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Running Head: Reptile trap-bias and response to fire

Reptile responses to fire and the risk of post-disturbance sampling bias

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Abstract

Altered fire regimes are a driver of biodiversity decline. To plan effective management, we need to know how species are influenced by fire and to develop theory describing fire responses. Animal responses to fire are usually measured using methods that rely on animal activity, but animal activity may vary with time since fire, potentially biasing results. Using a novel approach for detecting bias in the pit-fall trap method, we found that leaf-litter dependent reptiles were more active up to six weeks after fire, giving a misleading impression of abundance. This effect was not discovered when modelling detectability with zero-inflated binomial models. Two species without detection bias showed early–successional responses to time since fire, consistent with a habitat-accommodation succession model. However, a habitat specialist did not have the predicted low abundance after fire due to increased post-fire movement and non-linear recovery of a key habitat component. Interactions between fire and other processes therefore must be better understood to predict reptile responses to changing fire-regimes. We conclude that there is substantial bias when trapping reptiles after fire, with species that are otherwise hard to detect appearing to be abundant. Studies that use a survey method based on animal activity such as bird calls or animal movements, likely face a similar risk of bias when comparing recently-disturbed with control sites.

Key words: *adaptive management, biological legacies, disturbance regime, keystone species, prescribed burning, state and transition model*

Introduction

Inappropriate fire regimes have the potential to drive species towards extinction (Barlow and Peres 2004; Burgman et al. 2007; Cleary et al. 2006; Underwood et al. 2009). Fires may occur too often, without time for populations to recover between events (Bradstock et al. 1997; Gandhi et al. 2001; Odion and Tyler 2002). Fire frequency could increase with climate change (Flannigan et al. 2009; IPCC 2007; Westerling et al. 2006), with the spread of invasive grasses (Ostoja and Schupp 2009), or through an increase in fuel reduction burning as a management response to increased fire risk (DellaSala et al. 2004; Morrison et al. 1996; van Wilgen et al. 2010). However, an equally extreme management response, to suppress all fires, may be detrimental for species that depend on fire for reproduction or provision of suitable habitat (Greenberg and Waldrop 2008; Menges et al. 2006). Detailed knowledge of where the bounds of suitable habitat are after fire, for the range of species sharing a community, are needed as a guide for management.

Developing such an understanding requires knowledge of the drivers of post-fire faunal succession, and vegetation change has often been implicated (Briani et al. 2004; Madden et al. 1999; Valentine and Schwarzkopf 2009). The habitat accommodation model of succession predicts that species enter a community when their preferred habitat type has developed, and then decline as the plant succession proceeds beyond their optimal habitat conditions (Caughley 1985; Fox 1982; Fox et al. 2003; Letnic et al. 2004). However, there may be circumstances where a consistent sequence or temporal pace is not observed. For example, in North America, recolonisation of burnt old-field patches by plants was dependent on patch size (Schweiger et al. 2000). This meant that larger patches developed late-successional characteristics while small patches remained in an early seral stage, with concomitant responses by small mammals (Schweiger et al. 2000). Factors that influence the recovery of vegetation after fire may therefore alter the timing of peak abundance for particular animal species.

Reptiles often show a strong response to habitat structure and so habitat accommodation models have been particularly useful for describing sequences of species recovery after fire (Caughley 1985; Friend 1993; Greenberg 2000; Letnic et al. 2004). However, recent research shows that some reptiles do not follow a linear sequence of recovery. Lindenmayer et al (2008b) suggested that rapid vegetation growth after fire in eastern Australia may have undermined any possibility of sequential colonisation by reptiles. Driscoll and Henderson (2008) found that many reptile species in mallee woodlands of southern Australia showed either no response to time since fire or, for one species, an interaction between location and time since fire. In that study, habitat elements may not have responded linearly after fire, or reptiles may have responded more strongly to environmental variables such as soil type (Pianka 1969).

Sampling biases may also make it difficult to understand how species respond to fire. Responses to fire are often measured using a sampling method that depends on animal activity, such as calling by frogs or birds and movement into stationary traps by terrestrial animals (e.g. Cunningham et al. 1999; Driscoll 1998; Ford et al. 2010; Yarnell et al. 2007), including reptiles (Schlesinger 2007). However, if movement rates differ between recently burnt and long-unburnt habitat, abundance estimates based on pitfall trap captures will be confounded with movement (Anderson 2003; Driscoll and Henderson 2008; Schutz and Driscoll 2008). Pitfall trap biases have been described for some beetles (Greenslade 1964; Koivula et al. 2003) and ants (Melbourne 1999), although two studies addressing this issue for reptiles found no biases when comparing different levels of grass cover (Schlesinger 2007) or shrub cover (Craig et al. 2009). Nevertheless, there remains a risk that movement rates depend on time since fire which could bias the interpretation of fire effects.

We therefore address two problems in this study. First, we address survey bias by examining post-fire spikes in capture rates, and by modelling detection with zero-inflated binomial models (MacKenzie et al. 2006). Then, with knowledge of trap-bias, we examine the response of reptiles to time since fire and to key habitat elements, as a step towards building a general predictive theory of faunal responses to fire. Specifically, we ask (1) is there evidence of increased movement activity related to time since fire; (2) how do reptiles respond to time since fire and key habitat elements, and; (3) are those responses consistent with expectations from the habitat accommodation model?

Developing management practices that conserve biodiversity in the face of altered fire regimes is now critical in many regions of the world (Driscoll et al. 2010a; Fattorini 2010; Louzada et al. 2010; Pons and Clavero 2010; van Wilgen et al. 2010). To better inform management, research that addresses the responses of a range of plants and animals to fire is needed. However, for some of these animal groups there is a potential for biased sampling at different times since fire. Our research provides an informative case-study in this respect by demonstrating how sampling bias can be recognised and then used to better interpret the results from fire experiments.

