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Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression

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Summary

1. Conservation of biodiversity in fire-prone regions depends on understanding responses to fire in animal communities and the mechanisms governing these responses.

2. We collated data from an Australian semi-arid woodland reptile community (4796 individuals captured over 6 years) to: (i) determine the ability of commonly used shorter-term (2 years) surveys to detect reptile responses to time since fire (TSF) and (ii) investigate whether ecological traits of species reliably predicted their responses to fire.

3. Of 16 reptile species analysed, four had responses to TSF consistent with shorter-term surveys and three showed no response to TSF. Nine species had responses to TSF not detected in previous studies using smaller but substantial subsets of the same data.

4. Among the 13 affected species, times of peak abundance ranged from 1 to 50 years after fire. Nocturnal, burrowing species tended to be early successional and leaf-litter dwellers to be late successional, but these were only weak trends.

5. *Synthesis and applications.* We found only limited support for a generalizable, trait-based model of succession in reptiles. However, our study revealed that the majority of common reptile species in our study region specialize on a post-fire successional stage and may therefore become threatened if homogeneous fire regimes predominate. Our study highlights the importance of interpreting results from time- or sample-limited fire studies of reptiles with the knowledge that many ecological responses may not have been detected. In such cases, an adaptive or precautionary approach to fire management may be necessary.

Key-words: disturbance, fire management, habitat accommodation model, life-history traits, mallee, prescribed burning, sampling effort, Type II error

Introduction

Animal species in many ecosystems are threatened by altered fire regimes (Brisson, Strasburg & Templeton 2003; Gregory, Sensenig & Wilcove 2010; Pons & Clavero 2010) often caused by inappropriate management. Implementing management without understanding its ecological consequence or effectiveness could alter ecological communities, reduce biodiversity and waste resources (Driscoll *et al.* 2010a; Andersen, Woinarski & Parr 2012; Taylor *et al.* 2012; Nimmo *et al.* 2013). Predictive models of ecological responses to fire are needed so that management can be conducted within fire regimes suitable for the range of species in an ecosystem.

With sufficient knowledge, prescribed burning can restore natural processes. For example, prescribed fire promoted dispersal of the collared lizard among glades which restored its natural metapopulation structure (Templeton, Brazeal & Neuwald 2011). Such successful fire management relies on understanding the extent to which animal species specialize on a successional stage and the contrasting responses to fire among species in the ecological community (Driscoll *et al.* 2010b). Currently, this information is unavailable for many communities in fire-prone regions (Bradstock & Cohn 2002; Clarke 2008).

Predicting impacts of changing fire regimes can be assisted by conceptual succession models that describe

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biodiversity outcomes under different circumstances (e.g. Letnic *et al*. 2004). Fox's (1982) habitat accommodation model predicted that an animal species will enter the succession when its key habitat becomes available. Some reptile studies have supported this model, reporting that burrowing and nocturnal reptiles tend to prefer early successional habitats, while leaf-litter-dwelling reptiles prefer late-successional habitats (Caughley 1985; Letnic *et al*. 2004). However, the capacity for the habitat accommodation model to predict reptile responses to fire (following Caughley 1985) is limited (Driscoll & Henderson 2008; Lindenmayer *et al*. 2008; Nimmo *et al*. 2012). Models based solely on habitat availability may be too simplistic as they do not incorporate the range of mechanisms governing animal responses to fire (Clarke 2008; Blaum *et al*. 2011).

Development of animal succession models is also hindered by insufficient data, particularly for some vertebrate taxa (Clarke 2008). Rare animals often go unstudied (Manley *et al*. 2004), and incorrect inferences can be drawn from sparse data (Doak, Gross & Morris 2005). Woinarski *et al*. (2004) demonstrated that the survey effort required to detect fire responses in reptiles is substantially greater than employed in many surveys. Short-term (2 years) survey data from Australian semi-arid woodlands previously showed that the majority of reptile species had no detectable response to post-fire succession (Driscoll & Henderson 2008; Driscoll *et al*. 2012). Longer-term, intensive data collection could increase statistical power and improve our understanding of fire ecology in animal communities (Woinarski *et al*. 2004; Driscoll *et al*. 2010b).

In this study, we used a large data set collected over 6 years to quantify the response of reptiles to fire and investigate whether ecological traits could explain the response of individual species. We examined whether this large data set could detect more cases of changes in reptile abundance with time since fire than previous studies using smaller data sets. We investigated mechanisms of succession by considering relationships between responses to fire and habitat use and life-history traits, previously suggested to be important for reptile succession (Caughley 1985; Friend 1993; Letnic *et al*. 2004; Driscoll & Henderson 2008). Our focus on ecological traits may inform more generalized mechanistic models of reptile succession in other fire-prone ecosystems (Blaum *et al*. 2011). Such knowledge, based on adequately sampled ecological communities, is urgently needed to assist fire management and biodiversity conservation by enhancing our understanding of species' responses to variation in fire regimes.

