

An investigation of potential threatening processes for the Vulnerable great desert skink, *Liopholis kintorei*



'Every step is a step closer to another great desert skink burrow system.'

Steve McAlpin, spring 2013

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ABSTRACT

Although there is a great body of knowledge regarding the status of and threats to extant mammal populations in Australia there remains limited comparable information on reptiles. One in five reptilian species are threatened with extinction globally, with one in four species of Australian reptile considered to be in decline. Several prominent threatening processes have been identified as being the likely cause of reptile population declines and local extinctions including: 1. grazing history; 2. human induced habitat loss and fragmentation; 3. habitat homogenisation caused by changes in recent fire regimes; 4. increased predation pressure caused by the introduction of cats and foxes; 5. harvesting, and more recently; 6. climate warming.

Since European settlement within Australia only a single record exists of an Australian reptile becoming extinct—Christmas Island forest skink (*Emoia nativitatis*) in 2014 however, ten reptile species are listed under the *Environmental Protection and Biodiversity Conservation (EPBC) Act 1999* as Critically Endangered, 20 as Endangered and 33 as Vulnerable. Of these, at least six species are arid zone specialists, including the great desert skink *Liopholis kintorei*, which is nationally listed as Vulnerable.

Liopholis kintorei is a large social skink that constructs complex burrow systems. Although its known distribution covers a significant area of arid Australia—1 500 000 km², it is Nationally listed as Vulnerable with approximately seventy known discrete populations with observed localised population declines or extinctions. Several potential threatening processes have been identified: 1. habitat alteration caused by recent changes to fire regimes; 2. increased predation pressure caused by

the introduction of the feral cat and European red fox, and more recently; 3. climate warming. However, no supporting field data are available to confirm these as threatening processes, and as such the underlying mechanism driving the observed declines are yet to be explored.

I investigated the threatening processes previously identified for this species. Specifically, I aimed to: 1. examine the effect of fire on *L. kintorei* burrow-system occupancy and breeding success at different spatial and temporal scales; 2. identify predators of *L. kintorei* and assess potential predator pressure at the burrow system; 3. further understand the potential role of climate warming as a threatening process by examining current and future thermal constraints on *L. kintorei* activity patterns. In addition, I aim to increase our understanding of *L. kintorei* dispersal patterns by characterising age- and sex-based patterns of within-patch movement, philopatry and dispersal. This knowledge is critical for guiding effective conservation.

To examine the effect of fire on burrow-system occupancy and breeding success, experimental burns simulating different fire types (clean burn, patchy burn and no burn) were conducted at 30 *L. kintorei* burrow systems selected within a 75 ha focal study area. Burrow-system occupancy was monitored daily for one month, then monthly for an additional three months. Breeding success was assessed once at all 30 burrow systems. Eight additional 1-km² sites within *L. kintorei* habitat that had experienced some degree of fire two years earlier were selected throughout Newhaven Wildlife Sanctuary. Burrow-system occupancy and breeding success of *L. kintorei* at these sites was assessed once. There was no significant effect of fire on burrow-system occupancy one month after experimental burns; however, burrow-

system occupancy was significantly higher at unburnt sites four months after experimental burns and two years post-fire. In addition, breeding success was significantly higher at unburnt sites than at clean-burnt and patchy-burnt sites. It was concluded that fire adversely affects *L. kintorei*, particularly when all ground cover is lost.

To assess the predation pressure at *L. kintorei* burrow systems and how this interacts with fire-induced habitat modifications, I collected daily track data of potential predators for one month at 30 great desert skink burrow-systems where vegetation cover varied significantly after experimental burns. I used these data to evaluate potential predation pressure at the burrow-system and assess whether fire influenced predator pressure. I supplemented this analysis by documenting predation via the inspection of large mammalian predator scats collected from great desert skink habitat. The level of feral cat activity at a burrow-system entrances was significantly higher than that of any other potential predator, however fire had no effect on the visitation rates of feral cats, dingoes or large snakes to great desert skink burrow-systems. The remains of great desert skink were found significantly more frequently in feral cat scats, compared to fox and dingo scats. I provide the first direct evidence that feral cats are a significant predator for great desert skink, thus supporting the hypothesis that feral cat predation is a key threatening process.

The direct impact of recent global warming on activity potential has been hypothesised to have caused extinctions in desert lizards, including the Australian arid zone skink *L. kintorei*. I tested the general relevance of this hypothesis through a detailed characterisation of the above- and below-ground thermal and hydric

conditions available to, and used by, *L. kintorei*. I integrated potential body temperatures with observed body temperatures to construct daily activity budgets, including the inference of subterranean behaviour. I then assessed the likelihood that contemporary and future local extinctions in this species, and those of similar burrowing habits, could be explained by the direct effects of warming on its activity budget and exposure to thermal extremes. During the study period, I found that *L. kintorei* spent only 4% of its time active on the surface, mainly at dawn and dusk, and that overall potential foraging activity will likely be increased, not restricted, with climate warming. The burrow system provides an exceptional buffer to current and future maximum extremes of temperature (≈ 40 °C reduction from potential surface temperatures), and desiccation (burrows near 100% humidity). Any climate warming impacts on this species are likely to be indirect.

Finally, I aimed to describe within-patch movement, philopatry and dispersal patterns for this species. These data will contribute to our limited knowledge of movement and dispersal patterns of this threatened species and will help to guide effective conservation. I combined molecular analyses with capture-mark-recapture data to characterise age- and sex-based differences in dispersal by: (i) assessing the difference in relatedness at different spatial scales among individual adult males, adult females and juveniles to infer dispersal patterns; (ii) to evaluate sex based differences in directly observed movement among burrow systems for adult male and adult female lizards, and; (iii) characterise differences in adult and juvenile philopatry to their natal burrow system via the use of parentage analysis. Capture-mark-recapture data showed that maximum movements between burrow systems were <130 m with

significantly greater distances observed for adult males. Spatial autocorrelation analyses revealed significant positive local genetic structure at the burrow system for adult female and juvenile individuals, but not for adult males. Furthermore, parentage assignments showed that the location of mother and full sibling offspring most often coincide in the same burrow system. From these data I concluded that *L. kintorei* exhibits male-biased dispersal whilst adult females and juveniles exhibit high natal philopatry.

This research identifies the key threatening processes for *L. kintorei* within spinifex grasslands and contributes to our understanding of *L. kintorei* dispersal patterns. It will be necessary for key populations across its wide distribution to be formally identified and these key threats actively managed to ensure that the distribution of this species does not continue to decline significantly.

DECLARATION

I hereby declare that this is my original work and that it contains no material previously published or written by another person, except where due acknowledgement is made. This work has been carried out while enrolled as a student for the degree of Doctorate of Philosophy in the School of Biological Sciences, Macquarie University. This thesis has not been submitted previously for examination at this, or any other, university.

All animals were handled in accordance with the Macquarie University Animal Ethics Committee under protocol number ARA2013/020 (Appendix 1.). Sample collection was licensed by the Northern Territory Government (NRETAS; Licence Number 017; Permit 41144).

Danae Moore

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PREFACE

This thesis has been written in the style of a thesis by manuscript.

Chapter 3 has been published in *Wildlife Research*. Publication details are:

Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. (2015). Is fire a threatening process for *Liopholis kintorei*, a nationally listed threatened skink? *Wildlife Research* **42**(3), 207-216. <https://doi.org/10.1071/WR14227>.

Chapter 4 has been published in *Austral Ecology*. Publication details are:

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Chapter 5 has been published in *Journal of Animal Ecology*. Publication details are: Moore, D., Stow, A., and Kearney, M. R. (2018). Under the weather?—The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *Journal of Animal Ecology* **87**(3), 660-671.
doi,10.1111/1365-2656.12812.

Chapter 6 has been written for submission thus the term 'we' has been used throughout.

