

Responses of reptiles to fire and increasing time after fire in *Banksia* woodland

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ABSTRACT

In the study of the impact of fire on terrestrial vertebrates in Australian ecosystems, most work has focussed on small mammal species while often richer reptile assemblages have received little attention. Studies on mammals have found that dramatic changes in abundance after fire can be related to changes in vegetation structure; but it is not clear to what extent generalizations based on mammals can be extended to reptiles.

In a three-year study, reptiles were sampled in six areas of *Banksia* woodland unburnt for different lengths of time from 0 to 23 years. The reptile assemblage varied mainly in the first two years after fire, mostly due to differential survival of adult and immature specimens immediately after fire. One species, the small agamid *Tympanocryptis adalaidensis*, was most abundant 3-6 years after fire and this could be related to changes in vegetation structure. Apparent patchiness in the local distribution of most reptiles made results difficult to interpret.

In general, reptiles were tolerant of fire-induced changes to their environment. Fire-related changes in population structure disappeared within a few years of fire and the reptile assemblage then appeared stable. This may have been due to the rapid regeneration and subsequent structural stability of *Banksia* woodland after fire.

INTRODUCTION

Australian ecosystems have developed under a long association with fire (Kemp 1981; Singh *et al.* 1981) and its significance to flora and fauna is widely-acknowledged. Fire is recognized as a valuable management tool and has been extensively used in management within the forestry industries of southern Australia (McCaw and Burrows 1989) and the pastoral

industries of northern Australia (Lewis 1985). As noted by Friend (1993), however, its application in conservation has been restricted by a lack of understanding of its impacts, particularly upon fauna.

A number of studies, both in Australia and overseas, have found that diversity of plants and animals is highest soon after fire, with diversity declining in long-unburnt sites (Taylor 1973; Recher and Christensen 1981; Willan and Bigalke 1982). Willan and Bigalke (1982) also recorded a slight increase in small mammal diversity in long-unburnt sites. The general pattern of highest diversity soon after fire is associated with nutrient release and changes in the structural complexity of the vegetation as it regenerates and senesces after fire.

Detailed studies on vertebrate fauna in Australia have focussed mainly on mammals. In a detailed review, Friend (1993) concluded that small mammals have 'a reasonably consistent and predictable' seral response, with the response of a species to fire being consistent with its life history parameters such as shelter, food and breeding requirements. Similarly, Taylor (1991) concluded that with reference to small mammals, 'fire has been seen as a factor mainly influencing the availability of different successional stages of vegetation'. Numbers of most small mammal species decline dramatically after fire and individual species may achieve maximal abundance at a specific stage after fire when the vegetation satisfies their habitat requirements. This can give rise to successional-like changes in the levels of abundance of the species present (Fox and McKay 1981). Mammal species that have been most adversely affected by changes in fire regimes since European colonization are those that have the most specific habitat requirements in relation to post-fire stages of vegetation.

Observations on the impact of fire upon small mammals provide a theoretical framework for examining studies on other fauna, including reptiles. According to Friend (1993), reptiles are generally considered to be more resilient to the short-term impacts of fire than small mammals, but long-term changes in abundance have been recorded. Two studies (Cheal *et al.* 1979; Mather 1979, in Friend 1993) found that lizard species richness and abundance were

lower in a long-unburnt than a recently-burnt site and associated this with understorey density and height. Caughley (1985) recorded little change in the lizard assemblage with time after fire but did find successional-like trends in relative abundances of the species. She associated this with changes in vegetation structure and composition, particularly in the case of the small agamid *Ctenophorus fordii*, which was most abundant soon after fire when the vegetation consisted of bare ground and dense clumps of regenerating plants. Kahn (1960) and Lillywhite and North (1974) made similar observations with the small iguanid *Sceloporus occidentalis*. Mushinsky (1985) examined the impact of fire frequency upon reptiles and found that some fire frequencies increased reptile density and diversity; he suggested this was due to the impact of regular fires on vegetation structure and particularly on the availability of open areas.

There appears to be some consistency between observations on the impact of fire on small mammals and reptiles. This has led Friend (1993) to suggest the development of a model to predict the response of a species to fire on the basis of its life history parameters. Available data on reptiles are limited, however, and this paper reports on a study of reptiles in relation to time since fire to see whether generalizations based on data collected on small mammals can be applied to this taxon.

METHODS

Study Area

The study area was near Mooliabeenee, approximately 80 km north of Perth at 31°20'S., 116°02'E. and consisted of six areas of *Banksia* woodland. These areas were similar in topography and the vegetation consisted of an understorey dominated by *Eremaea pauciflora* and an overstorey to 6 m of *Banksia attenuata*, *Banksia menziesii* and scattered specimens of *Banksia ilicifolia* and *Eucalyptus todtiana*. The areas ranged in size from approximately 40 to over 100 ha but all were connected to larger regions of *Banksia* woodland; the layout of the areas is given in Bamford (1992a). Work was carried out on these areas from April 1983 to March 1986.

Sampling spanned the period 0-23 years after fire. Area 1 was burnt on 20 March 1985 and was previously burnt in 1962-63; it was thus sampled more than 20 years after and in the first year following a fire. Area 2 was burnt on 21 September 1984 and was sampled for a year following this fire to get some data on the impact of a low intensity, spring fire compared with all other fires, which occurred in summer-autumn and were of high intensity. Area 3 was burnt on 13 March 1983, 12 years after previously being burnt, and was sampled over the period 0-3 years after fire. Areas 4, 5 and 6 were burnt in March 1980, summer 1971-72 and summer 1962-63 respectively, and were thus sampled

over the periods 3-6, 11-14 and 20-23 years after fire.

Sampling

Reptiles were studied using a mark-release-recapture program based on five consecutive nights' trapping each month with grids of 50 pitfall traps (hereafter referred to as pitfalls). Two such grids were placed in each area and within each grid, pitfalls were located at 5 intervals; each grid was therefore 45 m long by 20 m wide. The pitfalls consisted of 40 cm lengths of 15 cm diameter PVC pipe. They were capped when not in use and had 1.5 mm mesh bases to prevent specimens from tunnelling out.