Materials and methods

STUDY REGION

We surveyed reptiles in two reserves on the Eyre Peninsula, South Australia (Fig. 1): Hincks Wilderness Area (33°45′ S, 136°03′ E;
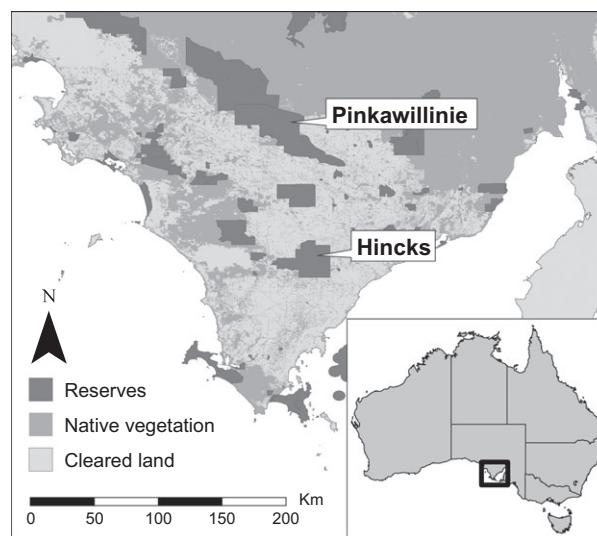

Fig. 1. Location of Hincks Wilderness Area and Pinkawillinie Conservation Park where reptiles were captured on the Eyre Peninsula, South Australia.

66658 ha) and Pinkawillinie Conservation Park (32°54′ S, 135°53′ E; 130148 ha). The region is semi-arid, with an annual mean rainfall of 321 mm. The main topographical features are white sand dunes, occurring in either large, parabolic fields or longitudinal ridges interspersed by swales of heavier, reddish-brown soils (Twidale & Campbell 1985). The dominant vegetation is low (<6 m) mallee woodlands, characterized by multi-stemmed *Eucalyptus spp.* (*E. costata* and *E. socialis*), commonly associated with the shrubs *Melaleuca uncinata* and *Callitris verrucosa* (Specht 1972). Spiky hummock grass *Triodia irritans* forms an important understorey habitat for many reptile species. Summer lightning commonly ignites mallee, typically resulting in large, severe wildfires on a decadal time-scale (Bradstock & Cohn 2002).

DATA COLLECTION

We used a space-for-time natural experiment to examine the effect of time since fire (TSF) on reptile abundances (Driscoll *et al*. 2010b). We defined a field season as the austral spring/summer period (November–February) when reptiles are most active. Our study covered six consecutive field seasons from Dec 2004–Feb 2010. We surveyed 25 sites, 11 at Hincks and 14 at Pinkawillinie, representing a range of times since fire (0–50 years, see Table S1 in Supporting Information). All sites were in the same broad mallee vegetation type, at least 200 m from the reserve boundary. *Triodia* was present at all but one site (P7). It was not possible to match other fire regime variables such as fire frequency, season or intensity among sites, but we considered potential effects of these variables in the Discussion section.

At each reserve, we used two trapping protocols, differing in the number and configuration of traps within a site and the seasons in which they were used. Eleven sites (five at Hincks, six at Pinkawillinie) had 22 pitfall traps arranged in pairs at 40-m intervals along a 400-m transect, with a 20-m drift fence intersecting each trap pair (Driscoll & Henderson 2008). The transects were aligned perpendicular to the dunes to sample both dune and swale habitats, and were surveyed in seasons 1–4 (Table S1, Supporting Information). Fourteen sites (six at Hincks, eight at

Pinkawillinie) had 25 pitfall traps in a 1-ha grid, with five rows of five traps spaced at 25-m intervals, each intersected by a 10-m drift fence (Smith, Bull & Driscoll 2012a). Each grid straddled a single dune to sample mainly on deep, sandy soil. Grids were surveyed in seasons 5–6 (Table S1, Supporting Information). Grid and transect sites were in the same general areas of the reserves (mean distance apart within reserves = 5·7 km, range = 0·6–16·3 km). Some trapping sites were within the same fire boundary (i.e. the area burned by a single fire event).

Each trap consisted of a 20-litre bucket buried flush with the ground surface. Trapped animals could shelter in a half PVC pipe placed at the bottom of each bucket and covered with a wood block which also acted as a floating refuge in the rare case of heavy rain. Traps within each reserve were opened and closed at the same times for an average of 30 nights per season (Driscoll & Henderson 2008; Driscoll *et al.* 2012; Smith, Bull & Driscoll 2012a). We sampled 592 traps over 32 246 trap nights (Table S1, Supporting Information).