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Firstly, I would like to thank Steve McAlpin— Steve has a great love for the great desert skink, *Liopholis kintorei* and has gained unparalleled knowledge about this species primarily through long hours of observations in the field. Steve has immersed himself in *L. kintorei* habitat across arid Australia hour after hour, year after year. His willingness to share so openly his knowledge has ensured a solid foundation for this study.

It has been a pleasure to work with Rachel Paltridge—one of central Australia's finest and most dedicated biologists. Her depth of knowledge about the arid-zone ecosystem is immense and I feel privileged to have been so closely guided by her throughout this study.

I have also had the pleasure of working with two wonderful people, Adam Stow and Mike Kearney, my supervisors. They have gently and consistently guided me through the research process. Although I have lived remotely throughout the duration of this work, I have not once felt that this has been a setback. Even during times when Adam was in the midst of serious field work, deep in the Amazon basin, he was always available, sending confirmation emails, submission edits and signatures. Likewise, Mike never let distance get in the way of a good catch-up. A coffee break at a conference in Tromso, Norway, was considered a good time to answer a few questions and nut out another complex R script. It has been wonderful to share my home in the desert with their families—these visits have been looked forward to by my family, and we hope that although the study has ended, these visits won't!

Trish Macdonald and Joss Haiblen generously provided a significant part of the funding that made this study a reality. Trish and Joss encouraged me to take on this study whilst raising a young family. They understood its importance, not only ecologically, but more so, for me personally. I still clearly and warmly remember the deciding conversation with them both, outside the workshop at Newhaven. They supported and loved my family over the years, and I look forward to many more relaxed times ahead. I also received funding from Australia and Pacific Science Foundation, Macquarie University and Australian Wildlife Conservancy.

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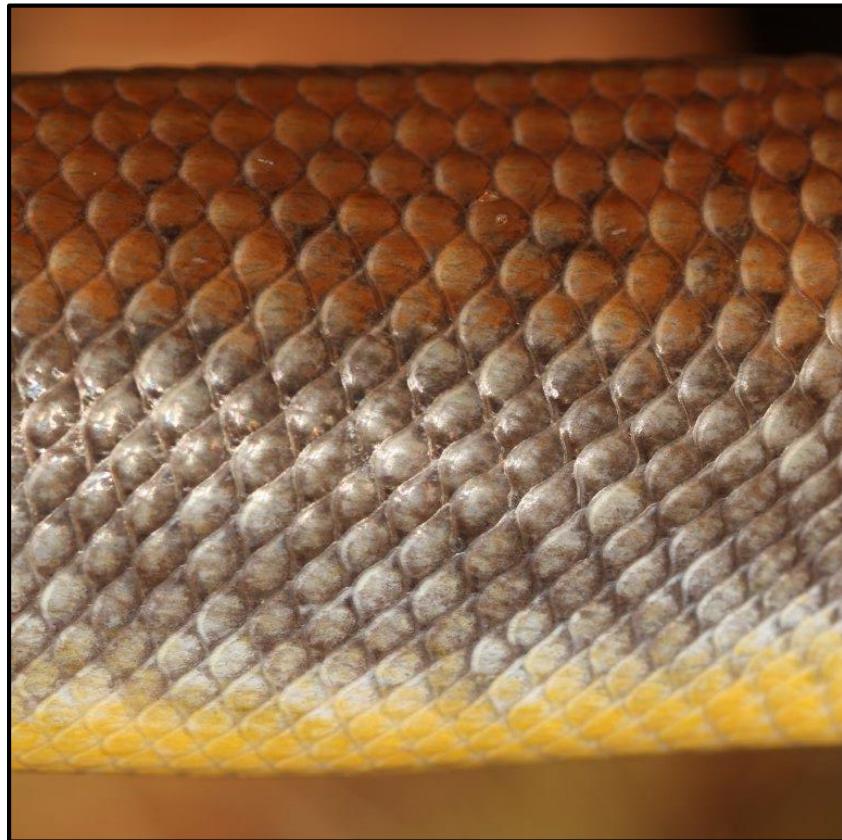
Georgina Spinaze and Margaret Henley gave their generous care at the perfect times both in the field but primarily at home, giving love and good food to our family to recharge our souls. I will not be able to thank you both enough for this love and care. It has been invaluable over these years of my research.

And my family...although small, they are the biggest part of my life. Josef and Eremaea have been by my side for the entire research with Smokey joining soon after I began this study. Josef's fine fire management skills were called upon during the field work—he conducted the experimental burns under the difficult conditions of dealing with *red devil* spinifex in early summer! He has taken the kids on picnics and

bushwalks on countless occasions, providing the quiet space I needed to prepare this thesis. Thank you so much Josef, you have been, as you always are, wonderful.

CHAPTER 1

GENERAL INTRODUCTION



A lateral view of a *Liopholis kintorei* displaying vivid desert colours (J. Schofield).

Preface

The following chapter reviews the literature relevant to this thesis, and introduces the current study, outlining its aims and scope.

Major threatening ecological processes in arid Australia

Changed fire regimes in arid Australia and the effects on fauna

This sub-chapter discusses recent changes in fire regimes in arid Australia, and how these changes may potentially contribute to faunal declines and extinctions. Focus has been given primarily to reptiles, as *Liopholis kintorei* is the focal reptile species of this thesis. The topic of fire regimes in the Australian landscape is more broadly discussed in the following sub-chapter.

Traditional Aboriginal burning practices within arid Australia resulted in a heterogeneous landscape with small patches of habitat at various stages of regeneration post- fire. With the cessation of traditional burning practices following European settlement, fire regimes shifted towards infrequent, intense, broad-scale wildfire events, resulting in vast tracks of homogenous habitat at the same stage of recovery post-fire (Burrows *et al.* 2006). Depending on the amount of rainfall within the first few years following fire, vegetation cover over large areas would have remained low, reducing habitat availability and diversity.

The effects of fire on fauna can be influenced by a range of multi-scale processes such as climate and rainfall patterns, fire history, habitat characteristics, resource distribution and predator pressure (e.g. Masters 1996; Letnic *et al.* 2004; Letnic and

Dickman 2006; Pianka and Goodyear 2012; Bird *et al.* 2013; Pastro *et al.* 2013; Greenville *et al.* 2016; Bennison *et al.* 2018). Studies within the arid zone focusing on small mammal species assemblage and abundance in relation to time since fire (e.g. Masters 1993; Southgate and Masters 1996; Letnic 2003; Letnic *et al.* 2004; Letnic *et al.* 2005; Pastro *et al.* 2011; Letnic *et al.* 2013) have suggested that many small native mammal species do not show a predictable response to fire, and there has been no consistent preference detected for burnt or unburnt habitats (Southgate and Masters 1996; Letnic 2003; Letnic *et al.* 2004; Letnic *et al.* 2005; Letnic and Dickman 2010; Letnic *et al.* 2013). This overall lack of consistency may be due in part to the fact that many of these studies were short-term and conducted post episodic flooding rainfall events associated with the La Niña phase of the El Niño/Southern Oscillation (Letnic *et al.* 2005; Letnic and Dickman 2010; Letnic *et al.* 2013; Pastro *et al.* 2013), where the possible short-term and long-lasting effect of fire may have been masked by the prolific growth of ephemeral plants and annual grasses. However, few species do show consistent responses, for example, the desert mouse *Pseudomys desertor* shows a strong preference for long-unburnt habitat, suggesting this species requires thick vegetation cover (Masters 1993; Southgate and Masters 1996; Letnic 2003; Letnic *et al.* 2004; Letnic and Dickman 2005). Other species such as crest-tailed mulgara *Dasycercus cristicauda*, brush-tailed mulgara *Dasycercus blythi* and Wongai ningaui *Ningaui ridei* may also be associated with long-unburnt habitats (Masters 1993; Letnic 2003). Masters (1993) suggested total cover was an important factor explaining the distribution of small mammals within spinifex grasslands at Uluru Kata-Tjuta National Park, southern Northern Territory. This study showed that six native small mammals

