a new model of another form, is necessary to describe adequately the range of responses, which represent a mammalian secondary succession or species replacement series that responds to the vegetation changes occurring as part of the plant pyric succession. The need to maintain a mosaic of regeneration ages for management and maintenance of a diverse small-mammal community (Pickett and Thompson 1978) has been demonstrated.

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