Opened traps were checked every morning, and captured reptiles were identified following Wilson & Swan (2010). *Pogona spp.* could not be reliably identified with field guides and keys but likely consist of two allopatric clades on the Eyre Peninsula with a boundary between Hincks and Pinkawillinie (J. Melville, Museum Victoria, personal communication, 2008). Location differences in ecological responses of *Pogona spp.* may represent species differences. At transect sites all animals were uniquely marked to allow recaptures to be omitted from the analysis. We used toe clips for skinks and agamids, fluorescent ventral marks for geckos (Smith, Bull & Driscoll 2012a) and ventral paint spots for snakes and pygopodids. Since recapture rates of legless reptiles within trapping sessions were <20%, we assumed a very low recapture rate between seasons. At grid sites, only three species were uniquely marked (*Amphibolurus norrisi* (Agamidae), *Ctenotus atlas* (Scincidae) and *Nephrurus stellatus* (Gekkonidae)). For other species at the grid sites, the number of individuals was deduced assuming similar recapture rates as at the transect sites in the same reserve (0–0·22, mean = 0·06) [count–(count × recapture rate)].

During our study, unplanned wildfires burnt three sites (P3 and P4 in late December 2005 and I4 in early December 2006) and a prescribed fire was conducted at one site (I3 in April 2006). Driscoll *et al.* (2012) reported increased capture rates immediately after fire for four of our study species (*Ctenotus atlas, Diplodactylus calcicolus, Lerista distinguenda* and *Morethia obscura*) but not for seven others. This reflected increased local movement shortly after the fire, rather than changes in local abundance. Records for those four species that occurred in the same season and after the fire (the post-fire trapping session in season 2 for P3 and P4 and all of season 3 for I3 and I4) were removed from the analysis. Excluding these species, Driscoll *et al.* (2012) found no differences in detectability for any species across three habitat categories (0–2, 5–10 and >20 years post-fire). Other pitfall studies have similarly found little evidence for habitat-related variation in reptile detectability (Schlesinger 2007; Craig *et al.* 2009; Smith, Bull & Driscoll 2012a). We therefore assumed that detectability was similar among successional stages and used the number of captures as an index of abundance.

ANALYSIS

Each site in each field season was treated as an individual observation for analysis. For each observation, TSF was calculated as the number of years since the most recent fire at the beginning of the season. The only exceptions to this were sites P3 and P4 which were burnt part-way through season 3 and were thus treated as separate observations before and after the fire in that season, with TSF calculated from the beginning of the trapping session. We analysed data from 16 reptile species with an equal or greater number of captures than observations ($N = 28$ Hincks, $N = 38$ Pinkawillinie, Table S2, Supporting information) (Didham *et al.* 1998). To account for variation in trap effort among sites, we used the number of captures per 500 trap nights as our response variable.

To predict the effect of TSF on capture rates, we fitted a generalized linear mixed model with a Poisson error distribution and a log link function to data from each species using the lme4 library (Bates, Maechler & Bolker 2012) in R 2.15.1 (R Development Core Team 2012). The data indicated some nonlinear, unimodal responses, so we fitted TSF and its quadratic form (TSF^2) as fixed effects after standardizing both terms [(x–mean (x)/standard deviation (x)] (Quinn & Keough 2002). For species with a suitable sample size at both reserves, location was fitted as a fixed effect and we included its interaction with both TSF terms. To account for our grouped sampling design (2–4 sites were sampled within a single fire boundary), we fitted fire (a factor naming individual fire events) as a random effect. To account for repeated sampling of sites over time, we fitted site as a random effect. We also included season (1–6) as a random effect to account for variance caused by differences in trapping protocol and survey years. To model extra-Poisson variation in the data, an observation-level random effect (1 to the number of observations) was fitted to each model (Maindonald & Braun 2010).

We followed Driscoll & Henderson (2008) and inferred significant effects of TSF on abundance where $P < 0·1$. For models in which TSF^2 was not significant, we removed the quadratic term and refitted the model. We then removed the interactive terms (TSF × location and TSF^2 × location) if they were not significant. For each model, we plotted the fitted values against the residuals to visually assess normality and homogeneity of variance (Zuur *et al.* 2009). To provide an estimate of model fit, we calculated marginal R^2 (variance explained by the fixed effects only) and conditional R^2 (variance explained by the full model, including random effects) following equations 29 and 30 in Nakagawa & Schielzeth (2013). We estimated abundance from the final models using predictSE.mer in the AICcmodavg package (Mazerolle 2012).