In the first year of the study, only single grids were operated in areas 1, 4, 5 and 6, two grids being used in subsequent years and for all sampling in areas 2 and 3. Sampling on all grids was limited to two nights in January 1986 and no nights in February 1986. Therefore, expected captures on each grid for these months were calculated from the proportion of captures in previous years that occurred in January and February. Across all grids, captures in these months accounted for only 20 per cent of all captures. While numbers of captures could be estimated by this approach, numbers of species could not be similarly estimated. Therefore, analyses which required values for the number of species excluded estimated annual samples.

The experimental design used in this study was based on the opportunistic availability of sites; in the south-west of Western Australia it is very unusual to find a set of juxtaposed stands of vegetation varying in time since fire as did the sites used in this study. The sampling layout constituted pseudo-replication (*sensu*. Hurlbert 1984) because replicate grids were placed within the same site and the time-frame from 0-23 years after fire was spanned by a series of sites. This design places some restrictions on valid statistical analysis.

For analysis, the annual number of captures (including recaptures between months) of all species and of each species per grid were used as indices of abundance in relation to time since fire. As an index of abundance, the annual number of captures is almost certainly affected by differing trappability of species but was assumed to reflect differences in absolute abundance of the same species between sites.

Annual numbers of captures were analysed using a subdivided chi-square approach as described by Zar (1974). This involves testing a data set for significant variation, identifying the values which contribute most greatly to a significant result and then conducting another test with these values removed. If no significant variation is found in the modified data set from which outstanding values have been removed, values in the modified data set can be pooled and compared with each of the removed values to confirm the significance of the removed values. For this analysis, total annual captures per grid were treated as

one data set, but annual captures per grid of all individual species except *Pogona minor* had to be pooled for each site as values were low, resulting in unacceptably small expected values.

Numbers of species and the Shannon-Weiner Diversity Index (H') were calculated for each annual sample. No analyses were conducted on these values, however, because both were affected by the large numbers of species represented by few individuals.

Samples of the same species from different areas were examined in detail to determine whether differences existed between them in population structure, as reflected by the distribution of snout-to-vent length (SVL) and the proportion of immature and adult specimens. From data on reptile morphometrics collected during the project, it was possible to estimate the size at sexual maturity for most species and, therefore, to recognize immature specimens on the basis of SVL and month of capture. All species bred in spring-summer and all except *Menetia greyii*, *Tympanocryptis adelaidensis* and possibly male *Morethia lineocellata* reached sexual maturity at the end of their second year or later (Bamford 1986, 1992c). Where it was possible to compare proportions between areas or sets of areas, proportions were converted with the arcsine transformation before analysis (Zar 1974). Alternatively, mean SVL measurements were compared with Student's *t*-Test. In the study of population structure, *Varanus gouldii* and *Varanus tristis* were excluded as it was suspected that the pitfalls selectively trapped immature specimens of these species.

RESULTS

The Impact of Fire upon Levels of Abundance

Thirty species of reptiles were recorded during sampling (Table 1). An additional five species (the gekkonid *Underwoodisaurus milii*, the scincids *Tiliqua occipitalis* and *Morethia obscura* and the elapids *Pseudonaja nuchalis* and *Vermicella bertholdi*), were observed in the study region but were never trapped. The majority of species were trapped only in small numbers and therefore the impact of fire upon them could not be examined. Only eight species were represented by sufficient captures to allow species-specific analyses to take place.

Numbers of captures of all species, numbers of species and diversity (H'), based on annual samples in each grid, are presented in relation to fire in Figure 1. Annual numbers of captures varied significantly ($\chi^2 = 63.84$, $P < 0.001$), but this was due entirely to one annual sample of 72 individuals collected in area 3, 0-1 years after fire. There was no apparent pattern in species richness or diversity with time after fire.

Despite the lack of general trends in the reptile assemblage in relation to fire, numbers of captures of

individual species were examined to see if trends were present (Fig. 2). Significant trends were found in *Pogona minor* ($c^2 = 53.00$, $P < 0.001$), *Tympanocryptis adelaidensis* ($c^2 = 101.24$, $P < 0.001$), *Lerista elegans* ($c^2 = 99.33$, $P < 0.001$), *Lerista christinae* ($c^2 = 106.16$, $P < 0.01$), *Menetia greyii* ($c^2 = 36.41$, $P < 0.001$) and *Morethia lineocellata* ($c^2 = 116.70.33$, $P < 0.001$); but not in *Ctenotus lesueurii* ($c^2 = 5.60$) or *Cryptoblepharus plagiocephalus* ($c^2 = 9.55$).

Significant variation in captures of *Pogona minor* was lost ($\chi^2 = 29.95$) with the removal of low captures in area 2 (0-1 years after a spring fire), and high captures in area 4 (4-5 years) and area 6 (20-21 years) from the data set. Comparison of each of these values with the pooled, modified data set confirmed their significance ($c^2 = 6.28$, $P < 0.025$, $c^2 = 9.47$, $P < 0.005$ and $c^2 = 6.15$, $P < 0.005$ respectively). These results suggest that numbers may be low shortly after fire but high and variable with greater time after fire.

With *Tympanocryptis adelaidensis*, all significant variation was due to large numbers of captures in area 4 (3-6 years) ($\chi^2 = 10.52$ for the modified data set without captures from area 4). This was confirmed by the comparison of area 4 captures with the pooled, modified data set ($\chi^2 = 96.4$, $P < 0.001$).

Tympanocryptis adelaidensis appears to be scarce after fire, abundant from 3-6 years after fire and then less abundant with greater time after fire.