Materials and Methods

Study Region

Our research was conducted in mallee woodland communities of South Australia (Fig 1). Mallee communities consist of multi-stemmed *Eucalyptus* species that form low open woodlands (Specht 1971). On the Eyre Peninsula of South Australia, these woodlands are dominated by *Eucalyptus incrassata*, *E. brachycalyx,* and *E. socialis,* with some *Callitris verrucosa*. The shrubby understorey includes *Melaleuca uncinata*, *Baeckea crassifolia*, *Phebalium bullatum*, and spinifex (*Triodia irritans*), a sharply spined clumping grass (Robinson and Heard 1985; Specht 1971). Spinifex (*Triodia* species) has a strong influence on the distribution of reptiles (Driscoll 2004; Masters 1996). The distribution of spinifex is influenced by the depth of sand, with more spinifex occurring on sand dunes than in the swales between dunes (Cohn 1995).

Mallee on the Eyre Peninsula overlies parabolic and longitudinal dunes with a solid limestone calcrete base (Twidale and Campbell 1985). The climate is mediterranean with annual rainfall 300-400mm (Schwerdtfeger 1985). Over half of the mallee on the Eyre Peninsula has been cleared, mostly before 1939, leaving a small number of very large mallee reserves and many small remnants (Australian Native Vegetation Assessment 2001; State of the Environment Report 2003). Natural fire regimes in mallee communities are poorly understood, but fire return intervals of less than 15 years are regarded as short (Bradstock and Cohn 2002), and mallee may remain unburnt for more than a century (Haslem et al. 2011).

Survey Design

We sampled three fire age categories (0-2 years since fire, 5-10 years, ≥ 20 years) from four or five locations (Table 1, Fig. 1). This contrasts with a previous study by Driscoll and Henderson (2008) who only used the latter two age classes. Unexpected events altered the number of treatments at some locations. Planned burns failed at Hambidge so the 0-2 age class was not available. Unplanned fires at Pinkawillinie and a planned burn then an unplanned fire at Hincks left two sites in the 0-2 year age category at both locations. Two new ≥ 20 years sites were established at Pinkawillinie, and one at Hincks (Table 1). Thus we used six sites burnt within the past two years, seven sites burnt within 5-10 years, and seven sites burnt twenty or more years ago.

We sampled each site using 22 pitfall traps, with 11 trap pairs spaced at 40 m intervals along a 400 m transect. Transects were aligned perpendicular to the angle of the sand dunes so that they traversed both sandy dunes and the clay inter-dunes across their length, sampling the full range of soil types in the landscape. Traps within pairs were 10 m apart and a 20 m drift fence was erected across them (for full details see Driscoll and Henderson 2008). Each trap contained approximately 500 cm^3 of sand, a halved PVC pipe 5cm in diameter, and a block of wood for sheltering trapped animals. All sites were surveyed for seven consecutive nights per month in four austral summers (2004-5, 2005-6, 2006-7, 2007-8; only two of the three summer months were sampled in 2005-6). The first two years of data were published in Driscoll and Henderson (2008) and we use some of these data again (described below). Reptiles were individually or batch marked and released at the point of capture. There were not enough recaptures to allow estimates of population density or detection probability.

Recaptures were excluded from our index of animals captured, but were used in estimating detection probability.

Taxonomy generally follows Wilson and Swan (2003), however, we combined *Pogona* records because recent research suggests there may be two allopatric taxa in the study area (Jane Melville, Museum Victoria, personal communication). Keys for separating *Lerista distinguenda* from *L. taeniata* were inadequate (Cogger 1996), and these taxa were pooled for analysis. However *L. taeniata* represents the majority of animals at Pinkawillinie, and *L distinguenda* at other locations (A. L. Smith, unpublished data). Percentage cover of spinifex was estimated within a 10 × 5m quadrat adjacent to each trap-pair.

Probability of Detection

Captures One Week to Ten Months after Fire

We examined potential bias of capture rates with time since fire by measuring reptile abundance before and after fires. An increase in reptile capture rates in the first few days after fire would imply an increase in movement. Immigration is likely to occur more slowly (e.g. Calsbeek 2009; Warner and Shine 2008). We speculate that immigration may lead to density increases over an intermediate period, possibly months or longer. Increases observed following the first breeding season after a fire are more likely to represent population changes from a combination of immigration (if that occurs at all) and increased births or survival. In mallee communities, increased survival of species favouring open habitats is likely to last for at least a decade (Driscoll and Henderson 2008; Smith et al. In press) because the vegetation is slow to recover in the semi-arid environment (Bradstock and Cohn 2002).

To examine changes in capture rates that could be associated with fire, a time series of data was required, with some sites burnt during the time series and others that remained unburnt for comparison. Because fire occurrence is not predictable, the data we have for examining these possible responses are opportunistic. For examining responses to natural unplanned fires, there are no other realistic options (Driscoll et al. 2010b). By including data reported in Driscoll and Henderson (2008) (three weeks from 2004-5 and two weeks from 2005-6), we were able to use a four-year data series. Unplanned fires at Pinkawillinie in December 2005 allowed us to sample the sites P3 and P4 six weeks after the fire. Four year data series were also available from P1 and P2 which had previously burnt in 2001. At Hincks, North Heggaton and South Heggaton, planned fires burnt the sites I3, N4 and S4 in April 2006, which we sampled eight months later. An unplanned burn at Hincks in December 2006 razed I4, and we sampled this site, beginning the day after the fire was extinguished. One other site at Hincks (I1) and two sites at both North and South Heggaton were not burnt during the study and had comparable four year data series (see Table 1 for site and burn details).

For each of the sites with four-year data series, we used a permutation test (Good 1994) to determine if there was significantly more animals captured in the period after each fire. As the test statistic, we used the number of animals captured in a seven-day survey period, averaged across the three capture sessions after the fire (or one capture session from the same summer at Pinkawillinie) minus the number of animals captured per week averaged across all other sample weeks. For example, I4 was burnt in December 2006, so our test statistic was the average weekly abundance from the December 2006, January and February 2007 samples, divided by the average of weekly samples from 2004-5, 2005-6 and 2007-8. For each of 1000 permutations, we randomly allocated sample periods to capture data and recalculated the test statistic, with P calculated as the proportion of test statistics that were equal to or larger than the actual value. We tested species with at least five captures at the site examined. We adjusted the P values, separately at each site, using the p.adjust function with method = "BH" (Benjamini and Hochberg 1995) in R (R Development Core Team 2011).