For species that were significantly affected by TSF, we examined relationships between their fire response and their ecological traits using Fisher's exact tests. For these analyses, we inferred significant relationships when $P < 0·05$. Species captured at both locations were included once in the analysis. We grouped species into two fire categories based on the year at which they reached their peak abundance over the 50-year successional time frame of our study (Table S3, Supporting information). The 'early' category included species with a peak abundance between 0 and 25 years, and the 'late' category included species with a peak abundance between 26 and 50 years after fire. *Brachyurophis semifasciatus* had a peak abundance close to 26 years after fire, so we ran two alternative analyses, classifying it as early in one and late in another. We used our personal observations, published literature and expert opinion (M. Hutchinson, South Australian Museum) to classify each species by its activity pattern (nocturnal/diurnal), shelter type (burrow/not burrow), foraging

habitat (open ground/within vegetation) and diet (generalist/specialist) (Table S3, Supporting information). These groupings have been suggested to be important drivers of fire responses in reptiles (Caughley 1985; Friend 1993; Letnic *et al.* 2004; Blaum *et al.* 2011). *Lerista edwardsae* may be diurnal, nocturnal or both (M. Hutchinson, personal communication), so we classified it nocturnal in one analysis and diurnal in another.

Results

We recorded 4796 individual reptiles from 44 species in seven families (Table S2, Supporting information). Sample sizes of 16 species were suitable for analysis (Table 1). Of those 16 species, we identified significant main effects of TSF (or TSF^2) and/or interactive effects between TSF and location on the abundance of 13 species (Table 1, Fig. 2a–u). The abundance of three species (*Amphibolurus norrisi*, *Ctenophorus cristatus* and *Morethia obscura*) was not significantly affected by TSF (Table 1). All eight species analysed at both locations had significant effects of location, with four more abundant at Hincks and four more abundant at Pinkawillinie (Table 1, Fig. 2a–u).

The significant responses to TSF in four species (*Ctenophorus fordi*, *Ctenotus atlas*, *Lucasium damaeum*, *Nephrurus stellatus*) had been previously reported and were generally in the same direction (Driscoll & Henderson 2008; Driscoll *et al.* 2012). *Amphibolurus norrisi* and *Ctenophorus cristatus* previously showed a response to TSF (Driscoll & Henderson 2008) but did not in this study. Our analysis revealed significant responses to TSF in nine species that were not found previously (Table 1, Fig. 2): *Aprasia inaurita*, *Brachyurophis semifasciatus*, *Ctenotus euclae*, *Ctenotus schomburgkii*, *Diplodactylus calcicolus*, *Lerista distinguenda*, *Lerista edwardsae*, *Liopholis inornata* and *Pogona* spp. The variance explained by the models, including random effects (conditional R^2), ranged from 19 to 90% (Table 1).

Our analysis of ecological traits showed a significant relationship between fire category and shelter type ($P = 0.02$), but only when *Brachyurophis semifasciatus* was classified as early successional (Table S4, Supporting information). In this case, burrowers and tree dwellers were all early successional, leaf-litter dwellers were all late successional, and species that shelter in *Triodia* were both early and late successional (Fig. 3). There was a non-significant trend for activity type to explain fire responses ($P = 0.07$), but only when *B. semifasciatus* was classified as early successional and *Lerista edwardsae* as diurnal (Table S4, Supporting information). In this case, nocturnal species tended to be early successional, while diurnal species had a range of fire responses (Fig. 3). There were no relationships between fire category and foraging habitat or diet (Fig. 3, Table S4, Supporting information).

Discussion

We derived two important results from our study of post-fire succession in an Australian reptile community. First,

Table 1. Response of 16 reptile species to time since fire (TSF) and location (Hincks was the reference level)