Sources of significant variation were complex in *Lerista elegans*, with high captures in area 1 (0-1 and 20-22 years) and low captures in area 3 (0-3 years) and area 5 (11-14 years) being important ($c^2 = 5.38$ for the modified data set containing areas 2, 4 and 6 only). This wide source of significant variation suggests a patchiness in abundance independent of time since fire. Further analysis determined significant variation between the pooled, modified data set and area 1 (0-1 years) ($c^2 = 39.3$, $P < 0.001$), area 1 (20-22 years) ($c^2 = 23.6$, $P < 0.001$) and area 3 (0-3 years) ($c^2 = 10.5$, $P < 0.001$), but not between the pooled, modified data set and area 5 (11-14 years) ($c^2 = 2.0$). These results suggest that abundance may be greatest the longest time after fire, with high numbers of captures in area 1 (0-1 year) the result of individuals surviving after fire in the short term, although sampling in area 1 could not be continued to investigate this. The same results could have been achieved, however, if *L. elegans* was very patchily distributed, as areas 2 and 3 had no indication of *L. elegans* surviving from pre-fire abundance.

Variation in captures of *Lerista christinae* was due to large numbers caught in area 3 (0-3 years) and few captures in area 1 (0-1 years and 20-22 years) ($\chi^2 = 8.41$ for the modified data set without captures from areas 1 and 3). These results were confirmed by the comparison of the pooled, modified data set with area 3 ($c^2 = 62.56$, $P < 0.001$) and area 1 (0-1 years $c^2 = 3.92$, $P < 0.05$; 20-22 years, $c^2 = 5.85$, $P < 0.05$). These results suggest that *L. christinae* is patchily abundant in *Banksia* woodland. There appeared to be a decline in

TABLE 1

Numbers of captures (including recaptures) of reptile species in all areas.

AREA	1	2	3	4	5	6	1
YEARS AFTER FIRE	0-1	0-1	0-3	3-6	11-13	20-23	20-22
TRAP NIGHTS	5900	7700	15 950	15950	12 450	12 350	7800
	Gekkonidae						
<i>Diplodactylus polyophthalmus</i>		1	6				
<i>Diplodactylus spinigerus</i>	2		1	4	7	1	4
	Pygopodidae						
<i>Aprasia repens</i>	1		6	3		1	2
<i>Delma fraseri</i>				1		1	1
<i>Delma grayii</i>	2						2
<i>Lialis burtonis</i>							2
<i>Pletholax gracilis</i>	2		3		9	2	
<i>Pygopus lepidopodus</i>			1				
	Agamidae						
<i>Pogona minor</i>	11	8	39	51	40	64	28
<i>Tympanocryptis adelaidensis</i>		1	10	51	8	7	3
	Varanidae						
<i>Varanus gouldii</i>		1	1				1
<i>Varanus tristis</i>			1	2		1	1
	Scincidae						
<i>Cryptoblepharus plagiocephalus</i>	8	17	27	20	21	9	15
<i>Ctenotus fallens</i>	2	9	9	5	3	6	4
<i>Ctenotus impar</i>			1				
<i>Ctenotus lesueurii</i>	5	2	13	14	9	7	7
<i>Ctenotus schomburgkii</i>			1				
<i>Egernia multiscutata</i>					2		
<i>Lerista christinae</i>			80	16	17	16	1
<i>Lerista elegans</i>	20	5		6	2	11	21
<i>Lerista praepedita</i>	3	3			4	3	
<i>Menetia greyii</i>	12	30	16	11	17	8	9
<i>Morethia lineocellata</i>			31	2	7	2	
<i>Tiliqua rugosa</i>				2	2		1
	Typhlopidae						
<i>Ramphotyphlops australis</i>	2						
	Elapidae						
<i>Demansia psammophis</i>			1				
<i>Notechis curtus</i>			1	1	1	3	3
<i>Rhinoplocephalus gouldii</i>			2		2	1	
<i>Vermicella calonotus</i>				1		1	
<i>Vermicella semifasciata</i>		1	1	1	3	2	1
N species	12	11	21	18	17	20	18
N captures	70	78	251	192	154	146	109

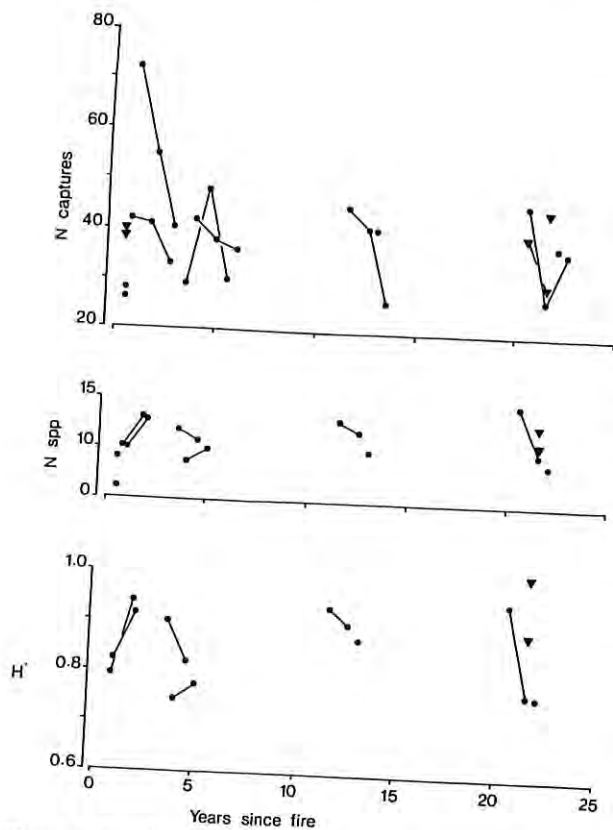


Figure 1. Number of captures (including recaptures) of reptiles per grid per year; number of reptile species per grid per year and Shannon-Wiener Diversity Index (H') of reptile captures per grid per year; against time since fire. Triangles represent data collected in area 1 before and after fire. Lines connect data collected on the same grid in different years. Number of species and diversity present data from complete years only, whereas number of captures includes values estimated from incomplete sampling in the third year of the study.

abundance in the first few years after fire (see Fig. 2); a sub-divided chi-square analysis of area 3 data only determined that significant variation was due to one annual sample only ($\chi^2 = 18.9$, $P < 0.005$ for all data; $\chi^2 = 7.12$ for modified data set excluding the highest annual capture).

