



Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko

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ABSTRACT

Altered fire regimes threaten the persistence of many animal species globally, thus understanding how fire affects demographic processes is critical for conservation. Using 2 years of mark-recapture data from the Australian gecko *Nephurus stellatus*, we investigated the effect of fire on (i) detectability to reliably measure post-fire changes in abundance, and (ii) survival and reproductive rates to investigate the mechanisms of successional change. Data were collected from two conservation reserves each with three different fire categories based on time since the last fire. “Early”, “medium” and “late” sites had 2–3, 7–9 and 42–48 years since fire, respectively. A robust design modelling framework was used to estimate the effect of fire category on abundance, survival and capture probability while also examining the influence of temperature and behaviour on detectability. Geckos showed trap-shy behaviour and detectability increased significantly with increasing temperature but was not affected by time since fire. Accounting for detectability, geckos were more abundant in the medium than the early sites, and were rare in the late sites. Although trends in survival are more difficult to address with short-term data, our results showed lower monthly survival rates, but higher fecundity in the early than the medium sites. These results were possibly related to successional changes in predation, the thermal environment, and food availability. We demonstrated how mark-recapture analysis can show the causes of animal fire responses while realistically accounting for detectability. Such information is necessary to provide a predictive framework to guide fire management for biodiversity.

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1. Introduction

Disruption of natural fire regimes from modern human land use has contributed to the decline of animal populations in many ecosystems around the world (Betts et al., 2010; Gregory et al., 2010; Lyet et al., 2009; Pardon et al., 2003; Sanz-Aguilar et al., 2011). Fire is widely used to create successional diversity in vegetation under the often untested assumption that this will benefit biodiversity more broadly (Parr and Andersen, 2006). However, if this practice is conducted at inappropriate spatial and temporal scales, animal populations may face local extinction (Bradstock et al., 2005; Templeton et al., 2001).

Well studied changes in plant demography after fire have led to conceptual and simulation based models to predict the effects of different fire regimes on vegetation (e.g. Bradstock et al., 2006; Moreira et al., 2009). Although there has been some progress in this direction for animal species (e.g. Bradstock et al., 2005) development has been slower than for plants because of the difficulty in obtaining animal life history data (Clarke, 2008). At the community

level, a functional trait-based approach for predicting fire responses in plants (e.g. Keith et al., 2007) holds promise for use in animal studies (Langlands et al., 2011; Moretti et al., 2009). However, this approach requires detailed information on life history traits, including survival, reproduction and dispersal (Langlands et al., 2011) which are not available for most animal species in fire-prone ecosystems. Understanding demographic changes of animal populations after fire is critical if we are to develop a predictive framework for ecological fire management (Clarke, 2008).

Post-fire succession in animal communities has traditionally been explained by a habitat accommodation model where the peak density of an animal species is correlated with that of its optimal post-fire habitat (Fox, 1982). However, fire-related patterns of abundance often vary spatially or temporally within species making simple habitat models unreliable (Driscoll and Henderson, 2008; Lindenmayer et al., 2008). Understanding the causes of fire-related changes in abundance will allow more accurate predictions of the effects of fire regimes on animal populations (Driscoll et al., 2010; Whelan et al., 2002). The profound habitat changes caused by fire are likely to influence survival in animal species by changing predation rates, food availability, reproductive success and thermal environments (Hawlena et al., 2010; Hossack et al.,

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2009; Le Galliard et al., 2005; Pike et al., 2010). Recent evidence shows that modified fire regimes can affect animal survival (Lyet et al., 2009; O'Brien et al., 2003; Pardon et al., 2003) highlighting the need for a taxonomically and ecologically broader understanding of successional changes in survival rates of animals.

While developing a trait-based approach to fire management is crucial, quantifying the effects of fire on animal abundance remains fundamental to fire ecology. Ecological fire management plans are usually based on empirical observations of apparent differences in abundance of target species in habitats of different time since fire (e.g. Petty et al., 2007; DENR, 2009). However, animals can also show behavioural responses to fire-driven succession (Fenner and Bull, 2007; Vernes and Haydon, 2001), meaning that detectability could change with time since fire. If this is true, descriptions of animal fire responses based solely on counts may not represent actual abundance, leading to misguided management (White, 2005). Despite this concern very few studies have controlled for detectability when investigating the effects of fire on animal abundance (Driscoll et al., 2010).

Driscoll and Henderson (2008) estimated abundance from counts to identify common reptile species with local distribution patterns influenced by post-fire succession in mallee woodlands of southern Australia. One of these was the starred knob-tailed gecko, *Nephrurus stellatus*, which they reported to show a strong fire-specialist response, with higher abundance in early than late successional habitats (Driscoll and Henderson, 2008). In this study we collected 2 years of mark-recapture data from *N. stellatus* to determine if (1) apparent effects of succession on abundance were confounded with fire related detectability differences, and (2) monthly survival rates differed with time since fire and could therefore account for observed differences in abundance. We also examined if post-fire succession affected three measures of reproductive capacity (age structure, sex ratio and female reproductive status) to help further explain any observed fire effects on abundance and survival. Our aim was to understand demographic responses to fire in a species that is likely to be sensitive to variation in fire regimes. Through this process, we sought to advance fire research on animals by developing a causative understanding of succession using biologically meaningful models of detectability.