(*Pseudomys desertor*, *Pseudomys hermannsburgensis*, *Dasyurus blythi*, *Ningaui ridei* and *Sminthopsis youngsoni*) had higher mean numbers at sites with more cover—i.e. sites with longer time-since-fire intervals. Only two species, spinifex hopping mouse *Notomys alexis* and hairy-footed dunnart *Sminthopsis hirtipes*, showed a preference for recently burnt habitat. However, another study on the short-term effects of fire on rodents at the same location found that population responses of sandy inland mouse *Pseudomys hermannsburgensis* and *Notomys alexis* showed no significant difference between burnt and unburnt habitats (Southgate and Masters 1996). These results reflected those of similar studies conducted within the Simpson Desert, western Queensland where the response to fire of small mammal species including *Pseudomys hermannsburgensis*, *Sminthopsis hirtipes*, and lesser hairy-footed dunnart *Sminthopsis youngsoni* varied with no consistent habitat preference between recently burnt and long-unburnt being detected (Letnic 2004; Letnic and Dickman 2005, Pastro *et al.* 2011). More recently, a study within arid Australia has reported that both rodent and dasyurid populations initially declined dramatically post-burn (2 years post burn). However, following this initial decline both rodents and dasyurid populations rapidly increased in abundance with both groups preferentially exploiting post-burn habitat (Bennison *et al.* 2018).

There is much support to suggest that many arid zone lizard species are fire specialists, reaching their peak in population densities only when post-fire habitats have regenerated to the required seral stage (Pianka 1992; Masters 1996; Pianka 1996 Letnic 2004) however, some uncertainty remains (Pastro *et al.* 2013). Fox (1982) first described the ‘habitat accommodation model of succession’ for small mammals which

suggested that, following a disturbance such as wildfire event, there should be a predictable sequence of species recovery, largely driven by vegetation recovery and subsequent production of more structurally complex habitat. This model has been applied to lizard communities in various habitats including the deserts of Australia (Masters 1996; Letnic *et al.* 2004; Driscoll and Henderson 2008). Additionally, the life history attributes of an individual species should enable predictable responses to the disturbance (Noble and Slatyer 1981; Caughley 1985; Friend 1993; Lindenmayer *et al.* 2008). Accordingly, different reptile species respond to fire in a variety of predictable ways — with increasing time since fire some reptile species decreased in abundance whilst others increased (Pianka 1996; Letnic *et al.* 2004; Masters 2006; Pianka and Goodyear 2012).

Fire succession cycles generate heterogeneity in habitats, both spatially and temporally (Pianka 1996; Pianka and Goodyear 2012), with each habitat being more suitable for a particular assemblage of species (Pianka 1996; Pianka and Goodyear 2012). Generally, species that require long-unburnt vegetation will decrease in number or disappear altogether after a fire while species that prefer open habitat will become more numerous. The underlying causes for changes in species composition after fire are unknown, however studies by Letnic *et al.* (2004) suggest that they reflect the differing thermoregulatory, shelter and dietary requirements of lizard species.

Numerous studies of arid Australia found consistent responses to fire across species. For example, the abundance of beaked gecko *Rhynchoedura ornata* — a nocturnal termite specialist — and central netted dragon *Ctenophorus nuchalis* — a

diurnal burrowing species that tolerates high body temperatures — increased following fire and decreased with increasing time since fire (Caughley 1985; Masters 1996; Pianka 1996; Letnic 2004; Pianka and Goodyear 2012). The military dragon *Ctenophorus isolepis* is another species that has reliably shown a consistent response to fire, preferring later successional stages of vegetation (Letnic 2004; Pianka and Goodyear 2012). This species is a poor burrower and requires the shade provided by vegetation structure to regulate its body temperature (Losos 1987).

A study conducted by Caughley (1985) within the mallee woodlands of temperate Australia identified three distinct reptile responses to fire: 1. burrowing species are most common in recently burned sites, presumably because they shelter within their burrow during the fire event and are able to thermoregulate effectively within their burrow; 2. heliothermic species that require vegetation cover are most abundant after six years (depending on rainfall) when vegetation cover recovers sufficiently, and; 3. leaf-litter specialist species do not peak in abundance until approximately 25 years post-fire, when the leaf-litter layer is well established. These distinct reptile fire responses have also been observed elsewhere. A long-term study conducted within the Great Victoria Desert of Western Australia by Pianka and Goodyear (2012) showed that the abundance of five species of shuttling heliothermic skinks in the *Ctenotus* genus diminished significantly after fire but re-established once vegetation cover regenerated. This pattern was reflected in studies conducted in the Simpson Desert, western Queensland, by Letnic *et al.* (2004) which observed that *Ctenotus* species were absent immediately post-fire, only becoming prominent in late succession assemblages. Letnic *et al.* (2004) suggested this result most likely reflected

the increasing opportunity to thermoregulate and shelter within an increasingly structurally complex habitat as the vegetation recovered from the fire. Despite many studies supporting the habitat accommodation model of succession, there remains uncertainty around how closely many lizard species follow the expected post-fire recovery trajectory (Driscoll and Henderson 2008, Nimmo *et al.* 2012; Pianka and Goodyear 2012; Nimmo *et al.* 2013; Pastro *et al.* 2013). Pastro *et al.* (2013) suggested that rainfall is a dominant factor driving lizard responses to fire and have shown no evidence of post-fire succession, instead suggesting that a range of factors including food availability, predator pressure and grazing history all contribute to lizard species abundance and assemblages.

Numerous land management and biodiversity conservation organisations have adopted programs for planning and implementing fire management activities (Allan and Southgate 2002). The implementation of such programs has become an increasingly important objective with the priorities largely focusing on the protection of fire sensitive plant communities, threatened fauna habitat and minimising the risk and impacts of broad-scale wildlife events (Allan and Southgate 2002; Greenville *et al.* 2009).

Introduced mammalian predators within Australia

One of the key causal agents of recent Australian biodiversity declines is predation by introduced predators, in particular by the feral cat *Felis catus* and the European Red Fox *Vulpes vulpes* (Woinarski *et al.* 2015; Woinarski *et al.* 2018). Both species now have extensive ranges across Australia. The impacts of these two introduced predators

have been particularly pronounced on medium-sized Australian mammals, with most of the 30 known Australian mammal extinctions over the last 200 years due to these two introduced predator species (Burbidge and McKenzie 1989; Dickman 1996; Woinarski *et al.* 2015; Doherty *et al.* 2017).

It is known that cats were certainly introduced to and spread from multiple locations within Australia during the period 1824-86 and by 1890 all of the continent had been colonised (Abbott 2002). As feral cats can survive independently of free water they were able to successfully colonise arid Australia. There remains a high level of uncertainty around the number of feral cats within Australia. It is estimated that around four million (ranging from approx. 1-11 million) cats inhabit the Australian mainland, with numbers increasing in the arid regions after above-average rainfall (Legge *et al.* 2017).

The feral cat is an opportunistic, generalist carnivore, consuming a diverse suite of prey (Doherty *et al.* 2015). Globally, the diets of cats are generally dominated by mammalian prey (Pearre and Maass 1998) with birds often being of secondary importance (Dickman 1996; Paltridge 2002). A study focusing on feral cat diets across Australia, found that the arthropods were the most commonly consumed food group across all studies, followed by rodents, birds, rabbits, reptiles, dasyurids and medium-sized native mammals (Doherty *et al.* 2015). Within arid Australia, reptiles have been found to be an important component of the diets of cats (Read and Bowen 2001; Paltridge 2002; Woinarski *et al.* 2018).