Zero-inflated Binomial Models

The number of animals trapped can provide a reasonable index of abundance in contrasting treatments if the probability of detecting an individual is the same across treatments. We examined the risk of different detectability in different time since fire categories by modelling detectability based on repeated surveys of each site. For each day of survey, we scored each site as either 1 (species captured) or zero (species not captured), providing a series of presence/absence records for each site across each day of the survey periods. We generated these sites by days datasets for each of the 17 most common reptile species in each of two survey years (2006-7 or 2007-8). Common species were those judged to have adequate data for our generalized linear modelling approach (described below). To each of these data sets we fitted a null detectability and occupancy model, and a model where time since fire category (0-2 years, 5-10 years, >20 years) was fitted as a detection covariate using zero-inflated binomial models (MacKenzie et al. 2006). We assessed the relative importance of each model using Akaike's Information Criterion for small samples (AICc: Burnham and Anderson 2002). Models were fitted using the unmarked R library (Fiske et al. 2011), with R 2.13.0 (R Development Core Team 2011).

Fire, sand and spinifex effects

We pooled data across the two sample years to maximise sample sizes for individual species in the three fire age categories (the same approach as Driscoll and Henderson 2008), because the majority of differences in capture rates between years reflected changes in activity associated with the temperature during the sampling weeks (see also, James 1994).

We examined the possible influence on reptile species' capture rates of three fixed effects: burn age-category, proportion of sand dune on the transect and percentage cover of spinifex (averaged across trap-pairs on a transect and square-root transformed). We used a generalised linear mixed model with Poisson link function, including location as a random effect to account for spatial blocking of the sample sites. We also included an observation level random effect (a factor delimiting each of the 20 sites) to model extra-Poisson variation in the data, thereby accounting for over-dispersion in residual variation (Maindonald and Braun 2010). We assessed the significance of the coefficients of sand and spinifex using the estimated coefficient divided by the standard error and assumed a t distribution, with degrees of freedom equal to the number of sites less the number of fixed effects that were estimated. This approximation was supported by comparison with MCMCglmm credible intervals, which are the rough counterpart of confidence intervals based on glmer output (MCMCglmm function in the MCMCglmm package, Hadfield 2010). Tests based on the likelihood were used to obtain p-values for differences between burn age categories. Wald statistics were too inaccurate for this purpose because of the large differences in Poisson mean. Two locations have sites nested within the same burn. We explored a mixed model that included burn nested in location as a random effect to accommodate this pseudo-replication. However, such random effects explained negligible variance and so we did not include them in our analyses.

We applied the model to the 17 most common reptile species and so adjusted the P values using the "BH" method. Analyses were completed using the glmer function from the R package lme4 (Bates et al. 2011). This function does not calculate confidence intervals. For presentation of significant burn age-category results we calculated least significant differences ($P < 0.05$) to define error bars, where non-overlap of error bars imply the probability of the observed difference is < 0.05 under the null hypothesis of no effect. We assessed the relative importance of the random location effect by comparing the range (maximum - minimum) of the random effects with the range of the fixed effects.

There was inadequate replication of fire categories within locations to test for the interaction. However, we checked for a possible interaction between location and burn age-category by examining the means for each fire age at each location. Possible interactions between location and sand or spinifex were examined graphically.

Results

We captured 2079 reptiles representing 40 species, 17 of which met our criteria for analysis (see Online Resource 1 for a full list of species captured in each fire age).

Probability of Detection

Captures One Week to Ten Months after Fire

Of the seven sites that were surveyed in four years and were not burnt during that time, one species at one site was significantly more abundant in the period corresponding with the post-fire period in nearby sites (*Egernia inornata* at I1, test statistic = 2.9, $P_{adjusted} = 0.04$). Therefore, with this one exception, seasonal changes in capture rates did not coincide with the post-fire period in sites that were burnt during the study.

At I4, surveyed one week to two months after a fire, four species had higher capture rates after the fire, compared with other survey weeks in years 1, 2 and 4 of the study (Fig. 2). An immediate increase in captures was observed for *Diplodactylus granariensis* and *Morethia obscura*, whereas the two *Lerista* species showed a gradual increase over the three month survey period (Fig. 2). *Diplodactylus granariensis* also had significantly higher capture rates in the post-fire surveys, eight months after the fire, at north Heggaton (test statistic = 2.2, $P_{adjusted} < 0.001$). However, such effects were not detected at two other locations for this species (south Heggaton, Pinkawillinie).

A number of rare species also had patterns consistent with higher activity after the fire at I4. These included five species that were only captured in the week after the fire at this site (*Pygopus lepidopodus* (2 animals), *Ramphotyphlops australis* (1), *Hemiergis peroni* (9), *Delma butleri* (4), *Delma australis* (1)). There were no other trapping sessions at I4 in which a species unique to that session was captured. Compared with data series at I1 and I3 (one and zero species unique to the December 2006 session, four and three unique to other sessions respectively), the observation at I4 is statistically improbable (Fisher's exact test, P =

0.009). In addition, at I4, five *Cyclodomorphus melanops* were caught in the week after the fire whereas only one other animal was captured at that site throughout the four year study. Seven species that occurred at I4 did not show evidence of increased capture rates in the months after the fire: *Aprasia inaurita*, *Ctenophorus fordi*, *Ctenotus atlas*, *Ctenotus euclae*, *Nephrurus stellatus*, *Pogona* sp. and *Ramphotyphlops bituberculatus*. Any differences in capture rates of these species in different aged vegetation therefore likely represent population size changes and not differences in movement activity.

Zero-inflated Binomial Models

Despite strong evidence of detection bias after fire at I4, the zero-inflated binomial models suggested that detectability did not vary with time since fire. For each species and year, we found that the zero-inflated binomial model with time since fire included as a detectability covariate always had a lower AICc and was never within two AICc of the null model. In all but one case, AICc weights for the null model exceeded 0.989 (Online Resource 2). We therefore made no further adjustment to our data (c.f. Ford et al. 2010) before fitting generalized linear mixed models.