	Model estimates			Model fit	
	Estimate	SE	*P*	$R^2_{(m)}$	$R^2_{(c)}$
Amphibolurus norrisi					
Intercept	0·74	0·26	<0·01	0·01	0·40
TSF	−0·07	0·27	0·80		
*Aprasia inaurita**					
Intercept	0·16	0·23	0·48	0·18	0·30
TSF	−0·45	0·26	**0·08**		
*Brachyurophis semifasciatus**					
Intercept	0·47	0·17	0·01	0·09	0·23
TSF	1·01	0·57	**0·08**		
TSF^2	−0·91	0·54	**0·09**		
Ctenophorus cristatus					
Intercept	1·18	0·27	<0·01	0·01	0·62
TSF	0·10	0·18	0·60		
Ctenophorus fordi					
Intercept	2·81	0·28	<0·01	0·66	0·90
TSF	0·59	0·41	0·15		
TSF^2	−1·55	0·53	**< 0·01**		
Location	−1·81	0·39	**< 0·01**		
Ctenotus atlas					
Intercept	1·70	0·24	<0·01	0·53	0·73
TSF	−0·21	0·65	0·75		
TSF^2	0·39	0·76	0·61		
Location	−1·26	0·25	**< 0·01**		
TSF × location	2·43	0·90	**0·01**		
TSF^2 × location	−1·83	0·92	**0·05**		
*Ctenotus euclae**					
Intercept	1·42	0·47	<0·01	0·43	0·80
TSF	−0·63	0·29	**0·03**		
Location	−2·83	0·72	**< 0·01**		
*Ctenotus schomburgkii**					
Intercept	−1·09	0·44	0·01	0·45	0·71
TSF	1·12	0·22	**< 0·01**		
Location	1·14	0·50	**0·02**		
*Diplodactylus calcicolus**					
Intercept	1·10	0·22	<0·01	0·59	0·64
TSF	1·39	0·77	**0·07**		
TSF^2	−2·51	1·00	**0·01**		
*Lerista distinguenda**					
Intercept	1·16	0·21	<0·01	0·27	0·68
TSF	0·53	0·19	**0·01**		
*Lerista edwardsae**					
Intercept	0·29	0·31	0·35	0·22	0·61
TSF	−1·15	1·02	0·26		
TSF^2	1·78	1·23	0·15		
Location	0·61	0·39	0·12		
TSF × location	2·29	1·18	**0·05**		
TSF^2 × location	−2·51	1·35	**0·06**		
*Liopholis inornata**					
Intercept	0·18	0·41	0·66	0·52	0·79
TSF	3·98	1·17	**< 0·01**		
TSF^2	−5·61	1·51	**< 0·01**		
Location	1·51	0·39	**< 0·01**		
TSF × location	−3·36	1·40	**0·02**		
TSF^2 × location	4·53	1·67	**0·01**		
Lucasium damaeum					
Intercept	1·22	0·36	<0·01	0·38	0·81
TSF	−2·65	1·01	**0·01**		

Table 1. (continued)

	Model estimates			Model fit	
	Estimate	SE	P	$R^2_{(m)}$	$R^2_{(c)}$
TSF^2	2·14	0·94	**0·02**		
Morethia obscura					
Intercept	0·46	0·19	0·01	0·01	0·19
TSF	0·09	0·20	0·65		
Nephrurus stellatus					
Intercept	1·28	0·34	<0·01	0·83	0·89
TSF	3·34	0·98	**< 0·01**		
TSF^2	−6·06	1·54	**< 0·01**		
Location	0·76	0·35	**0·03**		
TSF × location	−2·73	1·14	**0·02**		
TSF^2 × location	4·70	1·64	**< 0·01**		
*Pogona spp.**					
Intercept	0·42	0·21	0·05	0·38	0·48
TSF	−2·14	0·85	**0·01**		
TSF^2	2·24	0·97	**0·02**		
Location	0·59	0·21	**< 0·01**		
TSF × location	2·84	0·95	**< 0·01**		
TSF^2 × location	−3·29	1·06	**< 0·01**		

Significant effects are shown in bold. The variance explained by each model is provided for the fixed effects only ($R^2_{(m)}$ = marginal R^2) and for the full model ($R^2_{(c)}$ = conditional R^2). The asterisk (*) indicates that the TSF response was not detected with smaller data sets (Driscoll & Henderson 2008; Driscoll *et al.* 2012).

we detected significant fire response patterns in nine species that were not detected in previous analyses of substantial, although smaller, data sets. Most reptile species analysed showed a significant abundance response to TSF, indicating a high degree of successional specialization in the reptile community. Our findings highlight a risk that fire management decisions based on insufficient data could fail to incorporate the complexity of responses in animal communities, particularly for taxa that require large effort to accumulate adequate samples. Even with our extended data set, we could not analyse trends in 28 of the 44 reptile species detected. Second, while shelter site preferences and activity patterns of individual species were weakly related to succession, ecological traits groups were generally poor predictors of reptile responses to fire.

DETECTING FIRE RESPONSES IN REPTILES

Several studies have found limited effects of post-fire succession on reptile communities (Lindenmayer *et al.* 2008; Perry, Rudolph & Thill 2009), including previous studies in mallee vegetation (Driscoll & Henderson 2008; Driscoll *et al.* 2012). Woinarski *et al.* (2004) suggested that the survey effort used in many fire studies of reptiles was inadequate and our comparison with two previous studies supports this suggestion. Our enhanced ability to detect reptile fire responses may be attributed both to the amount of data (more capture records at each site and a greater number of sites with captures for some species) and to the increased resolution of successional trajecto-

ries. Driscoll & Henderson (2008) compared reptiles in two fire categories (burnt vs. unburnt), while we examined continuous responses over a 50-year succession. This may also explain the lack of a fire response in two species in this study that were previously detected (Driscoll & Henderson 2008). In another intensively sampled study (>7200 individuals from 56 000 trap nights), the majority of common reptile species (11 out of 17) had significant responses to time since fire (Nimmo *et al.* 2012). In that study, data were collected over only 2 years, but 280 sites representing a 100-year succession were surveyed for reptile presence/absence. An appropriate balance among the length of the survey period, the sampling intensity and the length and resolution of the succession must be achieved, and this is likely to vary among ecosystems and vegetation types (Woinarski *et al.* 2004; Gardner *et al.* 2008).