2. Methods

2.1. Study system

The study was conducted at Hincks Wilderness Area and Pinkawillinie Conservation Park on the Eyre Peninsula, South Australia (Fig. 1). The region is semi-arid, with an average annual rainfall of 322 mm. The main topographic features are white siliceous sand dunes, occurring in either large, parabolic fields or longitudinal ridges over calcrete limestone (Twidale and Campbell, 1985). Hincks and Pinkawillinie are dominated by mallee woodlands where low, multi-stemmed *Eucalyptus* species (predominantly *Eucalyptus costata*, *Eucalyptus brachycalyx* and *Eucalyptus socialis*) are associated with the shrubs *Melaleuca uncinata*, *Callitris verrucosa* and the spiky hummock grass *Triodia irritans* (Robinson and Heard, 1985; Specht, 1972). Summer lightning, the most common ignition source of mallee, typically results in large, severe wildfires on a decadal time scale (Bradstock and Cohn, 2002). Records of the complex fire histories of the two reserves have been kept by the South Australian Department for Environment and Natural Resources for over 40 years (DENR, 2011). *N. stellatus* is distributed widely across the Eyre Peninsula and in a small area of central-south Western Australia (Wilson and Swan, 2008). It is common in sandy areas, residing in self-dug burrows by day and actively

foraging for invertebrate prey by night (Cogger, 1996). Driscoll and Henderson (2008) captured *N. stellatus* consistently more often in recently burnt (3–7 years since the most recent fire) than long unburnt (18–39 years since the most recent fire) habitat across five conservation reserves. Little is known of the life history, but preliminary skeletochronological analysis suggests individuals can live for up to 4 years in the wild, possibly longer (A.L. Smith, unpublished data).

2.2. Trapping protocol

At each reserve we established two sample sites in each of three fire categories based on time since last fire. “Early” sites had 2–3 years since fire at the time of first data collection (2008), “medium” sites had 7–9 years and “late” sites had 42–48 years (Fig. 1). Sites were selected to ensure that other factors were similar, particularly the presence of sandy soil and *T. irritans*, an important habitat plant for many reptiles. In anticipation of low capture rates at the late sites (Driscoll and Henderson, 2008), two additional late sites were sampled at Pinkawillinie (Fig. 1). At each site 25 pitfall traps were set in a 1 ha plot, with five rows of five traps spaced at 25 m intervals. The distance between traps was based on typical movement distances (mean 16, range 0–103 m/day) from preliminary radio-tracking and mark-recapture studies. Traps consisted of 20 l buckets buried flush with the ground and intersected by a 10 m long, 30 cm high plastic drift fence. Fences alternated in angle so that each fence was perpendicular to the adjacent fences. Trapped animals could shelter in a 15 cm long half PVC pipe placed at the bottom of each bucket, covered with a 15 × 25 cm wood block which also acted as a floating refuge in case of heavy rain. Two temperature loggers (Gemini) in the shade at each reserve recorded temperature every hour during the trapping sessions. Readings from the two loggers were averaged.

We defined a field season as the spring-summer period when the geckos were most active and conducted our study over two seasons (November 2008–February 2009 and November 2009–February 2010). We collected capture data under Pollock's (1982) robust design where, in each field season, a series of three primary capture sessions incorporated several trap days, or secondary capture occasions (Kendall et al., 1995). Primary sessions included 5–15 secondary occasions (mean = 8). During each primary session traps in all fire categories were opened and closed at the same times. The intervals between primary sessions ranged from 0.5 to 1.9 months within seasons and from 8.8 to 9.6 months between seasons. Under this design abundance and detectability could be estimated from within primary sessions when the population was assumed to be closed to gains and losses (Kendall et al., 1995). Survival could be estimated from the intervals between the sessions when the population was assumed to be open (Kendall et al., 1995). This design allowed us to estimate survival rates during the activity season of the geckos, and between seasons when the geckos were mostly inactive. We treated data from each reserve separately as they were sampled at different times within seasons when daily temperatures varied and because capture rates in reptiles are strongly dependent on temperature. Traps were checked every morning between 0600 and 1000 h and all captured geckos (Appendix A) were taken to a base for processing where they were held for up to 24 h. Animals were therefore unavailable for capture on the secondary occasion following their capture. This may have biased rates of capture probability, but the effect was considered minor compared to the total length of the study and was consistent across fire categories. Only low rates of temporary emigration were evident during the trapping sessions (see results), so the bias caused on this parameter should also be minimal.