Captures of *Menetia greyii* varied significantly as a result of samples collected in areas 1 (0-1 year) and 2 (0-1 year) ($\chi^2 = 5.48$ for the modified data set without captures from areas 1 and 3). In both these areas, significantly more than expected *M. greyii* were caught than in the pooled, modified data set (area 1 (0-1 year) $\chi^2 = 7.03$, $P < 0.01$; area 2 (0-1 year) $\chi^2 = 29.58$, $P < 0.001$). While these results suggest that the abundance of *M. greyii* may be higher in recently-burnt than long-unburnt areas, this observation was not supported by all sites.

Captures of *Morethia lineocellata* were extremely variable and it was not possible to find a modified data set with no significant variation. Therefore, no patterns between significant variation and time since fire could be determined. This result could have been due to patchiness in the local distribution of the species.

The Impact of Fire upon Population Structure

Population structure in samples of *Pogona minor*, *Lerista christinae* and *Menetia greyii* are presented in Figure 3 and proportions of immature specimens are summarized for all species in Table 2.

Immature specimens dominated samples of *Pogona minor* collected more than three years after fire but were uncommon in some samples from more recently burnt areas. While area 1 (0-1 year) was an exception, almost all the immature specimens were caught within six weeks of the fire; these specimens had hatched before the fire. Without these immature specimens, area 1 would have had few captures after fire. In area 3, which was burnt at the same time of year as area 1, sampling did not begin until 8 weeks after fire and no immature specimens were caught in the first year. The cohort of immature specimens hatched immediately before an autumn fire appears to survive the fire but to disappear shortly after. Data from area 3 (1-2 years) suggest that breeding is limited or survival of immature specimens is poor in the second year after fire also. Data from area 2 (0-1 year, after a spring fire) suggest that the season (and possibly intensity) of fire is important to the survival of immature *P. minor*.

The proportion of immature specimens in samples of *Menetia greyii* was high in areas 3 (0-3 year) and 4 (3-6 years) compared with other areas, although numbers were too low to give a significant difference in the mean SVL ($T = -1.01$). Immature specimens hatched before the fire were caught in the autumn after fire in area 1 while immature specimens hatched before the fire in area 3 were not caught until the following spring when most had reached maturity; this reflected the 8-week delay in sampling in area 3. *Menetia greyii*, like other reptiles in the area, was rarely caught over winter. The sample from area 2 (0-1 years) was dominated by adult specimens and the significantly greater number of annual captures in area 2 compared with other areas was due to this. This large number of adults may have resulted from immigration, as *M. greyii* is believed to be nomadic with females concentrating in areas of low vegetation density to lay eggs (Bamford 1992b). Breeding was poor in the summer immediately following the spring fire, however, and no data were collected in the second summer after the fire.

In area 3, high captures of *Lerista christinae* were the result of large numbers of immature lizards, hatched before the fire, surviving in the first year after the fire. Immature specimens comprised only small proportions of samples with greater time after fire. Mean SVL was significantly less in area 3 (0-3 years) compared with all other areas ($T = -3.82$, $P < 0.005$).

With the exception of *Tympanocryptis adelaidensis*, samples of most other species from recently-burnt areas tended to be dominated by immature specimens compared with samples from long-unburnt areas (Table 2). On the basis of mean SVL of samples with a large proportion of immature specimens being less than