Driscoll *et al.* (2012) used a more conservative test of significance (α = 0·05 and adjustment for multiple tests) than used by Driscoll & Henderson (2008) and in the current study. However, if they had used α = 0·1, responses to TSF would have only been detected in six out of 17 species (Driscoll *et al.* 2012), less than half of the responses detected in this study. Only two species that were previously reported to respond to fire (Driscoll & Henderson 2008) did not have a significant response in this study, so the risk of Type I errors appears to be much lower than the risk of Type II errors. From a management perspective, Type II errors can have harmful and costly environmental outcomes, while Type I errors often lead to a relatively benign and inexpensive misdirection of management (Field *et al.* 2004; Reynolds, Thompson & Russell 2011). For example, a false finding that most species do not respond to fire could lead to an unrestrained application of prescribed burning which could threaten late-successional species and waste resources. Conversely, a false finding that many species did respond to fire would support a more cautious and targeted application of prescribed burning. Statistical thresholds can be optimized to minimize Type II errors when examining responses to fire in taxa which require large effort to accumulate adequate samples (Field *et al.* 2004). Furthermore, comparative research approaches such as we used in this study can be particularly informative when conducting studies to inform management.

We were restricted by available fire records (DENR 2011) to examining succession up to only 50 years after fire. Mallee can remain unburnt for well over a century (Clarke *et al.* 2010), and habitat features that develop beyond 50 years are important for many animal species (Haslem *et al.* 2011; Kelly *et al.* 2011). Studies that examine longer successional trajectories of reptiles are needed to understand the importance of habitat features that develop beyond our limited documentation (Nimmo *et al.* 2012). Furthermore, we were unable to analyse the effects of fire frequency, season or intensity which can affect animal abundances (e.g. Lindenmayer *et al.* 2008)
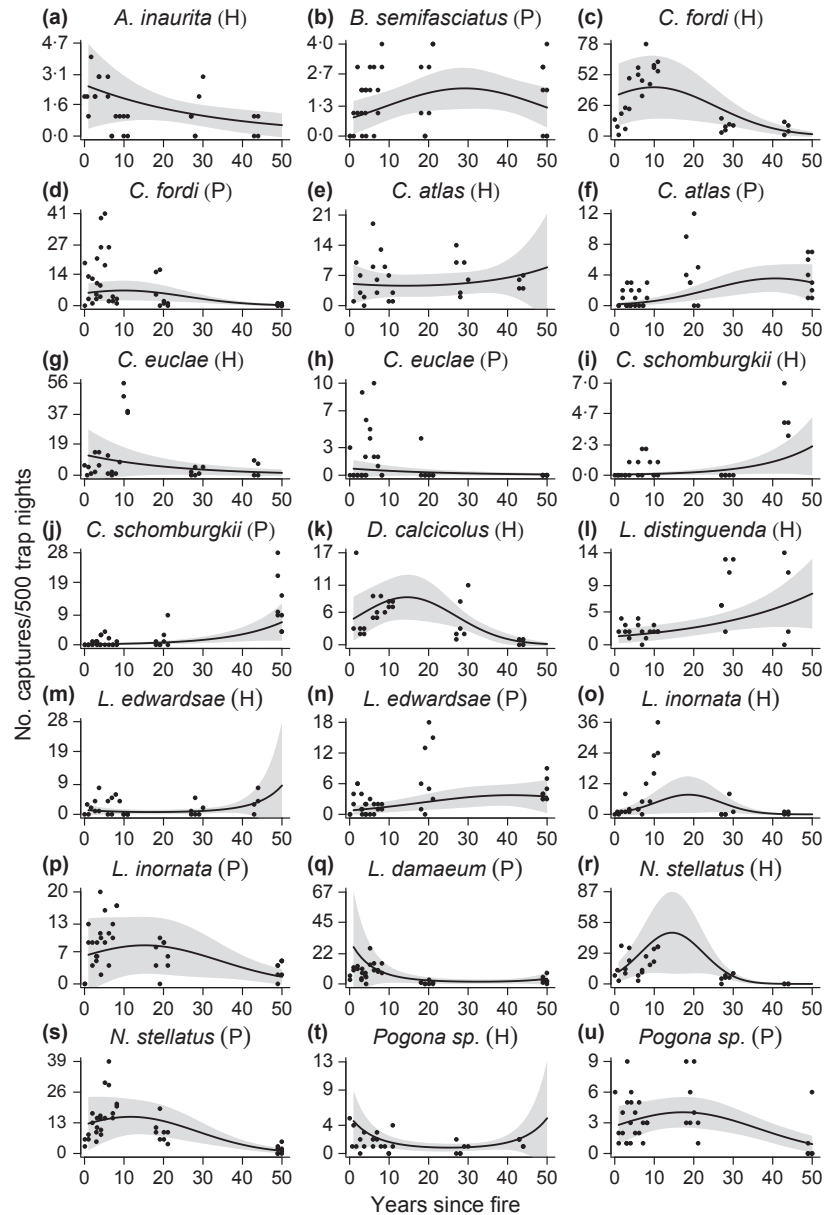
Fig. 2. The capture rate of 13 reptile species was significantly affected by time since fire ($P < 0.1$). Black dots are the observed data, solid lines are the model estimates, and grey shading shows the 95% confidence intervals of the estimates. H = Hincks, P = Pinkawillinie.