Size (snout-vent length) to sexual maturity (male = 55 mm, female = 70 mm) was established by examining reproductive organs

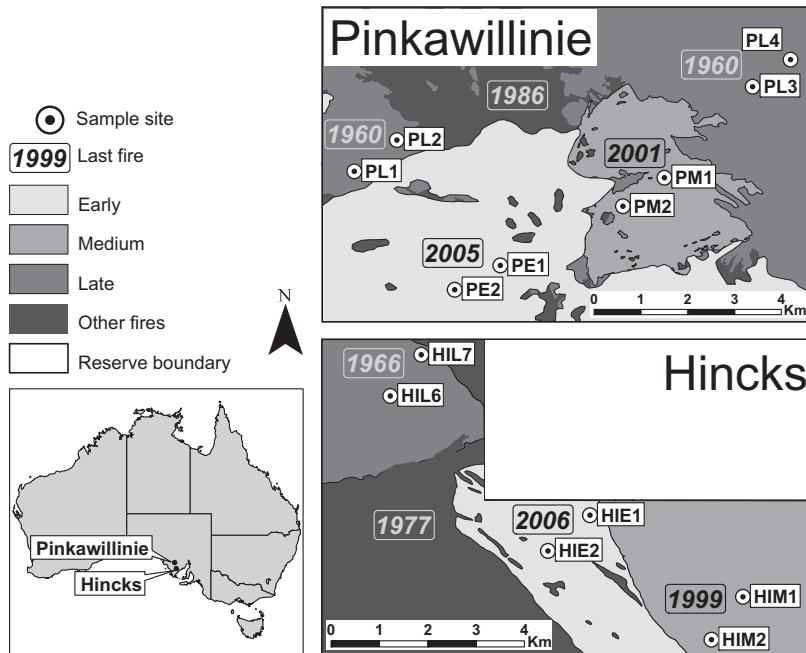


Fig. 1. Location of the sites where *Nephurus stellatus* were sampled at Hincks Wilderness Area and Pinkawillinie Conservation Park on the Eyre Peninsula, South Australia.

in 81 *N. stellatus* specimens at the South Australian Museum, following Godfrey and Hutchinson (2010). Geckos captured in the field were then measured and scored as either adult or juvenile. Adult sex was determined by external hemipenial bulges, present in males but not females. Adult females were scored as gravid when well developed eggs were visible.

For each initial capture, a single toe tip from the back foot was clipped as a batch mark, unique to each season (Funk et al., 2005). We used a Visible Implant Elastomer kit (Northwest Marine Technology) to apply a unique visual mark to each gecko by injecting a small amount of fluorescent elastomer under the ventral skin surface. Using different ventral positions allowed us to individually mark up to 300 animals annually. We rarely (3% of recaptures) found an animal with a clipped toe and an unreadable mark, indicating a high rate of mark retention. When a mark was not readable (in nine between-season recaptures when the animal had grown substantially) we sampled additional tissue and used microsatellite DNA genotypes (Smith et al., 2011) to match it to a capture from the previous year. These animals were re-marked with a new number. Each animal was released 5–10 m from the trap where it had been captured. If released during daylight, the gecko was placed in a concealed burrow and monitored to ensure it continued to dig itself in. Individuals that died in traps (1.3% of sampled animals) were not included in the analysis.

2.3. Habitat data

To quantify habitat differences among fire categories, we surveyed sites for structural vegetation characteristics and dominant species. At each site we established $25 \times 10 \text{ m}^2$ ($2 \times 5 \text{ m}$) plots on the NE side of each pitfall trap with a 2 m buffer between the plot and the trap fence. We recorded percentage canopy cover of trees (>2 m), tall shrubs (0.5–2 m), low shrubs (<0.5 m), dead (burnt) trees (>2 m), bare ground and leaf litter. We also recorded the percentage cover of the dominant plant species: *Eucalyptus* sp., *M. uncinata*, *C. verrucosa* and *T. irritans*. We analysed vegetation variables with Principal Components Analysis in the base package of R 2.12 (R Development Core Team, 2010) to illustrate similarities and differences among sites.

2.4. Reproductive capacity

Using initial capture data from each season and location separately, we applied Fisher's exact tests to determine if fire category influenced the age structure (ratio of juveniles to adults), sex ratio, and the reproductive status of adult females (detailed methodology in Appendix B).

2.5. Mark-recapture analysis

To estimate abundance, survival and detectability, we used the full-likelihood robust design model which includes the parameters capture probability (p), recapture probability (c), temporary emigration (γ), abundance (N) and survival (S) (Kendall et al., 1997). Temporary emigration has two components: γ'' , the probability of being unavailable at time i for animals that are on the study area at time $i - 1$, and γ' , the probability of being unavailable at time i for animals that are off the study area at time $i - 1$ (Kendall et al., 1997). It is therefore possible to model random ($\gamma'' = \gamma'$) and Markovian ($\gamma'' \neq \gamma'$) temporary emigration under the robust design (Kendall et al., 1997).