Although there are numerous examples of small mammal declines and local extinctions that have been correlated with either the arrival, or the increase in

abundance of cats (e.g. Dickman 1993; Gibson 1994; Dickman 1996; Johnson 2006; Moseby *et al.* 2011; Frank *et al.* 2014; Marlow *et al.* 2015; Moseby *et al.* 2015 McDonald *et al.* 2016; Davis *et al.* 2016; Hardman *et al.* 2016), specific attention has only recently been given to the broad-scale impacts of feral cat predation on reptiles (Woinarski *et al.* 2018). A recent study of continental-scale variation in the diet of feral cats (Doherty *et al.* 2015) reported that that reptiles formed a significant component (average frequency of occurrence 24% in cat dietary samples) of the diet of cats with a higher frequency of reptiles in cat dietary samples taken from arid regions. It is estimated that feral cats kill 466 million reptiles each year with numbers being greatest within arid regions (Woinarski *et al.* 2018). Predation by cats has been reported for 258 Australian reptile species, including 11 threatened species (Woinarski *et al.* 2018). At a more local scale, two studies conducted in arid and semi-arid Australia both found that the abundance of small lizards did not change significantly after the removal of feral animals including cats (Risbey *et al.* 2000; Moseby *et al.* 2009). Opposing results have been found however within northern Australia where a significant increase in the abundance of reptiles over a two-year period in cat-excluded plots was recorded (Stokeld *et al.* 2018).

The European red fox was first released into the wild in southern Victoria around 1871 to provide sport for hunters on horseback with hounds (Johnson 2006). The subsequent spread throughout southern parts of Australia was rapid with the species reaching the South Australian border by 1888, New South Wales by 1893 and Queensland and Western Australia in the early twentieth century (Dickman 1996). The early spread and establishment of foxes was thought to be facilitated by populations

of rabbits. Foxes reached their northern limits around 1965; at these latitudes their distribution is sparse and patchy (Johnson 2006). Tasmania remained fox free until recently; it is thought that either a deliberate or accidental introduction to the island occurred in the late 1990s (Parks and Wildlife Tasmania 2014).

Foxes are considered opportunistic predators—their diet varies greatly from carrion, to invertebrates, to vertebrates ranging in size from <2g to 15 000g. Their preferred prey however are mammals up to about 3 kg (Triggs *et al.* 1984; Jarman 1986; Dickman 1996; Paltridge 2002). Foxes have also been linked to major declines of mammals, in particular medium-sized mammals (Dickman 1996; Risbey *et al.* 2000; Johnson 2006; Woinarski *et al.* 2015). In addition, predation by fox is also recognised as a threat to threatened Australian lizard species, including the pygmy bluetongue lizard *Tiliqua adelaidensis* (Nielsen and Bull 2016). Few studies have also highlighted how complex interactions take place between fox populations, carnivorous reptiles and Australian reptile communities (Olsson *et al.* 2005; Sutherland *et al.* 2011; Read and Scoleri 2015). Similar to the feral cat, within arid regions of Australia reptiles are also an important seasonal prey item for foxes, particularly within the summer months when reptiles are active (Bayly 1978; Triggs *et al.* 1984; Caitling 1988; Read and Bowen 2001; Paltridge 2002; Woinarski *et al.* 2018).

Climate warming and its impact on lizards

Anthropogenic climate warming caused by increasing levels of carbon dioxide within the atmosphere have caused Australian air temperatures to increase by ~ 0.8°C over the past century, with this increase being consistent with global trends (Hughes 2003).

The average temperature in Australia is predicted to rise by 1.0 to 6.0°C by 2070 (Hughes 2003; BOM 2014; CSIRO 2014). Significant trends in regional rainfall have been observed with greater rainfall being recorded within the northern, eastern and southern parts of Australia, with the south-western region receiving less (Hughes 2003). Although future rainfall trends are difficult to predict with certainty, overall increases in potential evaporation are predicted (Hughes 2003; BOM 2017; CSIRO 2014).

Biological impacts of climate warming have been well documented over a long period and there is much evidence to support climate warming driven changes in the distribution and abundance of plants and animals globally (Parmesan 2006). The distributions of marine, freshwater and terrestrial organisms are being altered to remain within preferred environmental conditions—species are shifting to cooler environments and to higher altitudes as air temperatures rise (e.g. Davis *et al.* 2001; Hughes 2003; Parmesan 2006; Chen *et al.* 2011; Diffenbaugh and Field 2013; Poloczanska *et al.* 2013; Lenoir 2015).

Numerous studies support that under currently predicted climate warming scenarios a significant numbers of species extinctions will occur (Thomas *et al.* 2004; Sinervo *et al.* 2010; Urban 2015). Extinction estimates vary between studies, however a recent syntheses of published studies estimates a global mean extinction rate of 7.9%, with extinction risks being higher in South America, Australia and New Zealand (Urban 2015). Global extinction risks have not been isolated to a particular taxonomic group—reptiles are also vulnerable to extinction due to climate warming (Urban 2015). Numerous studies have focused on how climate warming may impact lizard

populations (e.g. Huey *et al.* 2009; Kearney *et al.* 2009; Huey *et al.* 2010; Sinervo *et al.* 2010; Huey *et al.* 2012; Scheffers *et al.* 2014; Sunday *et al.* 2014; Ofori *et al.* 2017). For example, a study conducted by Sinervo *et al.* (2010) focusing on reptiles, predicted that climate warming over the next 70 years will cause 20% of all lizard species to become extinct due to reduced fecundity caused by warming, i.e. induced restrictions on activity periods leading to a decrease in food intake. Kearney *et al.* (2009) suggest that the impact of climate warming on thermoregulating ectotherms within Australia will depend on two key aspects—how changes in vegetation cover may alter the availability and quality of shade and the animals' capacity to alter their seasonal timing of activity and reproduction (Kearney *et al.* 2009). Diurnal species are more likely to be impacted by climate warming than are nocturnal species. As day-time temperatures increase diurnal species are more likely to encounter stressfully high body temperatures during their normal activity period, therefore, the thermoregulatory priority for most terrestrial diurnal ectotherms under a climate warming scenario of 3°C would be to avoid overheating (Kearney 2009).

Many reptile species have several strategies that can be used to help buffer against the impacts of climate warming including: behavioral evasion, plasticity and evolutionary adjustments (Huey *et al.* 2018). Body temperatures can be increased or decreased by altering activity levels, shuttling between sun and shade, adjusting posture or orientation, perching, basking and/or utilising retreat sites. The use of such biological buffers will influence species responses to climate shifts.

Fire within the Australian landscape

The sub-chapters below focus further on the topic of fire within an Australian context, as this ecological process is a key focus of this study. The following topics are briefly discussed: 1. The prehistory of fire in Australia; 2. Australian fire regimes and the evolution of Australian plant communities; 3. Aboriginal and European impacts of fire use in Australia; 4. Contemporary fire regimes within arid spinifex grasslands, and; 5. General faunal responses to fire.

The prehistory of fire in Australia

The analysis of charcoal from sedimentary records within Australia has provided an insight into the past occurrence of fire over the last 65 MA (Mooney *et al.* 2012). The quantification of charcoal provides information on the relative changes to the amount of biomass burnt and therefore on fire activity over time (Mooney and Tinner 2011; Mooney *et al.* 2012). The most comprehensive survey of charcoal records within Australia has been provided by Kershaw *et al.* (2002). This study and others reveal that fire was a significant component of landscape dynamics within Australia as early as the Tertiary (Kershaw *et al.* 2002; Mooney *et al.* 2012). As environmental conditions continued to dry through the Cenozoic Era, fire activity increased (Kershaw *et al.* 2002). During the last glacial/interglacial cycle, covering approximately eighty thousand years, a strong relationship between fire and climate existed, with cold intervals characterised by less fire and warm intervals by more fire (Kershaw *et al.* 2002; Mooney *et al.* 2012).

Throughout the Holocene Epoch (the last 11.7 ka) four distinct periods of fire activity have been shown. Between 7-5 ka there was an interval of low fire activity, followed by an increase in fire activity across all Australian biomes except wet forests. A further increase in fire activity occurred after 2 ka years with maximum fire activity observed after the arrival of European settlers (Kershaw *et al.* 2002). Contemporary palaeo-fire studies (Kershaw *et al.* 2002; Mooney *et al.* 2011; Mooney *et al.* 2012) suggest that these more recent fire patterns have been atypical. Recent fire patterns have been characterised by an increase in biomass burning during the 19th century followed by a reduction in biomass burning within the 20th century. It has been suggested (Marlon *et al.* 2008) that the decrease in burning during the 20th century may be a direct result of landscape fragmentation caused by increased agricultural activity and active fire suppression, rather than being driven by changes in climate.