Fire, sand and spinifex effects

Two abundant species were captured most commonly in the 5-10 year-old burns, with very low numbers in recently burnt and long unburnt sites (*Ctenophorus fordi*, *Nephrurus stellatus*, Fig. 3). This pattern was consistent across all locations for *C. fordi*, and four of five locations for *N. stellatus*. *Nephrurus stellatus* had high abundance in the first two time-since-fire categories at Hincks. Two additional species had highest capture rates in the recently burnt sites (*Lerista dorsalis* and *Ctenotus atlas*, Fig. 3), results that were likely due to higher activity after fire. One of these (*Lerista dorsalis*) had significantly increased movement activity after fire (Fig. 2c) and burn age-category was no longer included in the model when I4 was excluded from the analysis. Highest abundance in the 0-y category was only observed at Hincks. The second species (*Ctenotus atlas*) did not have significantly more individuals immediately after fire in our permutation tests, but it was nevertheless more abundant in the first survey period after fire (abundance in weeks after fire minus abundance in other survey periods, at sites that were burnt: 6, 4.3, 3.4, -0.5; at sites that were not burnt: 0.7, 1.9,0.4). *Ctenotus atlas* occurred at three locations, and at Pinkawillinie had a pattern opposite to the main time-since-fire effect (3, 3, 17 individuals captured in 0, 5-10 and >20 y respectively). Fixed effects for all analyses are provided in Online Resource 3.

The agamid *Ctenophorus cristatus* had a negative relationship with the proportion of sand on the transect and a weak negative relationship with the sqrt (% spinifex) (Figs. 4a, b). *Lerista distinguenda*/*taeniata* captures where higher with a higher proportion of sand (Fig. 4c). *Ctenotus atlas* capture rates were positively correlated with sqrt (% spinifex) (Fig. 4d). Capture rates of all taxa examined varied substantially among locations, with the range of random location effects at least half as big as the range of fixed effect in nine species (Online Resource 4). An additional seven species with small random location effects were absent from some locations. The only taxon not in those response categories was *Lerista distinguenda*/*taeniata,* where *L. distinguenda* is rare at Pinkawillinie relative to *L. taeniata* (Online Resource 4).

Discussion

Probability of detection

The surprising number of species that were only captured in the week or weeks after fire at I4 is very informative because most of these were leaf-litter dwelling species. Their increased capture rates probably represent increased movement after the fire. It seems unlikely that these species would move into the burnt area given the lack of leaf litter. An increase in population density through reproduction is implausible because many of the increases occurred within a week of the fire and because the spike in capture rates was not sustained into the second year. Although species that depend on leaf litter are expected to be late-successional species, with low abundance for the first decade or two after fire (Caughley 1985), we have found no supporting evidence for low abundance after fire in this study, and only weak evidence in the previous study (Driscoll and Henderson 2008). However, the increased capture rate of litter-dwelling species immediately after the fire implies that these species are difficult to capture most of the time, making any response to fire hard to detect.

Our results therefore highlight an important methodological limitation: pitfall traps rarely capture cryptic species, but these species may represent the majority of late-successional species. To discover if poorly sampled species are also late-successional species, alternative research approaches are needed. This could involve manual searching for reptiles (Fogarty and Jones 2003), stationary visual surveys (Irvin et al. 2003) (both of which would need to consider detection probability, MacKenzie et al. 2006), or trapping immediately after fire then tracking the animals (Naef-Daenzer et al. 2005) to see if they disperse from the burnt area (Legge et al. 2008), hide again, or die.

The increase of two *Lerista* species from the first week after fire to the first and second month after fire at I4 was not observed in other years at that site, or at other sites in the same year. This pattern was opposite to that shown by other species, where there was a spike in capture rates followed by a gradual decline. If the *Lerista* species were not typical leaf-litter dwelling species, immigration from surrounding habitat might be a plausible explanation. Perhaps more likely, these animals remain in temporary shelter during and after a fire, and then emerge one to four weeks later, with increased movement as they seek to emigrate or find new shelter.

Increased movement activity after fire is not unique to mallee reptiles. In forests of south-eastern Australia, Irvin et al (2003) used a range of survey techniques but only found large numbers of the skink *Nannoscincus maccoyi* in the year after fire when it was forced to use logs as an alternative to its usual shelter in deep leaf litter. It became more cryptic in the following years as the leaf litter re-established (Irvin et al. 2003). We do not know if mallee reptiles are like *N. maccoyi* and find new shelter sites after fire. This is an important knowledge gap to resolve because if they hide, the reptile community may be robust to a broad range of fire regimes. If that were the case, it would allay concerns that we need to carefully design fire mosaics to conserve reptile diversity.

The modelling approach for estimating detectability depends on data from many sites with multiple surveys (MacKenzie et al. 2006), and so did not detect the site-specific survey bias that we have found using the permutation approach. In our study, this was potentially problematic, because our GLMMs suggested that the skink *Lerista dorsalis* was most abundant in the first years after fire, whereas our permutation analyses revealed that higher captures after fire was likely a detection bias. In the circumstances of our study, modelling detection was not adequate to account for detection bias.

Fire, sand and spinifex effects

Although other studies report that species decline in abundance after a fire, with a possible increased risk of extinction (Driscoll and Roberts 1997; Lindenmayer et al. 2008a; Lyon and O'Connor 2008), we did not detect such a pattern. Two common reptile species in this study have increased abundance after fire, a response that is commonly reported for reptiles (e.g. Matthews et al. 2010; Santos and Poquet 2010). The habitat accommodation model of reptile responses to fire (Caughley 1985; Driscoll and Henderson 2008; Letnic et al. 2004) predicts that burrowing species that forage in open areas will be favoured in the post-fire environment. The gecko *Nephrurus stellatus* fits this description. Consistent with previous research (Driscoll and Henderson 2008), a second species (*Ctenophorus fordi*) that does not use burrows as a regular retreat, showed the same response to time since fire as *N. stellatus*, implying that routine burrowing is not required to survive the fire and exploit the open post-fire environment (Driscoll and Henderson 2008).