Complex group structures in our data (i.e. sex, age, and site in addition to fire category groups) led to over parameterised models, giving us little power to detect fire effects on the parameters. To keep n/K ratios high (where n is the number of captures and K the number of parameters) we pooled data from the paired sites within each fire category, and from the four sites in the late category at Pinkawillinie. Parameter estimates were thus based on four hectares for the late category at Pinkawillinie and two hectares for all other units. Data from age and sex categories were also pooled. This was justified by preliminary analyses from both reserves, which showed low support for sex and age differences in capture probability.

For each primary session separately, we tested the assumption that the populations were closed using CLOSETEST 3 (Stanley and Richards, 2005). We tested the goodness-of-fit of a global model using RDSURVIV (Hines, 1996; Kendall and Hines, 1999). It is not possible to include group structure in this model, so we used the pre-defined model which accounted for time effects on survival,

time and behaviour effects on capture probability (either trap-happiness or trap-shyness) and for constant, random temporary emigration. The variance inflation factor \hat{c} was calculated for the global model as χ^2/df , which was used to adjust for overdispersion in our data.

We used the R package RMark 2.0 (Laake and Rexstad, 2008) to build models with script for fitting, selection and parameter estimation in program MARK 5.1 (White and Burnham, 1999). We took an information theoretic approach and used QAIC_c (which accounts for overdispersion and is recommended for small samples) to select the most parsimonious model in our candidate set (Burnham and Anderson, 2002). To assess the relative likelihood of each model in the candidate set we calculated Akaike weights (w_i) (Burnham and Anderson, 2002).

We developed a set of a priori hypotheses to investigate the effects of fire category on the parameters while also accounting for possible effects of temperature, trap-related behaviour and temporal variation (Burnham and Anderson, 2002). The effect of temperature on capture probability was modelled using daily minimum temperature (mt) for each secondary occasion (Table 1). Variation in capture probability over primary sessions was modelled by numbering the sessions from one to six (sn) (Table 1). We envisaged that the capture process could affect recapture rates by leading to either a trap-happy ($p < c$) or trap-shy ($p > c$) behavioural response. We thus examined capture probability models with ($p \neq c$) and without ($p = c$) trap related behaviour effects (Otis et al., 1978). We tested whether animals moved off the study area making a proportion of the population temporarily unavailable for capture during each primary session. Two time-constant models of temporary emigration were explored: no temporary emigration ($\gamma'' = \gamma'(0)$), and random temporary emigration ($\gamma'' = \gamma'(\cdot)$) (Table 1) (Kendall et al., 1997). Time-varying and Markovian models of temporary emigration were not included in the candidate set as their n/K ratio was too low. To investigate meaningful effects of time on survival while keeping n/K high, we allocated one of two parameters to each interval between primary sessions (sw) (Table 1). The “summer” parameter described monthly survival rates in the short intervals (mean = 1 month) within seasons when geckos were active. The “winter” parameter described monthly survival rates in the longer time intervals (mean = 9.2 months) between seasons when geckos were mostly inactive. Temporal changes in abundance over primary sessions (sn) were investigated and fire category group effects (g) were modelled for p , c , N , and S (Table 1). Our global model was $p(mt + sn + g)$, $c(mt + sn + g)$, $\gamma'' = \gamma'(\cdot)$, $S(sw + g)$, $N(sn + g + sn * g)$.

The candidate set for each parameter included its global formulation and all models nested within it, including constant, or “dot” models (\cdot). Using the step-down modelling approach of Lebreton et al. (1992) (discussed in Doherty et al., 2011), we determined the top model for each parameter sequentially. To begin, candidate models for capture probability were fitted while keeping the global parameterisation of γ , N and S constant (Appendix C). We then fitted candidate models for γ , S and N , in that order, with the other parameters updated based on information from model selection in previous steps. The final model with the lowest QAIC_c was used for parameter estimation. Our analysis allowed us to determine the

importance of fire on abundance and survival in *N. stellatus* using realistic models for capture probability and temporary emigration.

3. Results

3.1. Capture summary, reproductive capacity, and robust design assumptions

We recorded 532 captures (308 individuals, 224 recaptures) at Hincks and 215 captures (139 individuals, 76 recaptures) at Pinkawillinie (Appendix A). There was no effect of fire category on the age structure or sex ratio in either season or location (Fisher's exact tests $P > 0.05$, Appendix B). The proportion of females that were gravid was significantly higher in the early (93.8%) than the medium fire category (56.5%) in season two at Hincks (Fisher's exact test $P = 0.01$, Appendix B). Data from Pinkawillinie and from both sites in season one were too sparse for reliable inferences (Appendix B). All primary trapping periods in both data sets met the assumptions of closure (CLOSETEST: $P > 0.05$). Goodness-of-fit tests indicated that a general model fitted the data for Hincks ($\chi^2 = 14.28$, $df = 11$, $P = 0.22$) and Pinkawillinie ($\chi^2 = 11.42$, $df = 6$, $P = 0.08$), with some evidence of overdispersion. We therefore adjusted QAIC_c values and standard errors for Hincks ($\hat{c} = 1.3$) and for Pinkawillinie ($\hat{c} = 1.9$).