and may have contributed to the unexplained variation in our data. These are important parameters to target in future research of animal responses to fire regimes.

CAN WE PREDICT SUCCESSION OF MALLEE REPTILE COMMUNITIES?

Groups of ecological traits have been used to predict successional changes in plant (Keith *et al*. 2007), invertebrate (Langlands *et al*. 2011) and bird (Barlow & Peres 2004) communities following disturbance. This approach has had variable success in describing the response of reptiles to disturbance (Caughley 1985; Letnic *et al*. 2004; Driscoll & Henderson 2008; Lindenmayer *et al*. 2008; Nimmo *et al*. 2012). In our study, the small number of species with enough samples for analysis meant we had limited power to detect effects of ecological traits of individual

species on their responses to TSF. We found some trends for reptile fire responses to be related to their shelter type and daily activity patterns. However, the reliance on individual species driving these results showed that these trends are unlikely to have strong predictive power.

All but one of the burrowing species in our study were nocturnal, and there was a trend for these species to be early successional. The ability to use burrows probably reduces reliance on above-ground vegetation meaning sparsely vegetated areas can be occupied soon after fire (Caughley 1985). Letnic *et al*. (2004) suggested that shelter from above-ground vegetation is also less important for nocturnal than diurnal species, and our analyses showed some limited support for this. Nocturnal reptiles rely on heat transfer from substrates (Schlesinger, Noble & Weir 1997) that are likely to be warmer in recently burnt areas (Hossack *et al*. 2009).
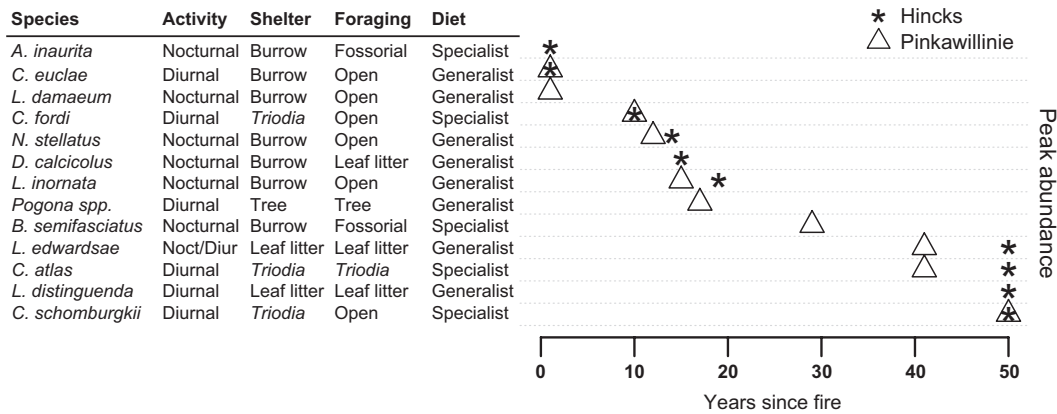
Species	Activity	Shelter	Foraging	Diet
A. inaurita	Nocturnal	Burrow	Fossorial	Specialist
C. euclae	Diurnal	Burrow	Open	Generalist
L. damaeum	Nocturnal	Burrow	Open	Generalist
C. fordi	Diurnal	*Triodia*	Open	Specialist
N. stellatus	Nocturnal	Burrow	Open	Generalist
D. calcicolus	Nocturnal	Burrow	Leaf litter	Generalist
L. inornata	Nocturnal	Burrow	Open	Generalist
Pogona spp.	Diurnal	Tree	Tree	Generalist
B. semifasciatus	Nocturnal	Burrow	Fossorial	Specialist
L. edwardsae	Noct/Diur	Leaf litter	Leaf litter	Generalist
C. atlas	Diurnal	*Triodia*	*Triodia*	Specialist
L. distinguenda	Diurnal	Leaf litter	Leaf litter	Generalist
C. schomburgkii	Diurnal	*Triodia*	Open	Specialist

Fig. 3. Ecological traits and peak abundance for 13 reptile species with a significant response to time since fire.