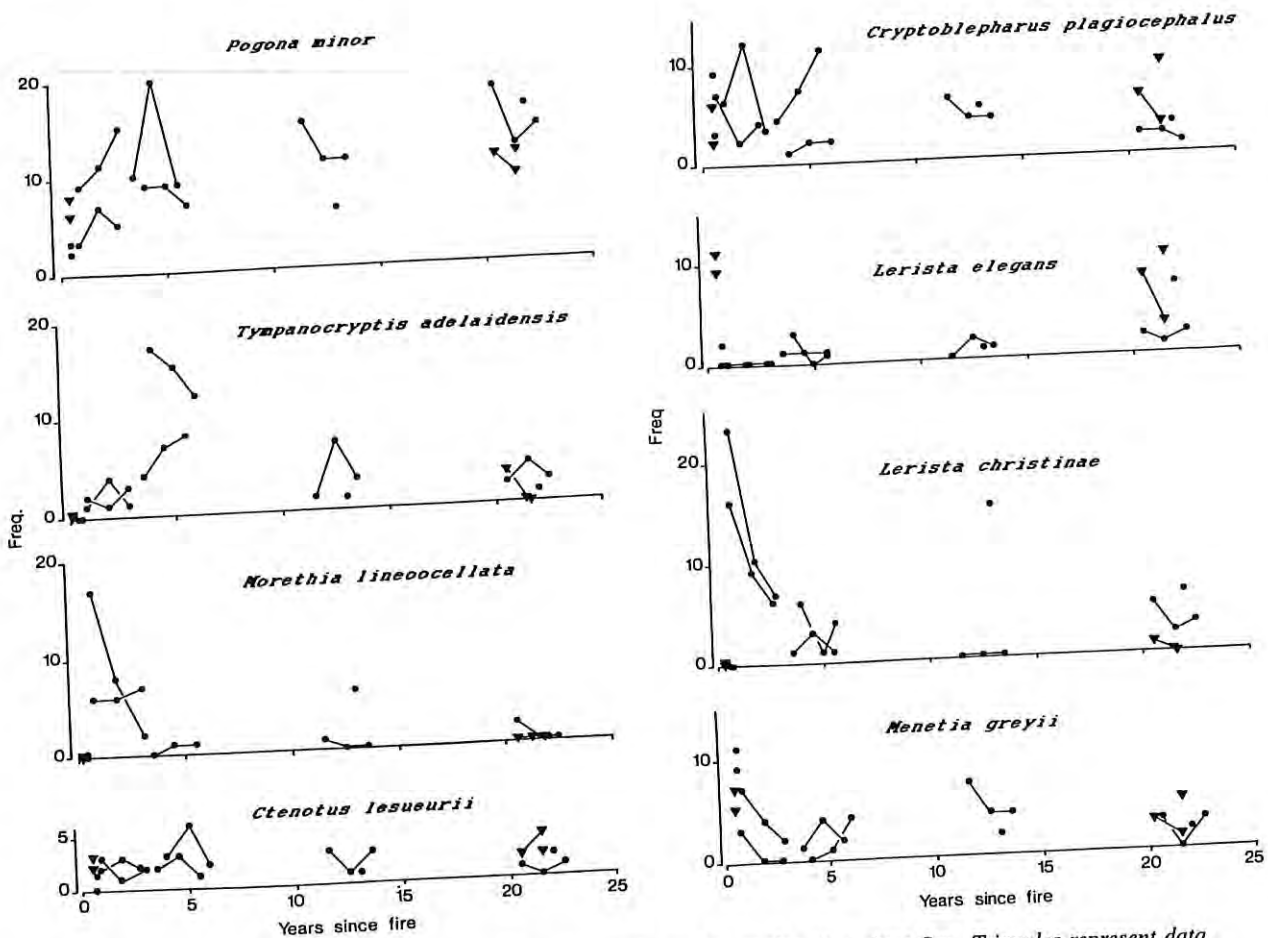


Figure 2. Numbers of captures of the most-often caught reptile species against time since fire. Triangles represent data collected in area 1 before and after fire. Lines connect data collected on the same grid in different years.

that of samples with fewer immature specimens, significant differences were found with *Cryptoblepharus plagiocephalus* ($T = -2.09$, $P < 0.025$), *Morethia lineocellata* ($T = -3.97$, $P < 0.005$) and *Ctenotus fallens* ($T = -3.051$, $P < 0.005$), but not with *Lerista elegans* ($T = -0.608$) and *Ctenotus lesueurii* ($T = -1.368$, although $P < 0.10$). *Morthis lineocellata* was distinctive in that the high proportion of immature specimens was recorded only in the second year after fire in area 3. *Ctenotus fallens* and *C. lesueurii* showed a similar tendency, but annual samples were too small to justify analysis. The representation of immature specimens in samples of *Cryptoblepharus plagiocephalus* differed from other species in that it was high only in area 2 (0-1 years, after a spring fire). The number of specimens involved was small but four of the five immature lizards recorded hatched in the summer after the fire while one was a survivor from the previous breeding season.

Pogona minor was the only frequently-caught species which showed a decline in the proportion of immature specimens in the first year after fire. Even those species caught too infrequently to examine individually, when pooled, revealed a trend for a greater proportion of immature specimens in recently burnt areas (Table 2). For all species except *P. minor* pooled

(Table 2), the mean proportion of immature specimens from samples collected over the period 0-6 years after fire was significantly greater than for samples collected over the period 11-23 years after fire ($T = 4.18$, $P < 0.005$).

DISCUSSION

In studies of relationships between reptile assemblages and time since fire, a number of patterns have been observed. These include: greater richness and abundance in recently-burnt compared with long-unburnt sites (Cheal *et al.* 1979; Mather 1979, in Friend 1993) and successional-like changes in relative abundance with increasing time after fire (Caughley 1985). None of these was recorded in the Mooliabeenee study.

Impacts that could be related to fire were generally restricted to the first few years and in most cases consisted of short-term changes in population structure. Three of the six species affected showed increases in numbers of captures in the first year or few years after fire, one showed an increase in the period 3-6 years after fire, one showed an increase 20-23 years after fire and one showed a decline in the first year after