3.2. Habitat variation

The first two components (PC) of the Principle Components Analysis explained a cumulative total of 90% of the variation in the vegetation plot data (PC1 = 83%, PC2 = 7%, Fig. 2). There was a clear separation between the late sites and the other sites along PC1. Ground cover variables appeared to contribute most to this separation, with leaf litter replacing bare ground with increasing time since fire (Fig. 2). The early and medium sites were separated mainly along PC2. There was more variation in vegetation among the late sites as they covered the full extent of PC2, while the early and medium sites were more centrally clustered (Fig. 2). There was little separation between reserves within fire categories indicating similar vegetation structure at both locations (Fig. 2).

3.3. Model selection and parameter estimates

Of the 14 models for capture probability at Hincks, the most parsimonious was $p(mt)$, $c(mt)$ ($w_i = 0.399$) (Appendix C). Capture probability increased significantly with increasing minimum temperature and geckos which had previously been captured had a lower capture probability than geckos on their first capture, indicating a trap-shy behavioural response (Fig. 3). Our n/K ratio for Pinkawillinie was very small (seven for the global model) and several of our models for capture probability were too general for our data. The two models with the lowest QAIC_c included trap-related behaviour effects but these both failed to produce estimates and standard errors for N . We thus chose the best fitting model with parameter estimates for N ($p(mt)$, $w_i = 0.085$, Appendix C) as our top model for capture probability at Pinkawillinie. There was little

Table 1
Variables used to parameterise capture (p) and recapture (c) probability, temporary emigration (γ), abundance (N) and survival (S).

Variable	Notation	Values	Used to parameterise
Minimum temperature	mt	Degrees Celsius	p , c
Primary session	sn	1–6 for each primary session	p , c , N
Fire category group	g	Early, medium, late	p , c , N , S
Season	sw	Summer or winter (monthly rates)	S
Constant	(\cdot)	No variation	p , c , γ , N , S

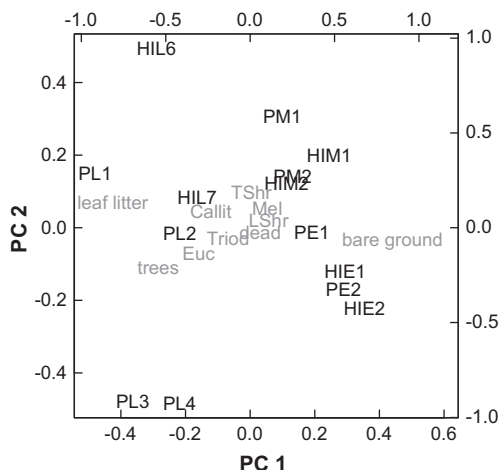


Fig. 2. Principle Components Analysis of vegetation structure and dominant plant species for each study site. Principle component 1 (PC1) explained 83% of the variation in the data, and PC2 explained 7%. The names of the study sites are shown in black, and the measured variables in grey (TShr = tall shrubs, LShr = low shrubs, Mel = *Melaleuca uncinata*, Callit = *Callitris verrucosa*, dead = dead trees, Triod = *Triodia irritans*, Euc = *Eucalyptus* spp.).

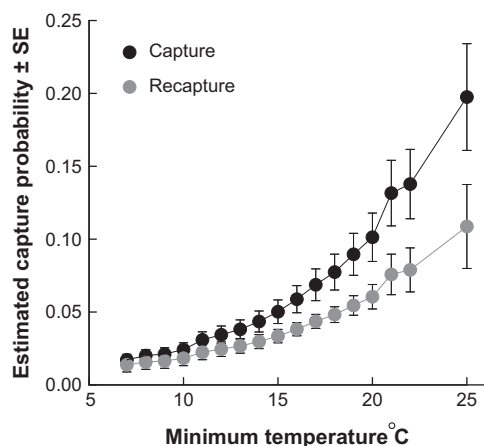


Fig. 3. Estimated capture (p) and recapture (c) probability (\pm SE) increased with increasing minimum temperature in *Nephurus stellatus* at Hincks and trap-shy behaviour ($p > c$) was detected.

support for an effect of fire category on capture probability at either Hincks or Pinkawillinie (Appendix C). Of the two models for temporary emigration (constant and zero) there was support for temporary emigration at Hincks ($w_i = 0.664$) with the proportion of animals unavailable for capture in each primary period estimated at $0.093 (\pm 0.090 \text{ SE})$. The model for no temporary emigration had the most support for Pinkawillinie ($w_i = 0.761$).