According to the habitat accommodation model, spinifex specialists including the skink *Ctenotus atlas* are expected to remain at low numbers after fire until the spinifex recovers after approximately six years (Caughley 1985). However, two factors are likely to have undermined this expectation. First, increased movement immediately after fire has given the false impression of increased abundance in the 1-2 year post-fire age category. Although this pattern was not statistically significant, we presented evidence showing that increased movement is a more likely explanation than a tripling of abundance in the first two years after fire. Second, although *C. atlas* does have a strong relationship with percent cover of spinifex (Fig. 4a), spinifex does not have the expected linear relationship with time since fire. For example, one long-unburnt site (P7) had no spinifex (despite suitable soil conditions) and no *C. atlas*, whereas a nearby site with the same time-since-fire (P8) had a substantial cover of spinifex and high numbers of *C. atlas*. Further, two other sites that burnt during the study had rapid re-establishment of spinifex through resprouting and no apparent change in *C. atlas* abundance (I3, I4). Processes in addition to fire must therefore influence spinifex re-establishment and subsequently the rate at which *C. atlas* populations increase after fire. Candidate processes include the rate of re-sprouting (Rice and Westoby 1999), possible interactions with grazing (Cohn and Bradstock 2000; Legge et al. 2008) and the influence of fire frequency on plant survival (Bradstock et al. 1998; Regan et al. 2003). Conceivably a state and transition model like that proposed for small mammals in the Australian arid zone (Letnic et al. 2004) may be a more useful concept than succession for describing changes in abundance of species that depend on a flammable habitat component (Fig. 5).

We found no evidence to support the concern raised by Driscoll and Henderson (2008) that some species may drop to extremely low numbers in the first two years after fire, and therefore face a substantial extinction risk. Cryptic species may have declined after fire, but we were unable to detect any effects. However, the "early successional" species with peak abundance after 5-10 years face a greater (though unquantified) risk of extinction when fire is excluded from the ecosystem for long periods of time (Gray et al. 2003) because that is when they have their lowest abundance. This problem could be exacerbated in fragmented landscapes that are subject to fire suppression (Hobbs 2003) because population sizes will be smaller than in large blocks of habitat and the potential for recolonisation may be lower for some species (Schutz and Driscoll 2008; Williams et al. in press).

Because we did not stratify our sampling by burn age and soil type, there was a risk that a strong response to soil type may have introduced additional variation that prevented us from detecting burn effects for some species. However, we found little evidence that soil type influenced the abundance of species at a site level. Only two species were correlated with the amount of sand on a transect. These few effects of sand in our study probably do not reflect the importance of soil type for reptile habitat specialisation (e.g. Pianka 1969; Woinarski et al. 1999). Rather, these few effects likely arise from our sampling design which avoided strong soil type differences among sites.

Driscoll and Henderson (2008) reported substantial differences between locations and our findings using the subsequent two years of data confirm that pattern. As suggested by Driscoll and Henderson (2008), a range of location-specific factors may drive these patterns such as soil, climatic and vegetation differences. These knowledge gaps await research attention.

Considering our experimental design more generally, we detected few fire effects compared with our previous study (Driscoll and Henderson 2008). This reflects reduced statistical power due to the altered sampling design, with fewer replicates of each fire age class. The high likelihood of unplanned and uncontrollable alterations to experimental design (Hurlbert 1984) in fire research suggests that space-for-time substitution may be a less risky approach to studying fire than attempting to study fire responses across multiple years (Driscoll et al. 2010b).

Conclusions

Pitfall trapping is widely used to survey reptiles but only two studies of which we are aware measure possible trap biases due to increased movement in more open habitat, and both found no evidence of bias (Craig et al. 2009; Schlesinger 2007). Our study is the first to show that a proportion of the reptile species in a community have increased capture rates in open habitat one to six weeks after fire. This additional activity can give the erroneous impression that a species has increased in abundance, even when data are pooled across broader sample periods (c.f. Figs. 2c, 3c). Studies that use data collected from shortly after disturbance that also have an increase in capture rates in disturbed sites (e.g. Kilpatrick et al. 2010; Todd and Andrews 2008) need to consider the risk of increased movement after disturbance as a possible interpretation. It may be wrong to assume that an increase in capture rate represents an increase in population density (Chelgren et al. 2011).

Given the possibility that leaf-litter species depend on late successional habitat and the observation that there are early successional species, a general recommendation to avoid extreme fire regimes is supported. Widespread frequent fires and complete fire suppression are unlikely to be ecologically sustainable fire strategies in many ecosystems including the mallee system (Cunningham et al. 2002; Perry et al. 2009). However, it is not yet clear how important a carefully managed fire mosaic might be for conserving reptile species (Bradstock et al. 2005; Driscoll and Henderson 2008; Parr and Andersen 2006). Some reptile species could remain in a landscape at low population density during less favourable seral stages (Greenberg 2000; Pianka 1996). If that is true, the bounds of suitable fire mosaics may be very broad for reptiles and require little management input. The actual risk of extinction in long-unburnt habitat for species with peak abundance within ten years of fire, and in recently burnt habitat for leaf-litter species remain important knowledge gaps to fill.

Our study emphasises that reptile responses to fire can be mediated by their association with habitat, and that sometimes habitat does not have a linear response to fire (Fig. 5). When the association with habitat is very strong (e.g. *Ctenotus atlas* with spinifex) fire becomes only one of the factors that influence abundance. Understanding the strength of association of species with habitat features is therefore critical for building theory with a predictive capacity. Both theory and management need to consider a broad range of processes to understand population dynamics in the face of fire. Rather than considering just time since fire (Madden et al. 1999; Richards et al. 1999), fire management for biodiversity conservation may need to be integrated with management of other processes (e.g. grazing, wood removal, predator control: Gill and Williams 1996; Letnic et al. 2005; Olsson et al. 2005). These interactions are important topics for future research (Driscoll et al. 2010b).

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Table 1. The fire history of sites surveyed in summer 2006-7 and 2007-8. Six sites were burnt in 2005 or 2006 in planned burns or unplanned fires started by lightning. Site codes from Driscoll and Henderson (2008).