Australian fire regimes and the evolution of Australian plant communities

Fire is recognised as a significant evolutionary force (Bond 2005). The presence of charcoal in sedimentary records within Australia reliably demonstrates a long history of fire in the Australian environment (Boman 1998; Kershaw *et al.* 2002; Mooney *et al.* 2011; Bowman *et al.* 2012). As a result of this long existence of fire, some Australian flora species have evolved to not only tolerate fire but depend on fire for reproductive success (Bell *et al.* 1993; Dixon *et al.* 1995; Wright *et al.* 2016). Adaptations such as thick bark and heavily insulated regenerative tissue, allowing epicormic resprouting and basal resprouting, are common traits found within many Australian fire-prone

plant communities (Bowman *et al.* 2012; Schubert 2014). Fire-stimulated flowering has been observed in taxa such as grass tree, *Xanthorrhoea* (Gill and Ingwersen 1976) and smoke- and heat-stimulated seed germination is needed by many Australian flora genera including *Acacia*, *Grevillea*, *Hakea* and *Eucalyptus* (Bell *et al.* 1993; Dixon *et al.* 1995; Enright *et al.* 1997; Morris 2000; Wright *et al.* 2016). Furthermore, some native Australian plant communities, such as Eucalyptus woodlands and *Triodia* grasslands, promote fire by the production of resin and oil-rich and decay-resistant leaves (Mutch 1970; Aston 1981; Nano *et al.* 2012). Fire has played a key role not only in the origins of plant adaptations but also in the distribution of plant communities (Kershaw *et al.* 2002; Pausas 2009). This has resulted in plant communities with characteristic fire regimes to which plants and animals have co-evolved (Pausas and Keeley 2009; Bowman *et al.* 2012).

Aboriginal and European impacts of fire use in Australia

A major focus of palaeo-fire studies within Australia has been the influence of human activities on fire regimes (Mooney *et al.* 2012). Recent palaeo-fire studies found no evidence to support the narrative that Aboriginal settlement within Australia — 40–60 ka — caused a significant shift in the fire regime (Mooney *et al.* 2011; Mooney *et al.* 2012). In addition, there is evidence showing that changes in vegetation observed around this time were not influenced by drivers such as fire and human activity (Stevenson and Hope 2005). However, it is well recognised that for a thousand years prior to European occupation Aboriginal people used fire extensively to sustain

interrelated cultural, political and resource values (Kimber 1983; Bowman *et al.* 2012; Nano *et al.* 2012).

Traditional Aboriginal fire regimes within the central and western deserts of Australia have resulted in a diverse mosaic of patches of vegetation at various stages of post-fire succession (Latz and Griffen 1978; Saxon 1984). This habitat heterogeneity is thought to be critical for the survival of a range of plants and animals which have since declined following the widespread cessation of traditional Aboriginal fire management post European settlement in Australia, in particular arid-zone mammals that fall within the ‘critical weight range’ (50–5,500 g; Burbidge and McKenzie 1989; McKenzie *et al.* 2007; Bowman *et al.* 2012).

Contemporary fire regimes within arid spinifex grasslands of the central and western deserts

Vast tracks of semi- arid and arid regions of Australia support hummock grasslands, characterised by the dominance of the highly flammable *Triodia* genus (Beadle 1981). These grasslands are associated with soils that are low in nutrients, occupy a diversity of landforms including sand plains, rocky hills, dune fields and gibber plains, and are commonly referred to as ‘spinifex country’ (Allan and Southgate 2002; Burrows *et al.* 2006). The presence of resin in many *Triodia* species and the arrangement of fine sclerophyllous leaves enhance the flammability of spinifex grasslands once mature, dome-shaped hummocks have formed (Allen and Southgate 2002; Nano *et al.* 2012). Mature spinifex grassland fires are severe, primarily wind-driven and can spread rapidly (Burrows 1991).

Episodes of extensive wildfires in arid spinifex grasslands are driven by time since fire and above average rainfall events (Letnic and Dickman 2006; Allan 2009; Greenville *et al.* 2009). The accumulation of biomass occurs quickly after major rainfall events, with little attrition during prolonged dry phases (Griffin *et al.* 1983). The growth of non-spinifex fuels, including forbs and annual grasses common post rain, increase fuel loads and connectivity between spinifex hummocks (Allan 2009; Nano *et al.* 2012). High fuel loads then readily burn in ideal conditions. Post-fire plant diversity is high, with grasses, herbs and forbs dominating as competition from spinifex is reduced (Allan and Southgate 2002). Fuel loads within spinifex grasslands are generally slow to recover from fire and the interval between fires ranges greatly depend on rainfall (Allan 2009).

Different *Triodia* species exhibit a range of resprouting responses to fire. Some species such as *Triodia basedowii* are obligate seeders and are killed by fire while other species, including *Triodia pungens*, of the stoloniferous variety, resprout and recover quickly post-fire (Nano *et al.* 2012). Consequently, fire frequency within spinifex grasslands is influenced by the dominant *Triodia* species. For example, semi-saline sandplains that are dominated by the resprouting stoloniferous form of *Triodia pungens* are more likely to carry fire sooner than sandplains dominated by the non-resprouting, obligate seeder *Triodia basedowii*.

For thousands of years, semi-nomadic desert Aboriginal people burnt country routinely to hunt game, to promote new plant growth, for communication and for other cultural reasons (Kimber 1983; Griffin and Friedel 1985; Burrows 1991). As a result of this burning practice a fine grain mosaic of burnt and un-burnt habitat at

different seral states was achieved (Jones 1969, Latz and Griffen 1978; Saxon 1984; Burrows *et al.* 2006).

European settlement of remote desert regions of Australia has resulted in Aboriginal people abandoning or modifying their traditional use of fire (Latz and Griffin 1978; Kimber 1983; Griffin and Friedel 1985; Burrows *et al.* 2006; Burrows 1991). Within central Australia traditional Aboriginal landscape scale mosaic burning had effectively ceased by the 1920 (Griffin and Friedel 1985). As a consequence, the seasonality, size and spacing of burnt patches has changed generally from small and close to large and distant (Griffin 1984). However, within central Australia fire remains an important aspect of Aboriginal people's lives today with people maintaining many uses, both practically and culturally, for fire (Vaarzon-Morel and Gabrys 2009).

Today, the location of Aboriginal settlements within remote arid Australia influences the size, seasonality and frequency of fires. An examination of fire size within the southern Tanami Desert by Allan (2009) shows that smaller fires ($> 50 \text{ km}^2$) occur within close proximity to Aboriginal communities and outstations and along main roads and travelling routes between Aboriginal communities. Extensive fires occurred beyond these regions burning thousands of kilometres. For example, during the 2000 - 2002 fire event a single fire burnt $5\ 716 \text{ km}^2$ in the southern Tanami Desert, Northern Territory (Allan 2009). These patterns have also been reflected in desert regions of Western Australia within the Great and Little Sandy Deserts (Bird *et al.* 2012). The number and size of fires lit by Aboriginal people within close proximity to communities (within 50 km) and tracks (within 5 km) was compared to those that were ignited by lightning outside these areas over a ten-year period. Although the

number of fires that were lit by Aboriginal people was much greater inside than outsides these areas, the average size of the fires was significantly smaller (Bird *et al.* 2012). For example, within the dry season, 2,514 fires were lit by Aboriginal people with a mean size of 109 ± 41 ha compared to just 163 fires being ignited by lightening, the latter fires burning on average $6,255 \pm 3099$ ha (Bird *et al.* 2012). Lightening is still a major ignition source of fires within spinifex grasslands and anthropogenic fire ignitions are also common, particularly along roads, hunting tracks and settlements (Nano *et al.* 2012).