No *N. stellatus* were captured in the late category at Hincks, restricting comparisons from that location to the early and medium categories. At both Hincks and Pinkawillinie abundance was best explained by fire category and primary session (Table 2). There were significant differences in abundance among primary sessions, even within seasons, at both locations (Fig. 4). Abundance was consistently lower in the early than the medium sites at Hincks (Fig. 4a). Despite twice the trapping effort, the late category at Pinkawillinie had consistently lower abundance (mean population density = $0.7/\text{ha}$) than the early ($7.8/\text{ha}$) and medium ($14.7/\text{ha}$) categories (Fig. 4b).

At both reserves there was strong support for seasonal differences in monthly survival rates (Table 2). Survival was significantly lower in summer than winter (Fig. 5a and b). At Hincks there was

an additive effect of fire category (Table 2), with summer survival significantly lower in the early sites than the medium sites (Fig. 5a). There was no difference in survival between fire categories over winter (Fig. 5a). At Pinkawillinie, the best fitting model with fire effects on survival had only minimal support ($w_i = 0.117$), but showed lower mean summer survival rates in the late ($0.309 \pm 0.281 \text{ SE}$) than the early ($0.477 \pm 0.159 \text{ SE}$) and medium ($0.601 \pm 0.116 \text{ SE}$) sites. Although, these were not significant differences, the large variance resulting from data limitations may have masked an effect of fire category on survival.

4. Discussion

4.1. Post-fire abundance and detectability

Ignoring detectability in ecological studies can lead to spurious results and misguided management (White, 2005). Fire regimes can influence detectability in mammals (Pardon et al., 2003) raising concerns about conclusions drawn from simple count data in fire ecology studies. We asked whether the early successional distribution of the gecko *N. stellatus* reported by Driscoll and Henderson (2008) was biased by differences in detectability among post-fire successional stages. Our mark-recapture analysis found no differences in detectability among fire categories. However, we observed a general trap-shy response in *N. stellatus*, probably because they learn to avoid stressful confinement in traps (Langkilde and Shine, 2006).

The significant effects of time since fire on estimated abundance of *N. stellatus* were consistent across all six primary sessions at both reserves, supporting Driscoll and Henderson (2008) who reported higher capture rates of *N. stellatus* in recently burnt than long unburnt habitat. We added further resolution to the successional trajectory by including early, medium and late fire categories. Vegetation structure was clearly different among post-fire categories, but similar among sites in the same fire category in the two reserves. Abundance increased from the early to the medium category and was lowest in the late category, implying a mid-successional fire response in *N. stellatus*. However, mallee vegetation may remain unburnt for over a century (Haslem et al., 2011). In that context, *N. stellatus* could be regarded as an early successional species relative to the normal longevity of its habitat.

4.2. Mechanisms of abundance variation

Geckos in early sites had lower survival rates during the summer activity season than in medium sites, which probably contributed to the lower abundance in the early fire category. The early sites had only small shrubs, little leaf litter, and extensive bare ground, probably exposing geckos to higher predation. Changes in predation rates with habitat succession have been reported for mammals (Conner et al., 2011) and reptiles (Hawlena et al., 2010). Common nocturnal predators in the two reserves, including elapid snakes, owls and foxes, could all reduce gecko survival, as could diurnal predators like varanid lizards that excavate gecko burrows (Olsson et al., 2005). The higher monthly survival rates in winter than summer support a predation hypothesis. *N. stellatus* remain inactive underground over winter, with low predation risk but probably have increased mortality during peak activity periods in summer from predation, disease and extreme heat, as other reptiles do (Bonnet et al., 1999; Shine, 1980). The fire effects on predator populations and the cascading impact on their prey should be incorporated into future research on the effect of fire on animal survival.

Although survival and abundance were lower in early sites, fecundity appeared to be elevated as indicated by the higher

Table 2
Candidate models for abundance (*N*) and survival (*S*) of *Nephrurus stellatus* at Hincks and Pinkawillinie.

<i>N</i>	<i>S</i>	No. parameters	QAIC _c	ΔQAIC _c	Weight	QDeviance
Hincks						
<i>sn + g</i>	<i>sw + g</i>	15	688.283	0.000	0.937	615.220
<i>sn + g + sn * g</i>	<i>sw + g</i>	20	693.998	5.715	0.054	610.221
<i>sn + g</i>	<i>sw</i>	14	698.229	9.946	0.006	627.283
<i>sn</i>	<i>sw + g</i>	14	700.305	12.022	0.002	629.359
<i>g</i>	<i>sw + g</i>	10	707.852	19.569	<0.001	645.297
<i>sn + g</i>	<i>g</i>	14	715.861	27.578	<0.001	644.916
(·)	<i>sw + g</i>	9	719.138	30.855	<0.001	658.660
<i>sn + g</i>	(·)	13	720.778	32.495	<0.001	651.942
Pinkawillinie						
<i>sn + g</i>	<i>sw</i>	12	331.982	0.000	0.616	152.769
<i>g</i>	<i>sw</i>	7	333.883	1.901	0.238	165.674
<i>sn + g</i>	<i>sw + g</i>	14	335.297	3.315	0.117	151.529
<i>sn + g</i>	(·)	11	338.537	6.556	0.023	161.569
<i>sn + g</i>	<i>g</i>	13	341.637	9.655	0.005	160.158
<i>sn + g + sn * g</i>	<i>sw</i>	22	350.487	18.506	<0.001	147.549
(·)	<i>sw</i>	5	353.651	21.669	<0.001	189.696
<i>sn</i>	<i>sw</i>	10	355.003	23.021	<0.001	180.256

Capture probability was modelled as $p(mt)$, $c(mt)$ for Hincks, and $p(mt)$ for Pinkawillinie. Temporary emigration was modelled as $\gamma'' = \gamma'(\cdot)$ for Hincks and $\gamma'' = \gamma'(0)$ for Pinkawillinie.