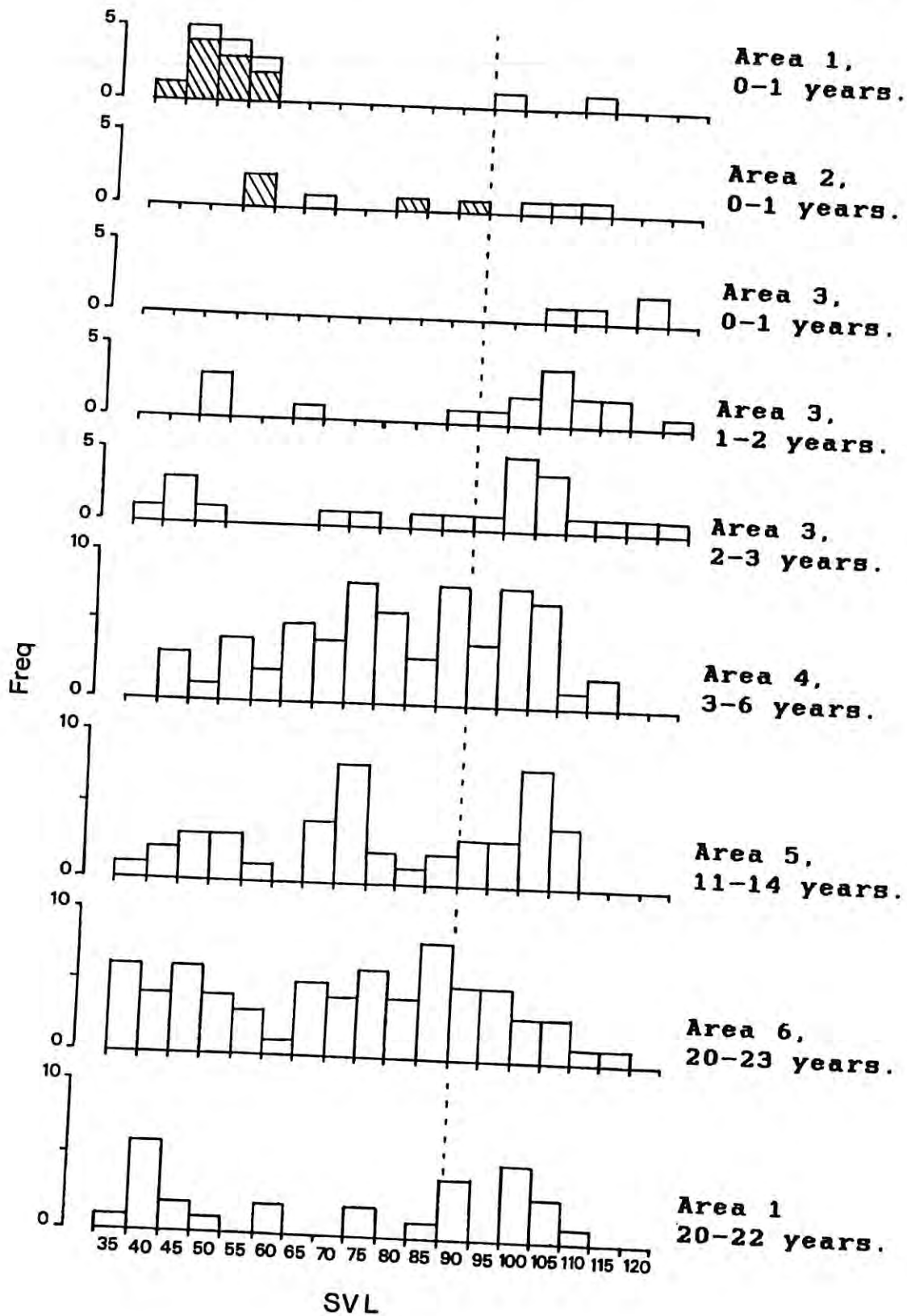


Figure 3 (a). Distribution of snout-to-vent length in samples of *Pogona minor*, in relation to time since fire. Only the lower value of each snout-to-vent length category is indicated. Hatching indicates immature specimens hatched before and area was burnt and caught in the first year after fire. The broken vertical line indicates SVL at sexual maturity. Note that sampling effort was not the same for each histogram; sampling efforts are given in Table 1.

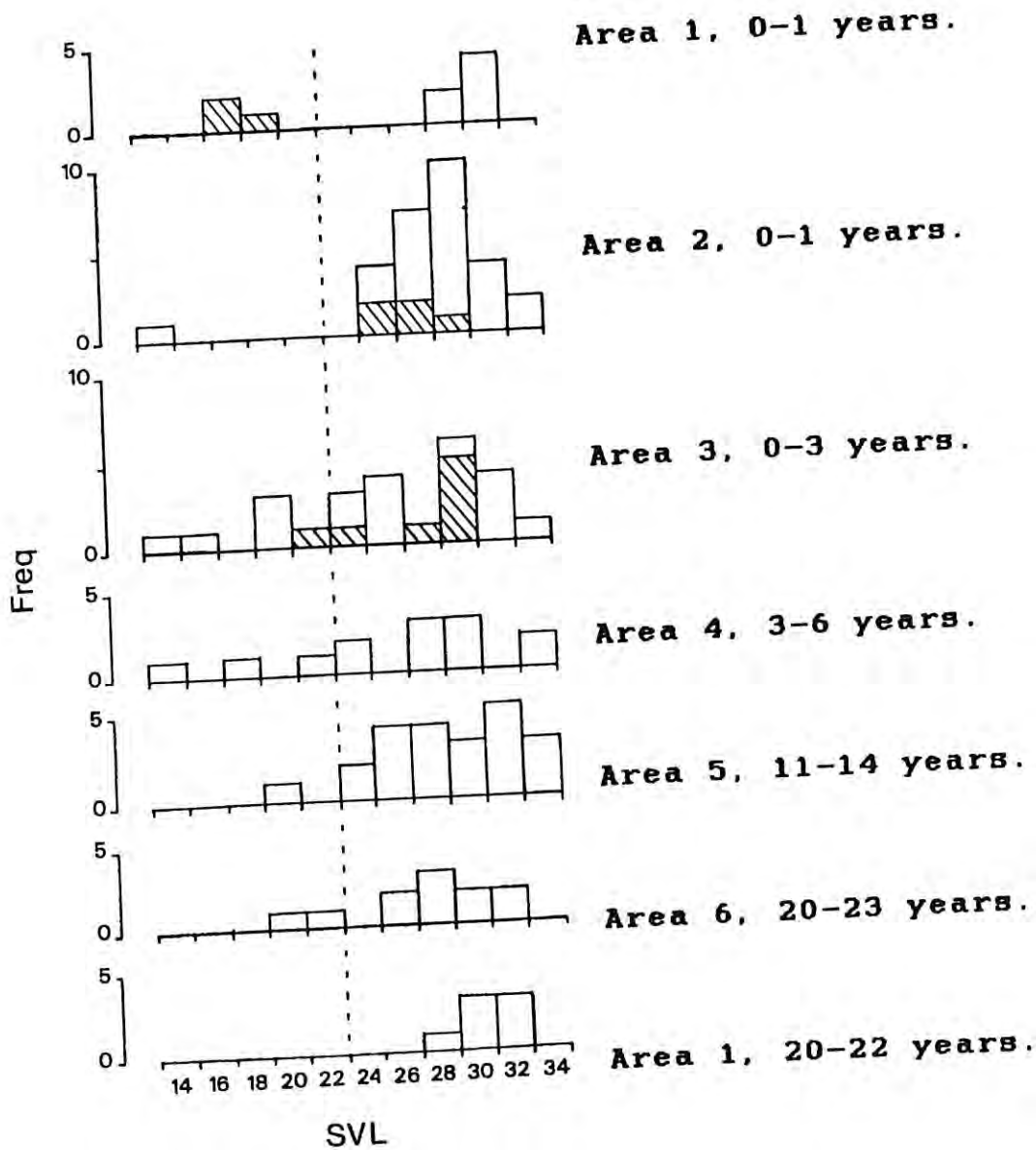


Figure 3 (b). Distribution of snout-to-vent length in samples of *Menetia greyii* in relation to time since fire. Only the lower value of each snout-to-vent length category is indicated. Hatching indicates immature specimens hatched before and area was burnt and caught in the first year after fire. Note that sampling effort was not the same for each histogram; sampling efforts are given in Table 1.