Historic records from central Australia suggest extensive fires occurred in the 1920s following an exceptional rainfall event, and then in the mid 1970s following a series of wet years (Griffin and Friedel 1985; Greenville *et al.* 2009; Allan 2009). More recently, extensive fire events have occurred during 2000 and 2002 following three years of above average rainfall and during 2011 after an exception rainfall year in 2010 (Allan 2009).

General faunal response to fire

Animal populations of Australia have been noted to respond to a single fire in four broad ways: 1. no response; 2. population declines and remaining at a low level for a certain period of time before recovering; 3. populations decline to extinction, and; 4. initial post-fire increase then decline over time as the original vegetation returns (Whelan *et al.* 2002; Nano *et al.* 2012).

The effect of fire on species is complex with multiple contributing factors. Whelan *et al.* (2002) describe three important principles emerging from recent fire

ecology research results that help to understand and predict the effects of fire: 1. fires have both a direct and indirect effect on individuals; 2. the population response will be affected by both the fire event and by processes occurring after the fire, for example rainfall, and; 3. the ecosystem is affected from the fire regime, not just a single fire event (Gill 1975). Thus, the impact on species from fire events results from a complex interaction of many factors at different time scales. It is therefore difficult to predict the effects of one particular fire on any species (Whelan *et al.* 2002).

Recent Australian reptile declines

Although there is a great body of knowledge regarding the status of and threats to extant mammal populations in Australia (Burbige and McKenzie 1989; Bohm *et al.* 2013; Woinarski *et al.* 2015) there remains limited comparable information on reptiles. One in five reptilian species are threatened with extinction globally, with one in four species of Australian reptile considered to be in decline (Woinarski *et al.* 2007; Wilson 2012; Bohm *et al.* 2013; Environment Australia 2018). Since European settlement within Australia only a single record exists of an Australian reptile becoming extinct—Christmas Island forest skink (*Emoia nativitatis*) in 2014. Ten reptile species are listed under the *Environmental Protection and Biodiversity Conservation (EPBC) Act 1999* as Critically Endangered, 20 as Endangered and 33 as Vulnerable (Environment Australia 2018). Of these, at least six species are arid zone specialists, including the focal study species of this research, *L. kintorei* which is nationally listed as Vulnerable.

Several prominent threatening processes have been identified as being the likely cause of reptile population declines and local extinctions including: 1. grazing history; 2. human induced habitat loss and fragmentation; 3. habitat homogenisation caused by changes in recent fire regimes; 4. increased predation pressure caused by the introduction of cats and foxes; 5. harvesting, and more recently; 6. climate warming (Woinarski *et al.* 2007, Wilson 2012, Bohm 2013; Environment Australia 2018).

Study species: great desert skink, *Liopholis kintorei*

One remarkable reptile species that has experienced dramatic population declines and local extinctions is the great desert skink *Liopholis kintorei*. This species was previously classified in the genus *Egernia* (Gardner *et al.* 2008), and is the largest member of a closely allied clade of desert adapted, burrow constructing skinks (Chapple and Keogh 2004). *L. kintorei* is a large, robust skink with well-developed limbs (Cogger 2014). It has an average adult snout to vent length (SVL) of 200 mm and weighs up to 350 g. (McAlpin 2001). The tail is thick, tapering and relatively short, slightly longer than SVL (McAlpin 2001; McAlpin 2011). It is a viviparous species with females giving birth annually to 1-7 young which are born in the summer months from late November to late January (McAlpin 2011). Sexual maturity is reached within approximately two years when a SVL of about 160 mm is attained (Storr 1968; Pearson *et al.* 2001; McAlpin 2011). Sexual dimorphism has been observed within the species with males having a more robust build (McAlpin 2011; Dennison 2015). *L. kintorei* is the only reptile species known to

construct and maintain a long-term home for family members, providing a rare example of lizards behaving cooperatively (McAlpin *et al.* 2011).

L. kintorei varies in colouration both across their range and within discrete populations (McAlpin 2001). The dorsal surface ranges from a bright orange through to a dull grey and the ventral surface ranges from a bright lemon-yellow to cream or blue-grey (McAlpin 2001). The flanks range in colour from cream to blue-grey and may be patterned with orange-brown vertical bars, particularly in juveniles (McAlpin 2001, Pearson *et al.* 2001).

Field observations suggest *L. kintorei* is crepuscular and nocturnal, with most activity outside the burrow occurring within the early to mid-morning and from late afternoon to late evening. (Chapple 2003; McAlpin 2011; Cogger 2014). Its activity patterns are flexible depending on specific environmental conditions (Chapple 2003). For example, during warm overcast rainy days the species has been observed foraging in the middle of the day (Moore pers. obs.).

The species is an obligate burrower, constructing and maintaining a complex burrow system with several entrances and interconnecting tunnels (Chapple 2003, McAlpin *et al.* 2011). These complex burrow systems provide protection from predation and extreme temperatures (Chapple 2003). External latrines, most commonly one or two per burrow system, are also characteristic of *L. kintorei* burrow systems (McAlpin 2001). Specific locations are used habitually by the occupants of the burrow system to defecate and a concentrated accumulation of scats occurs forming what is known as a communal latrine.

Large burrow systems are usually occupied by a family group consisting of an adult breeding pair with juveniles from usually two, and occasionally three, age-cohorts (Cogger 2014; Pearson *et al.* 2001; McAlpin 2011; Dennison 2015). Like other members from the subfamily Egerniinae, *L. kintorei* have a complex social structure and mating system (McAlpin 2011; Dennison 2015). *Liopholis kintorei* have strong burrow fidelity with the average occupancy of a burrow being four years (McAlpin *et al.* 2011). One burrow system was observed to be continually occupied for ten years (McAlpin 2011).

The feeding behaviour and diet varies depending on food availability. *L. kintorei* is known to forage away from their burrow in search of food and also to opportunistically ambush potential prey from the burrow entrance (McAlpin 2011). The species is omnivorous, feeding on the leaves, flowers and fruits of particular plants, a variety of small vertebrates and a range of invertebrates including scorpions, cockroaches, grasshoppers, beetles, spiders, ants and termites. Termites are consumed in large quantities and make up a large part of their diet, particularly after rain when the swarming of alates is triggered (McAlpin 2001; McAlpin 2011) and termites are actively foraging (Moore pers. obs.)

The species is endemic to the arid zone and is restricted to sandy and gravelly habitats (McAlpin 2001; Woinarski *et al.* 2007) within the western desert regions of the Northern Territory, Western Australia and South Australia (Fig. 1.1).

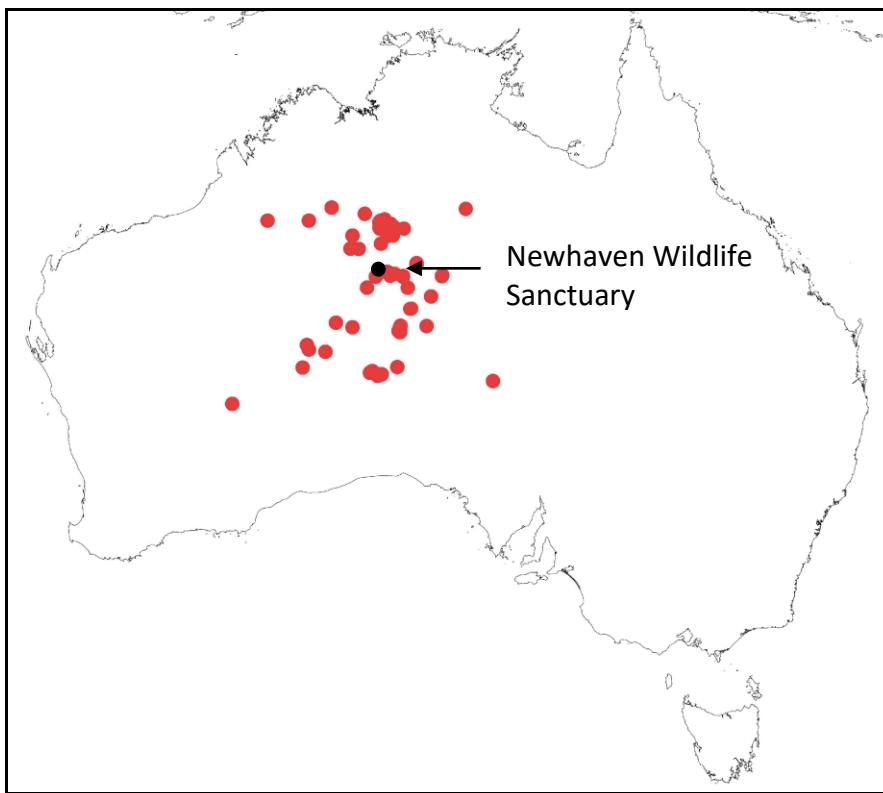


Fig. 1.1 The distribution of *Liopholis kintorei*, covering the western desert regions of the Northern Territory, Western Australia and South Australia. The approximate location of Newhaven Wildlife Sanctuary is indicated. Source: Atlas of Living Australia (2017).