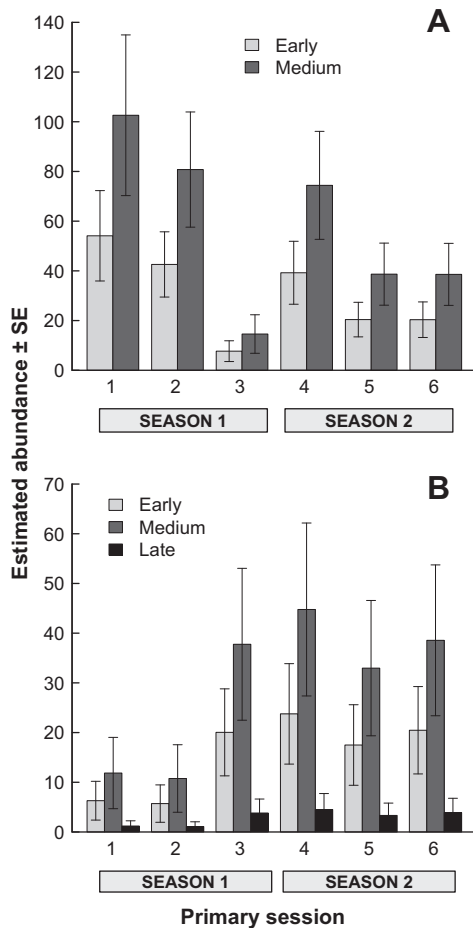


Fig. 4. Estimated abundance (*N*) (\pm SE) for *Nephrurus stellatus* at Hincks (A) and Pinkawillinie (B) where *N* was affected by fire category and session. The late category at Pinkawillinie had twice the sampling effort (100 traps) of all other units (50 traps).

proportion of gravid females at Hincks. Both surface and burrow temperatures are most likely higher in recently burnt areas than in habitats with advanced succession (Hossack et al., 2009) which could increase fecundity (Chamaillé-Jammes et al., 2006) and

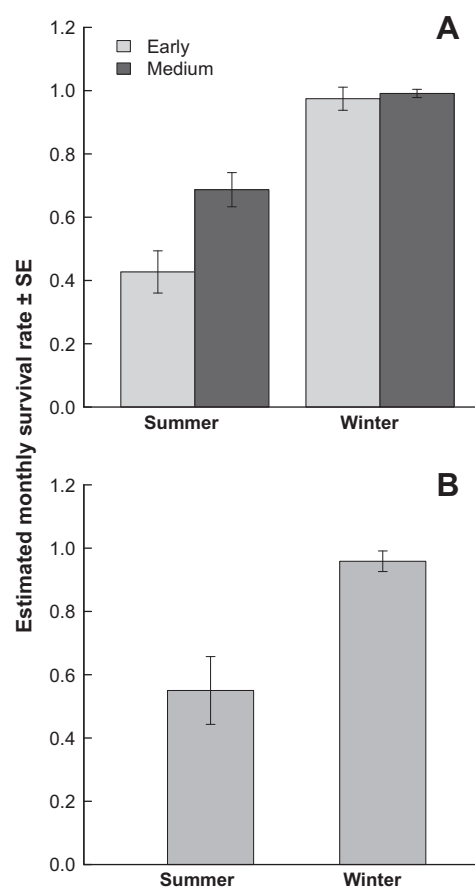


Fig. 5. Estimated monthly survival rates (\pm SE) for *Nephrurus stellatus* at Hincks (A) and Pinkawillinie (B). At Hincks survival was affected by fire category and season, and at Pinkawillinie by season only.

hasten embryo development (Angilletta et al., 2000). Diurnal temperatures influence many reproductive parameters in nocturnal geckos including nest success (Pike et al., 2010) and offspring sex ratios (Gamble, 2010). The higher proportion of gravid females in the early sites at Hincks could be a result of favourable thermal conditions. In addition, the early sites in this study had higher

invertebrate abundance (Teasdale pers. comm.) and the reduced vegetation structure could increase foraging success (Vernes and Haydon, 2001). Thus the early sites may have a thermal environment enhancing reproductive output in *N. stellatus*, plus a higher food resource base to increase fecundity. Although we found no effect of fire on sex ratios, the measures we used were limited by the difficulty in determining the sex of juveniles.