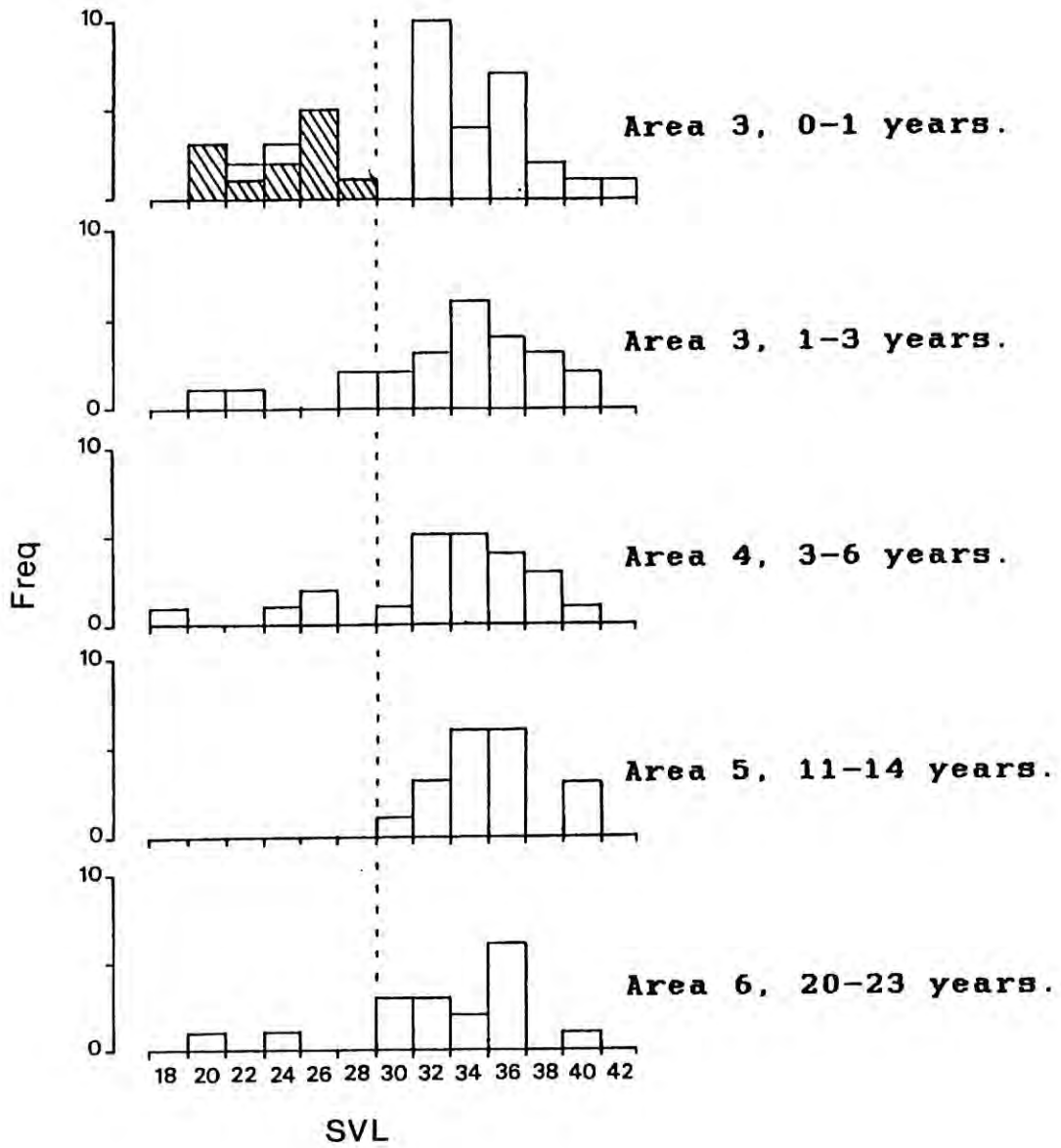


Figure 3 (c). Distribution of snout-to-vent length in samples of *Lerista christinae* in relation to time since fire. Only the lower value of each snout-to-vent length category is indicated. Hatching indicates immature specimens hatched before an area was burnt and caught in the first year after fire. Note that sampling effort was not the same for each histogram; sampling efforts are given in Table 1.

TABLE 2

Proportions of immature reptiles in samples in relation to time since fire. Data from areas of similar time since fire pooled to generate adequate sample sizes.