The two species in our study that shelter in leaf litter were late successional, probably reflecting the dense cover of this habitat feature in mallee habitats that are older than approximately 20 years (Haslem *et al.* 2011). There was no overlap in the times of peak abundance of burrowers and leaf-litter dwellers, so these categories of shelter type may have some predictive power of fire responses. Reptiles requiring *Triodia* for shelter did not share a common fire response (Caughley 1985) even though *Triodia* generally increases in density for 30 years after fire (Haslem *et al.* 2011). Variable effects of rainfall and grazing on *Triodia* growth (Driscoll *et al.* 2012; Nimmo *et al.* 2012) and use of supplementary habitat features by *Triodia* specialists (Driscoll & Henderson 2008) may obscure relationships between *Triodia* and its inhabitants.

Unfortunately, detailed ecological information on most reptile species is scarce. Traits we could not examine included reproduction, longevity and dispersal, but these are probably of great importance in determining fire responses (Templeton, Brazeal & Neuwald 2011; Smith, Bull & Driscoll 2012a). A better understanding of species-level ecology (e.g. Templeton, Brazeal & Neuwald 2011) and detailed measures of habitat structure and other fire regime characteristics in addition to simple measures of time since fire (e.g. Di Stefano *et al.* 2011) will help to improve predictive models of fire responses in animal communities.

FIRE MANAGEMENT FOR FAUNA CONSERVATION

Management that increases early successional and more open habitats is often suggested to benefit reptiles that rely on basking opportunities for thermoregulation (Greenberg, Neary & Harris 1994; Pike, Webb & Shine 2011). Bury (2004) claimed that 'most reptiles are adapted to open terrain, so fire usually improves their habitat'. Unless statements like this are based on adequate data, the resulting management recommendations might harm some species. In our study, four skink species were most common in long-unburnt habitats (*Ctentous atlas*, *C. schomburgkii*, *Lerista edwardsae* and *L. distinguenda*). In studies with smaller sample sizes, only one of these responses was detected (*C. atlas*), while a higher proportion (44%) of reptiles showed early or mid-successional responses (Driscoll & Henderson 2008; Driscoll *et al.* 2012). Fire studies on reptiles might be biased towards detecting early successional responses. A suite of reptile species probably specialize on late-successional habitats, but go unstudied because they have behavioural traits that make them hard to detect (Driscoll *et al.* 2012; Smith *et al.* 2012b).

If reptiles can survive at low densities in suboptimal habitat, their risk of extinction under adverse fire regimes will be lower than if they are completely eliminated (Driscoll & Henderson 2008; Driscoll *et al.* 2010b). In our study, the effect of TSF on some species was small indicating that they can persist at lower numbers in suboptimal post-fire habitats. Other species were almost absent from their suboptimal seral stage (e.g. *Nephrurus stellatus* and *Ctenotus schomburgkii*) highlighting a risk that some species may be locally eliminated by fire or by a lack of fire (Smith, Bull & Driscoll 2012a). Management that is likely to be of greatest benefit to reptiles in mallee ecosystems would aim to protect long-unburnt habitat (e.g. 40–50 years old, and potentially older) from fire because these seral stages are uncommon (Clarke *et al.* 2010). Actions to help achieve this include promoting small, patchy fires to prevent widespread wildfire and minimizing the application of back-burning in long-unburnt habitat while fire-fighting (Driscoll *et al.* 2010b). Quantifying appropriate spatial and temporal scales of fire mosaics for fauna (e.g. Kelly *et al.* 2012; Taylor *et al.* 2012; Nimmo *et al.* 2013) is a key priority for continued research.

Our study showed that the majority of common reptile species in our study region specialize on a post-fire successional stage and may become threatened if homogeneous fire regimes (widespread burning or complete fire suppression) predominate. Although long-term, intensive studies are not always possible, it is important that results from

time- or sample-limited fire studies of reptiles are interpreted with the knowledge that many ecological responses may not have been detected. While avoiding homogeneous fire regimes, it is important that responses to alternative fire regimes are monitored across a range of taxa, so that management practices can be updated in light of new information (e.g. Keith, Williams & Woinarski 2002).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Fire and sampling information for each of the study sites.

Table S2. Total number of each of the 44 species in seven families captured during the study.

Table S3. The peak abundance, fire category and ecological traits for each of the 16 species analysed.

Table S4. Results from Fisher's exact tests to determine whether fire responses could be explained by ecological traits.