Although fecundity was higher, it did not result in increased abundance or a higher ratio of juveniles to adults in the early sites, suggesting high juvenile mortality that countered increased fecundity. Survival of lizard eggs can decrease if critical temperature and moisture thresholds are exceeded (Warner and Shine, 2009). Thus, even though the early sites had a higher reproductive capacity, survival of the eggs, once laid, might be diminished in a thermally extreme habitat. Hatchlings would also be particularly vulnerable to desiccation and predation in the exposed habitat of the early sites.

There were temporal changes in abundance over the study period, but no interactive effects between fire category and primary session to indicate population growth rates varied among successional stages. Abundance (for no obvious reason) declined at Hincks over the 2 years but stayed stable at Pinkawillinie, at least over the final four sessions. Our 2 year study was too short to clarify how succession influences population growth rates in a perennial species like *N. stellatus* (Pianka, 1970). A substantially larger data set is required for mark-recapture analyses which incorporate a recruitment parameter to model the effect of fire on population growth (Pradel, 1996).

Mortality cannot be separated from permanent emigration using only mark-recapture data (Pollock et al., 1990), thus lower survival rates in the early sites could also reflect higher rates of dispersal. The influence of successional changes on patterns of dispersal needs more study. The effect of fire on survival that we observed is likely to be related to successional changes in predation, the thermal environment, and resource availability. Examining the relative contribution of these mechanisms will be necessary to advance our understanding of animal survival at different post-fire stages.

4.3. Declines in long-unburnt mallee

We found a substantial decline of *N. stellatus* in old mallee habitat. At Pinkawillinie, although there was minimal support for models with fire effects on survival, those models showed lower mean summer survival rates in the late sites. Small population numbers in those sites reduced precision in the estimates, but lowered survival rates could drive abundance declines in long unburnt sites. Reproductive success may decrease if advanced habitat succession limits opportunities for optimal nest site choice and thermoregulation (Pike et al., 2010). In addition, the dense leaf litter, and high *Triodia* and tree canopy cover may inhibit dispersal and movement, making it harder for individuals to forage and find mates. Quantifying the effect of fire on reproduction, dispersal and movement is essential to better understand the processes behind fire responses in species with specialist successional niches.

Our investigation of detectability in long unburnt mallee was limited at both study locations. At Hincks no geckos were captured in the late sites. At Pinkawillinie, models with fire effects on capture probability had little support, although estimates from the best fitting model with fire effects on capture probability ($p(mt + g)$) revealed higher values in the late than the early and medium categories but very large standard errors (Appendix C). The limited power of our data in the late category might have masked an effect of fire on detectability. Since we trapped late sites intensively at Pinkawillinie it is unlikely that continued trapping would greatly increase the precision of capture probability estimates. Focussing on direct measures of movement, through

radio-tracking or direct observation, may provide a better idea of whether detectability differs between recently and long unburnt habitat (Koch and Hero, 2007). Alternatively, an occupancy approach across a large number of sites may provide more information about detection differences among fire categories (MacKenzie et al., 2005).

5. Conclusions

Given the recent severe changes in land use, ecological fire management must be conducted on temporal and spatial scales that are appropriate to the contemporary landscape (Keith and Henderson, 2002). In Australia, most mallee vegetation has been cleared for agriculture and small habitat remnants (approx. 1000 ha) can be completely incinerated by unplanned fire (DENR, 2011), which may disadvantage late successional species (Driscoll and Henderson, 2008). Prescribed burning may therefore be particularly important for small remnants which are at risk of complete incineration. Fire would best be used to protect late successional habitats on which many mallee animals rely (Bradstock et al., 2005; Brown et al., 2009; Driscoll and Henderson, 2008; Friend, 1993) and our data show that such management actions will also benefit early/mid-successional species. Where prescribed fire is not practical or appropriate, other actions such as canopy thinning may provide an alternative management strategy for providing fire breaks (Pike et al., 2011), although their effects on the broader community need to be assessed.

Understanding the effects of fire on animal population dynamics is fundamental to effective conservation planning in fire-prone ecosystems around the world (Clarke, 2008). The development of accurate predictive models for fire management relies on our ability to understand not only patterns, but also processes behind fire responses in animal communities (Driscoll et al., 2010; Whelan et al., 2002). Our study questioned previous research on fire ecology in reptiles, which has typically reported fire related distributions based on simple count-based abundance estimates. By incorporating realistic models for detectability in our study of *N. stellatus*, our results showed that counts from pitfall trap data (e.g. Driscoll and Henderson, 2008) can provide a reliable picture of post-fire abundance of reptiles. The early post-fire environment lowered survival rates in *N. stellatus* but high fecundity and increasing vegetation cover probably drove the populations towards a peak in both abundance and survival at approximately 8 years after fire. A continued focus on the demographic effect of fire will increase our ability to effectively guide fire management for biodiversity conservation (Driscoll et al., 2010).

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Supplementary material

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