Site code	Location Name	Year last burnt prior to surveys	Burn type '05-6	Age 2006-7	Latitude	Longitude
A1	Hambidge	2000		6	-33.4382343	135.8695555
A2	Hambidge	2000		6	-33.425131	135.8478811
A3	Hambidge	1965		41	-33.45925	135.8675567
A4	Hambidge	1965		41	-33.4261074	135.8236423
I1	Hincks	1999		7	-33.7632891	136.0797203
I3	Hincks	1977 + April 2006	planned	0	-33.7631529	136.0593281
I4	Hincks	1977 + Dec 2006	unplanned	0	-33.809309	136.1451495
I7	Hincks	1977		29	-33.7547989	136.0343191
N1	Heggarton N	1997		9	-33.3658658	136.542489
N3	Heggarton N	long unburnt		>30	-33.3685451	136.527118
N4	Heggarton N	long unburnt + April 2006	planned	0	-33.3646362	136.5348834
P1	Pinkawillinie	2001		5	-32.9001251	135.8778749
P2	Pinkawillinie	2001		5	-32.9056547	135.878542
P3	Pinkawillinie	1986 + Dec 2005	unplanned	1	-32.9099813	135.8670276
P4	Pinkawillinie	1986 + Dec 2005	unplanned	1	-32.9141698	135.8708898
P7	Pinkawillinie	1986		20	-32.9100385	135.8157418
P8	Pinkawillinie	1986		20	-32.9019816	135.7890342
S2	Heggarton S	2001		6	-33.4134099	136.5284644
S3	Heggarton S	long unburnt		>30	-33.4067317	136.5171501

S4	Heggarton S	long unburnt + April 2006	planned	0	-33.408034	136.5273637

Fig. 1 Reptiles were sampled at twenty sites representing up to three fire ages in five locations on the Eyre Peninsula, southern Australia.

Fig. 2 Abundance of four lizards in 11 trapping periods at I4 with significantly more animals captured in the three sample periods after a fire (dashed vertical line). Numbers indicate the test statistic (mean occurrence in samples during the summer after the fire minus mean occurrence in all other sample periods).

Fig. 3 Predicted abundance of lizard species (at mean levels of spinifex and sand) in the three burn-age categories: <2 y = sites burnt in planned or unplanned fires in the year prior to this study; 5-10 y, >20 y = sites burnt 5-10 or >20 years respectively prior to this study. Error bars are 95% confidence limits. The number of locations at which each species occurred and included in the analyses for that species is indicated.

Fig. 4 Predicted abundance (with 95% CIs) of four lizard species that had a significant relationship with the proportion of transects on sand dunes (a, c) and with the square root of percent cover of spinifex (b, d) (note log scale on y axes). The number of locations at which each species occurred and included in the analyses is indicated.

Fig. 5 Conceptual state and transition model for the post-fire population trajectory of a species that depends on a flammable habitat component (such as the skink *Ctenotus atlas* that depends on the clumping grass *Triodia irritans*). Depending on the rate of re-establishment of the key habitat component, the species may decline then recover, barely change abundance at all, or become extinct after fire

Figure 1

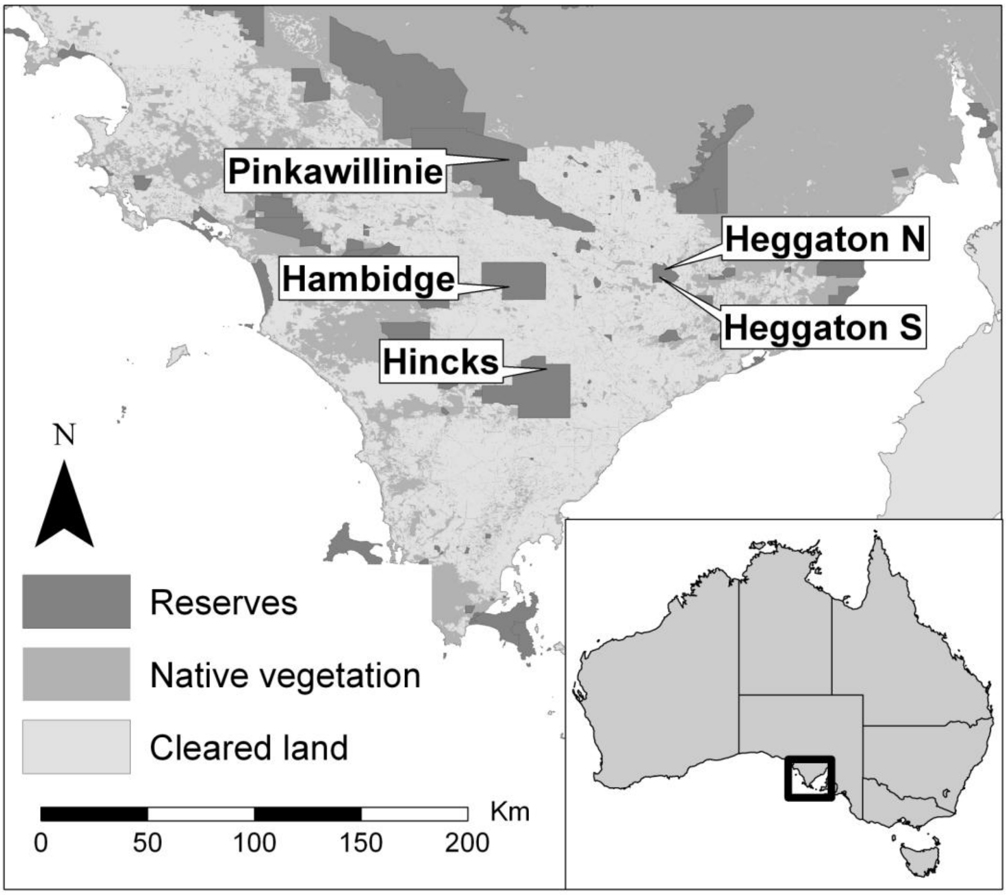

Pinkawillinie
Heggaton N
Hambidge
Heggaton S
Hincks
N
Reserves
Native vegetation
Cleared land
Km
0
50
100
150
200