Although its known distribution covers a significant area—1 500 000 km²—only approximately 70 discrete populations are known (McAlpin 2001). Consequently, they are an internationally listed vulnerable species (IUCN 2016). The limited number of known populations may reflect the difficulties associated with surveying such remote areas. However, it could also be a reflection of their specific habitat requirements within various regions.

In the north of their known distribution, within the Tanami Desert and the eastern areas of the Great Sandy Desert, *L. kintorei* populations are found in semi-

saline spinifex sand plains. These sand plains are associated with ephemeral drainage lines and are dominated by soft spinifex *Triodia pungens* (McAlpin 2001). In southern regions, populations have been found inhabiting open Mulga woodlands dominated by *Acacia aptaneura* and *Acacia minyura* with an understory of sparse tussock grasses dominated by *Eragrostis eriopoda* (McAlpin 2001). However, sand plains and wide flat swales of adjacent dune fields dominated by either hard spinifex *Triodia basdowii* or soft spinifex *Triodia pungens* and *Triodia schinzii* are considered favoured habitats within this region also (McAlpin 2011). Further to the west within the Gibson Desert favoured habitat is gently undulating gravelly downs known as ‘rira’ where the understory is dominated by hummock grasses primarily *Triodia basedowii* (McAlpin 2011).

Several potential threatening processes have been identified as being the likely cause of *L. kintorei* population declines including: 1. habitat homogenisation caused by changes in recent fire regimes (McAlpin 2001; Woinarski *et al.* 2007; Cadenhead *et al.* 2015); 2. increased predation pressure caused by the introduction of cats and foxes (McAlpin 2001), and more recently; 3. climate warming (Sinervo *et al.* 2010).

Introduction to current study

Thesis aims and scope

This thesis comprises a series of separate but related studies that together will strengthen our knowledge-base on the key threats for this species. *Liopholis kintorei* is an internationally listed vulnerable species (IUCN 2016) and although several key threatening processes have been identified as the likely causes of population declines

and local extinctions (refer to section above), no formal studies have been conducted exploring these potential threats. Consequently, no conservation recommendation can be confidently provided. The overall objective of this research project was to gain an improved understanding of the ecological mechanisms that underpin *L. kintorei*'s response to key threats and consequently to provide advice on conservation land management practices aimed at protecting this species from further declines and local extinctions. In addition, the study aimed to increase our understanding of *L. kintorei* dispersal patterns—such knowledge is critical for guiding effective conservation.

To meet this broad objective, I investigated three key potential threats: 1. fire; 2. introduced predators, and; 3. climate warming and examine *L. kintorei* dispersal patterns.

Four specific aims were developed:

1. To experimentally determine the effect of fire on *L. kintorei* burrow system occupancy and breeding success;
2. To determine predators of *L. kintorei* and investigate the magnitude of mammalian predation and potential predator pressure at *L. kinotrei* burrow systems;
3. To characterise *L. kintorei* activity patterns and the thermal and hydric conditions available within *L. kintorei* preferred habitat — the semi-saline spinifex plains of the eastern Great Sandy Desert Bioregion. Using these data, determine the effect of future climate warming on *L. kintorei* activity periods and assess to what extent the burrow system may buffer this species from climate warming.

4. To describe age- and sex-based differences of within-patch movement, dispersal and philopatry.

Thesis Structure

This thesis comprises four data chapters addressing the key research objectives described above. Following this general introduction (Chapter 1), Chapter 2 provides an overview of the study site, including the general location of Newhaven Wildlife Sanctuary and the specific location of the focal study sites within Newhaven. Climatic conditions for the region, vegetation composition and fire history of the focal study site are briefly described.

In Chapter 3, I aim to examine the effect of fire on *L. kintorei* burrow-system occupancy and breeding success at different spatial and temporal scales by employing two approaches, namely, a manipulative field experimental approach and a ‘natural experiment’ approach. Experimental burns simulating different fire types (clean burn, patchy burn and no burn) were conducted at 30 *L. kintorei* burrow systems selected from within a 75 ha focal study area. Burrow-system occupancy was monitored daily for one month, then monthly for an additional three months. Breeding success was assessed once at all 30 burrow systems. Eight additional 1-km² sites within *L. kintorei* habitat that had experienced some degree of fire two years earlier were selected from across Newhaven Wildlife Sanctuary. Burrow-system occupancy and breeding success of *L. kintorei* at these sites was assessed once.

In Chapter 4, I identify the key terrestrial predators of *L. kintorei* within semi-saline spinifex sandplains. I assessed the predator pressure at 30 individual burrow

systems daily for one month and analysed mammalian (feral cat, European fox and dingo) and reptilian (sand goanna) scats collected from *L. kintorei* habitat.

In Chapter 5, I discuss the potential role of climate warming as a threatening process for lizards living in extreme desert environments by considering the thermal constraints on *L. kintorei*. Specifically, I assess if the reported local extinctions for *L. kintorei* could be explained by a restriction of activity period due to an increase in field body temperatures (Sinervo *et al.* 2010). I assess the potential for future activity restrictions under climate warming scenarios and evaluate the extent to which the burrow system provides a buffer against current extreme maximum temperatures and those predicted by future climate warming.

In Chapter 6 I describe age- and sex-based differences of within-patch movement, dispersal and philopatry. I use a combination of molecular analyses with capture-mark-recapture data. I discuss the conservation implications of these results in the context of fire which is simultaneously a key threatening process and a critical conservation land management tool within hummock grasslands of arid Australia.

Chapters 3, 4, 5 and 6 are presented in the format required for the journal in which they have been published, or intend to be published, with the exception of table and figure numbers which have been altered to read sequentially and consistently throughout this thesis. Because each data chapter has been written as a stand-alone piece of work for publication, there is some repetition among them, particularly in reference to site location and species description. Each of the publications can be found in the Appendix of this thesis.

A final discussion chapter summarises the key findings of this research, discusses the implications of these findings within a conservation context and makes suggestions of further research.

References

- Abbott, I. (2002). Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. *Wildlife Research*, **29**(1), 51-74.
- Allan, G. E. (2009). Managing fire in the southern Tanami Desert. In *Desert Fire: fire and regional land management in the arid landscapes of Australia Desert Knowledge Cooperative Research Centre Report 37*. (Eds G.P. Edwards and G.E. Allan.) pp. 17-78. (Desert Knowledge Cooperative Research Centre, Alice Springs.)
- Allan, G. E., and Southgate, R. I. (2002). Fire regimes in the spinifex landscapes of Australia. In *Flammable Australia: the Fire Regimes and Biodiversity of a Continent*. (Eds R. A. Bradstock, J. E. Williams and A. M. Gill.) pp. 145–176. (Cambridge University Press: Cambridge, UK.)
- Andersen, A. N. (2005). ‘Termites of Northern Australia.’ (Barker Souvenirs: Alice Springs, NT.)
- Ashton D.H. (1981). Fire in tall open forests (wet sclerophyll forests). In *Fire and the Australian Biota*. (Eds AM Gill, RH Groves and IR Noble.) pp.339-366. (Australian Academy of Science, Canberra.)