SPECIES	AREAS	YEARS SINCE FIRE	SAMPLE SIZE	PERCENTAGE IMMATURE
<i>Pogona minor</i>	1,2,3	0-3	47	48.9
	4	3-6	56	57.1
	5	11-14	40	55.0
	1, 6	20-23	94	64.9
<i>Tympanocryptis adelaidensis</i>	3	0-3	12	25.0
	4	3-6	52	26.0
	1,5,6	11-23	13	23.1
<i>Cryptoblepharus plagiocephalus</i>	2	0-1	17	33.0
	1,3	0-1	35	5.7
	4	3-6	20	15.0
	1,5,6	11-23	45	6.7
<i>Lerista christinae</i>	3	0-1	32	31.2
	3	1-3	24	16.7
	4	3-6	16	12.5
	1,5,6	11-23	31	0
<i>Lerista elegans</i>	1	0-1	17	29.4
	1,5,6	11-23	32	12.5
<i>Menetia greyii</i>	1,2,3	0-1	45	13.3
	3,4	1-6	15	20.0
	1,5,6	11-23	32	6.2
<i>Morethia lineocellata</i>	3	0-1	14	0
	3	1-3	22	50.0
	4,5,6	3-23	12	8.3
<i>Ctenotus fallens</i>	1,2,3	0-3	20	85.0
	1,4,5,6	3-23	16	31.2
<i>Ctenotus lesueurii</i>	1,2,3	0-3	20	70.0
	1,4,5,6	3-23	37	43.2
Other species	1,2,3	0-1	25	36.0
	3,4	1-6	30	6.7
	5	11-14	32	15.6
	1,6	20-23	34	8.8
all species except <i>P. minor</i>	1	0-1	55	38.2
	2	0-1	65	33.8
	3	0-1	86	22.1
	3	1-3	105	31.4
	4	3-6	138	23.9
	5	11-14	111	10.8
	6	20-23	80	13.8
1	20-22	73	9.6	

fire. In four of these species, however, patchiness in their local distribution complicated the results.

There was no indication, from changes in the frequency of recaptures or distances moved by recaptures, that observed impacts were due to changes in behaviour rather than to population changes. It is also unlikely that specimens identified as immature were actually stunted adults, as they were of the expected size at the expected time of year. The only exception was a single *Pogona minor* in area 2, caught when about 21 months old and therefore at the beginning of its first breeding season, but noticeably smaller than specimens of similar age elsewhere. The spring fire occurred when this specimen was about nine months old and may have inhibited its growth over the following summer.

Several different patterns in the short-term changes in population structure emerged. In *P. minor*, a decline in abundance after fire was linked to a decline in the abundance of immature lizards in the first six months after an autumn fire. *Pogona minor* is partly arboreal and the lack of understorey cover may have led to increased predation upon small specimens. A more strictly arboreal species, the gecko (*Diplodactylus spinigerus*), was infrequently caught but appeared to suffer a similar post-fire decline. Adult *D. spinigerus* are about the same size as recently-hatched *P. minor* and were very abundant in the first week after fire in area 1. Normally inconspicuous, their pale grey coloration made them very obvious as they clung to blackened twigs. They had survived the fire by sheltering in burrows of other species, including those of the large scorpion *Urodacus novaehollandiae* (personal observation).

The small, fossorial *Lerista christinae* was very abundant in area 3 after fire owing to large numbers of immature specimens from the breeding season before the fire. Survival of this cohort may have increased owing to the complete absence in the first year after fire of the predatory dasyurid marsupial *Sminthopsis griseoventer* (Bamford 1986).

Patchiness in local distribution in this and other species, such as *Lerista elegans*, may have concealed an increase in abundance with greater time after fire. Such an increase could have been associated with increased leaf-litter and would support the relationship between habitat selection and response to fire, but the data are inconclusive.

In *Morethia lineocellata* and possibly also *Menetia greyii*, *Ctenotus fallens* and *C. lesueurii*, high proportions of immature lizards in the first few years after fire were due to enhanced recruitment in the first breeding season after fire, not to enhanced survival of young from the season before the fire as seen with *L. christinae*. *Cryptoblepharus plagiocephalus* displayed a similar pattern, but only after a spring fire. Such enhanced recruitment might be expected to result in an increase in abundance levels in the reptile assemblage, but appeared to be too short-lived an

effect to have such an impact. Enhanced recruitment may have led to the significantly high levels of abundance of *Tympanocryptis adelaidensis* 3-6 years after fire, however. Enhanced recruitment may have gone undetected in this species because individuals mature in less than one year and rarely live for more than two (Bamford 1992c).

Tympanocryptis adelaidensis was the only species with a response to fire that could be interpreted using the hypothesis that a species' habitat preferences influence the impact of fire upon it. Bamford and Bamford (1992) found that captures of *T. adelaidensis* along two, 3 km transects of pitfalls, established through *Banksia* woodland without initial reference to vegetation structure, were concentrated in pitfalls associated with low densities of vegetation. This was at a site 100 km north of Mooliabeenee in an area unburnt for about 12 years. It was suggested that the species actually favoured locations where dense vegetation and open areas were juxtaposed. Such patchiness in vegetation density was evident 3-6 years after fire.

The response of *T. adelaidensis* to fire, involving a peak in abundance a few years after fire associated with patchiness in vegetation density, is similar to that observed in *Ctenophorus fordii* (Caughley 1985) and *Sceloporus occidentalis* (Kahn 1969; Lillywhite and North 1974). Mushinsky (1985) also stressed the importance of patchiness in vegetation density produced by some fire regimes for reptiles. *Tympanocryptis adelaidensis*, *C. fordii* and *S. occidentalis* are small representatives of two families often thought of as ecological analogues (Pianka 1971). A preference for patchy vegetation would appear to be responsible for their similar responses to fire.

Long-term changes with fire found with other studies upon reptiles and very evident with studies on mammals (Friend 1993), have been related to habitat preferences and changes in vegetation structure after fire. In the present study, however, only the response of *T. adelaidensis* to fire can be explained in terms of habitat selection. In other species for which sufficient data were collected, the response was brief and related to changes in survival of immature lizards. The absence of long-term responses in the present study may reflect the speed of regeneration of *Banksia* woodland after fire. Both understorey and overstorey plants resprout after fire and changes to vegetation structure over the period about 5-23 years after fire are minor. This brief period of rapid regeneration is within the lifespan of most of the reptiles recorded in the area (Bamford 1986). In this respect, the fast-maturing, short-lived *T. adelaidensis* is unusual and resembles *C. fordii* (Heatwole 1976). With low rates of population turnover, the populations of most reptiles may not be greatly affected by one or two years of altered recruitment after a fire, while those species with predictable responses to fire may tend to be fast-maturing and short-lived.

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