Figure 2

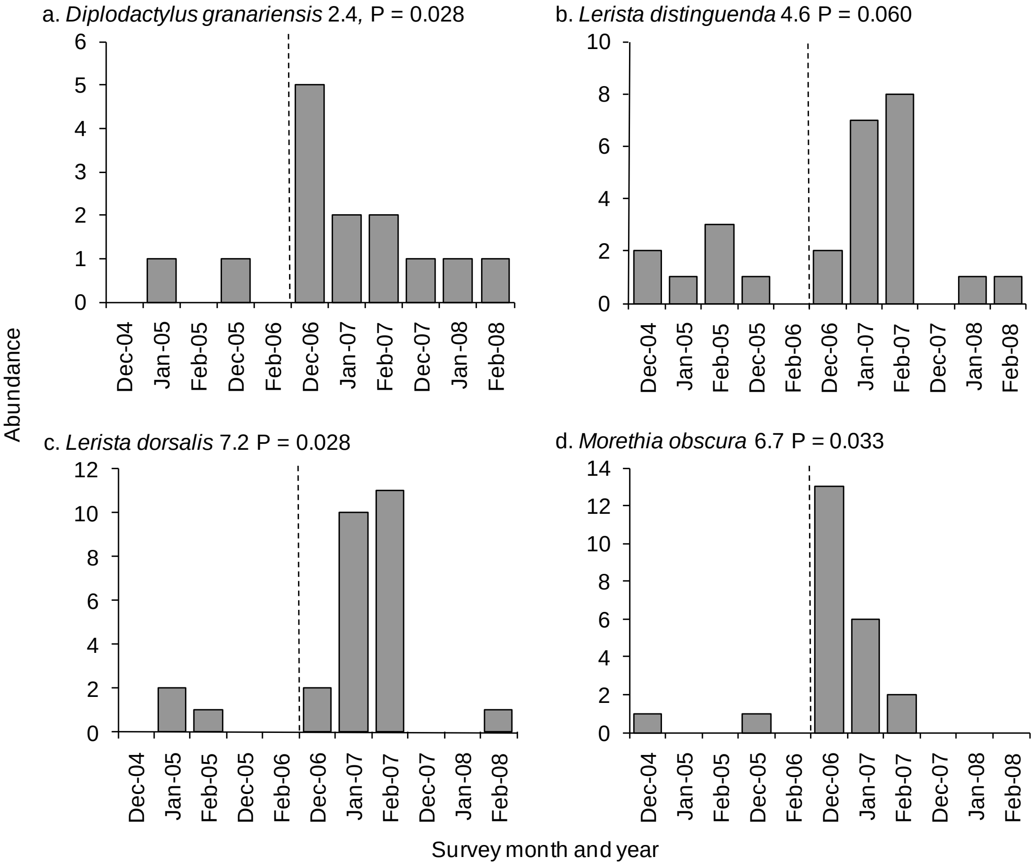

a. *Diplodactylus granariensis* 2.4, P = 0.028
b. *Lerista distinguenda* 4.6 P = 0.060
c. *Lerista dorsalis* 7.2 P = 0.028
d. *Morethia obscura* 6.7 P = 0.033
Abundance
Survey month and year
Dec-04
Jan-05
Feb-05
Dec-05
Feb-06
Dec-06
Jan-07
Feb-07
Dec-07
Jan-08
Feb-08
0
1
2
3
4
5
6
8
10
12
14

Figure 3

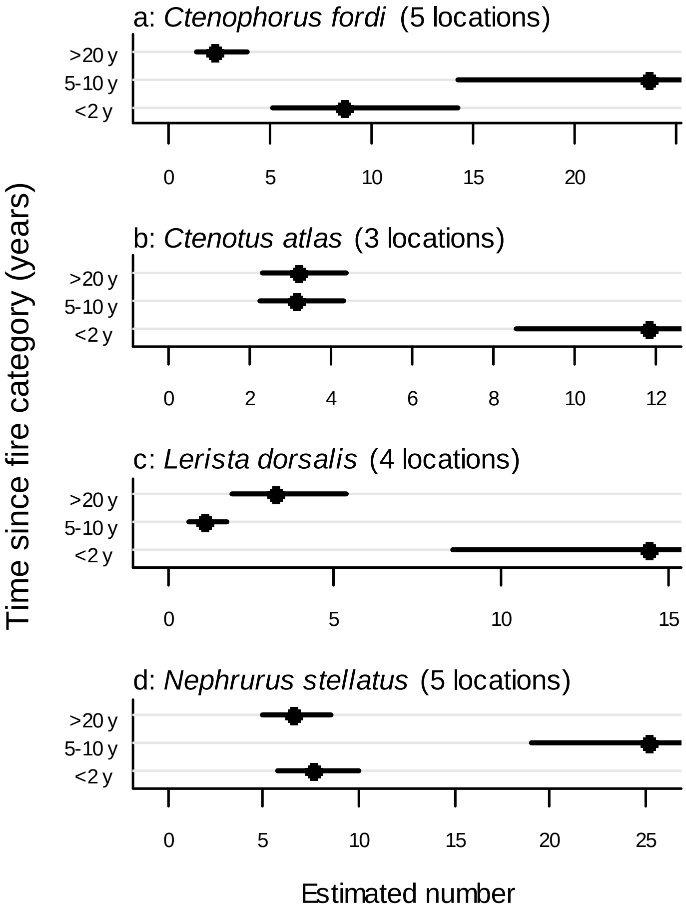

a: *Ctenophorus fordi* (5 locations)
>20 y
5-10 y
<2 y
0
5
10
15
20
b: *Ctenotus atlas* (3 locations)
>20 y
5-10 y
<2 y
0
2
4
6
8
10
12
c: *Lerista dorsalis* (4 locations)
>20 y
5-10 y
<2 y
0
5
10
15
d: *Nephrurus stellatus* (5 locations)
>20 y
5-10 y
<2 y
0
5
10
15
20
25
Estimated number
Time since fire category (years)

Figure 4

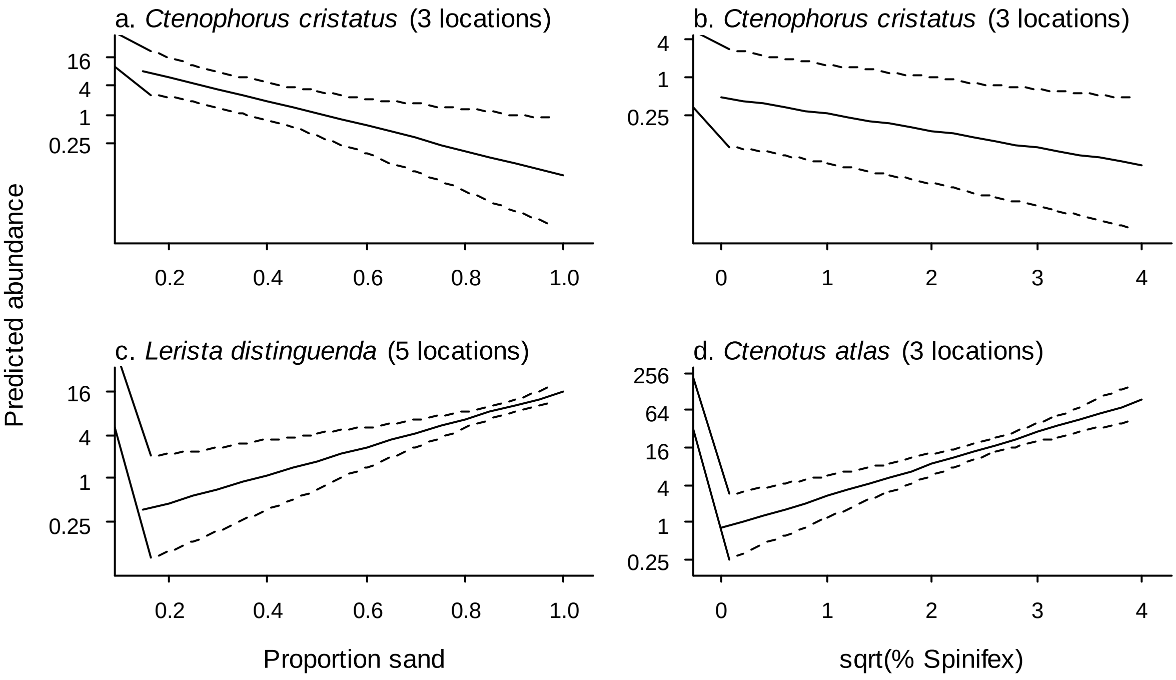
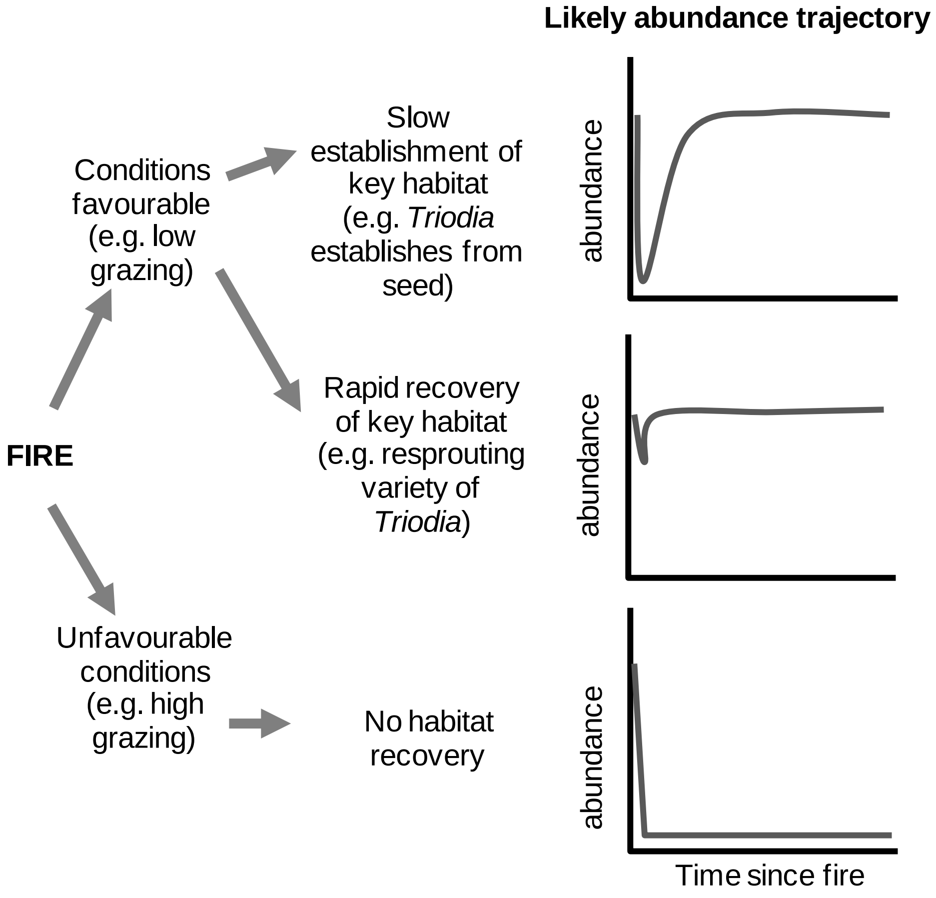

a. *Ctenophorus cristatus* (3 locations)
16
4
1
0.25
0.2
0.4
0.6
0.8
1.0
b. *Ctenophorus cristatus* (3 locations)
4
1
0.25
0
1
2
3
4
Predicted abundance
c. *Lerista distinguenda* (5 locations)
16
4
1
0.25
0.2
0.4
0.6
0.8
1.0
d. *Ctenotus atlas* (3 locations)
256
64
16
4
1
0.25
0
1
2
3
4
Proportion sand
sqrt(% Spinifex)

Figure 5


Likely abundance trajectory
FIRE
Conditions favourable (e.g. low grazing)
Slow establishment of key habitat (e.g. *Triodia* establishes from seed)
Rapid recovery of key habitat (e.g. resprouting variety of *Triodia*)
Unfavourable conditions (e.g. high grazing)
No habitat recovery
abundance
abundance
abundance
Time since fire