Bayly, C. P. (1978). A comparison of the diets of the red fox and the feral cat in an arid environment. *South Australian Naturalist* **53**(2), 20-8.

Beadle, N. C. W. (1981). 'The vegetation of Australia.' (Cambridge University Press: Cambridge, UK.)

Bell, D. T., Plummer, J. A., and Taylor, S. K. (1993). Seed germination ecology in southwestern Western Australia. *Botanical Review* **59**, 24-73.

Bennison, K., Godfree, R., & Dickman, C. R. (2018). Synchronous boom–bust cycles in central Australian rodents and marsupials in response to rainfall and fire. *Journal of Mammalogy*. Early online view. DOI:10.1093/jmammal/gyy105

Bird R. B., Codding, B. F., Kauhanen, P. G., and Bird, D. W. (2012). *Aboriginal hunting buffers climate-driven fire-size variability in Australia's spinifex grasslands*. 'Proceedings of the National Academy of Sciences of the United States of America', 109:10287–10292. doi: 10.1073/pnas.1204585109.

Böhm, M., Collen, B., Baillie, J. E., Bowles, P., Chanson, J., Cox, N., ... and Rhodin, A. G. (2013). The conservation status of the world's reptiles. *Biological Conservation* **157**, 372-385.

Bolton, B. L., and Latz, P. K. (1978). The western hare-wallaby *Lagorchestes hirsutus* (Gould) (Macropodidae), in the Tanami Desert. *Wildlife Research* **5**, 285–293. doi:10.1071/WR9780285.

Bond, W. (2005). Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **7**, 387-394.

- Bowman, D. M. J. S. (1998). The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist* **140**, 385-410.
- Bowman, D., Murphy, B. P., Burrows, G. E., and Crisp, M. D. (2012). Fire regimes and the evolution of the Australian biota. In *Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World*. (Eds R. Bradstock, R. Williams and A. Gill.) pp. 3–25. (CSIRO Publishing: Melbourne.)
- Burbidge, A. A., Johnson, K. A., Fuller, P. J., and Southgate, R. I. (1988). Aboriginal knowledge of the mammals of the central deserts of Australia. *Wildlife Research* **15**(1), 9-39.
- Burbidge, A. A., and McKenzie, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**, 143–198. doi:10.1016/0006-3207(89)90009-8.
- Burrows, N. D. (1991). Patch-burning desert nature reserves in Western Australia using aircraft. *International Journal of Wildland Fire* **1**(1), 49-55.
- Burrows, N. D., Burbidge, A. A., Fuller, P. J., and Behn, G. (2006). Evidence of altered fire regimes in the Western Desert region of Australia. *Conservation Science Western Australia* **5**, 14–26.
- Cadenhead, N. C. R., Kearney, M. R., Moore, D., McAlpin, S., and Wintle, B. A. (2015). Climate and fire scenario uncertainty dominate the evaluation of options for conserving the Great Desert Skink. *Conservation Letters* **9**, 181-190. doi:10.1111/conc.12202

Catling, P. C. (1988). Similarities and contrasts in the diets of foxes, *Vulpes vulpes*, and cats, *Felis catus*, relative to fluctuating prey populations and drought. *Wildlife Research* **15**(3), 307-317.

Caughley, J. (1985). Effect of fire on the reptile fauna of mallee. *Biology of Australasian frogs and reptiles*. (Eds G. Grigg, R. Shine and H. Ehmann.), 31–34. (Surrey Beatty: Sydney.)

Chapple, D. G., and Keogh, J. S. (2004). Parallel adaptive radiations in arid and temperate Australia: molecular phyogeography and systematics of the *Egernia whitii* (Lacertilia: Scincidae) species group. *Biological Journal of the Linnean Society* **83**(2), 157-173.

Chapple, D. G. (2003). Ecology, life-history, and behaviour in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monograph* **17**, 145–180. doi:10.1655/0733-1347(2003)017[0145:ELABIT]2.0.CO;2.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science* **333**(6045), 1024-1026.

Cogger, H. (2014). ‘Reptiles and amphibians of Australia.’ (CSIRO PUBLISHING.)

Cowles, R. B., and Bogert, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* **83**, 263–296.

CSIRO (2014). Climate change information for Australia.

<https://www.csiro.au/en/Research/OandA/Areas/Oceans-and-climate/Climate-change-information> [Accessed 2014].

Davis, M. B., and Shaw, R. G. (2001). Range shifts and adaptive responses to

Quaternary climate change. *Science* **292**(5517), 673-679.

Davies, H. F., McCarthy, M. A., Firth, R. S., Woinarski, J. C., Gillespie, G. R., Andersen, A.

N., and Murphy, B. P. (2016). Top-down control of species distributions: feral

cats driving the regional extinction of a threatened rodent in northern

Australia. *Diversity and Distributions* **23**(3), 272-283.

Dennison, S. (2015). *Social organisation and population genetics of the threatened*

great desert skink, Liopholis kintorei. PhD. Thesis. (Macquarie University,

Sydney.)

Dickman, C. (1993). Raiders of the last ark: Cats in island Australia. *Australian Natural*

History Magazine **24**(5), 44-52.

Dickman, C. R. (1996). Overview of the impacts of feral cats on Australian native fauna,

pp. 1-92. (Australian Nature Conservation Agency: Canberra.)

Dickman, C. R., and Newsome, T. M. (2015). Individual hunting behaviour and prey

specialisation in the house cat *Felis catus*: implications for conservation and

management. *Applied Animal Behaviour Science* **173**, 76-87.

Diffenbaugh, N. S., and Field, C. B. (2013). Changes in ecologically critical terrestrial

climate conditions. *Science* **341**(6145), 486-492.

Dixon, K. W., Roche, S., and Pate, J. S. (1995). The promotive effect of smoke derived from burnt native vegetation on seed germination in Western Australian plants. *Oecologia* **101**, 185-192.

Doherty, T. S., Davis, R. A., Etten, E. J. B., Algar, D., Collier, N., Dickman, C. R., Edwards, G., Masters, P., Palmer, R., and Robinson, S. (2015). A continental-scale analysis of feral cat diet in Australia. *Journal of Biogeography* **42**(5), 964-975.

Driscoll, D. A., and Henderson, M. K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* **141**, 460–471.
doi:10.1016/j.biocon.2007.10.016.

Driscoll, D. A., Lindenmayer, D. B., Bennett, A. F., Bode, M., Bradstock, R. A., Cary, G. J., Clarke, M. F., Dexter, N., Fensham, R., and Friend, G. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* **143**, 1928–1939.
doi:10.1016/j.biocon.2010.05.026.

Edwards, G. P., and Allan, G. E. (2009). *Desert Fire: fire and regional land management in the arid landscape of Australia*. Desert Knowledge CRC Report No. 37. (Desert Knowledge Cooperative Research Centre: Alice Springs, NT.)

Enright N. J., Goldblum, D., Ata, P., and Ashton, D. H. (1997). The independent effects of heat, smoke and ash on emergence of seedlings from the soil bank of a healthy Eucalyptus woodland in Grampians (Gariwerd) National Park, western Victoria. *Australian Journal of Botany* **22**, 81-88.

Environment Australia (2018). 'EPBC Act List of Threatened Fauna.' Available at
<http://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=fauna>. [Accessed 9 October 2014]

Fenner, A. L., and Bull, C. M. (2007). Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *Journal of Zoology* **272**, 444–450.
doi:10.1111/j.1469-7998.2007.00287.x.

Frank, A. S. K., Johnson, C. N., Potts, J. M., Fisher, A., Lawes, M. J., Woinarski, J. C. Z., Tuft, K., Radford, I. J., Gordon, I. J., Collis, M.-A., and Legge, S. (2014). Experimental evidence that feral cats cause local extirpation of small mammals in Australia's tropical savannas. *Journal of Applied Ecology* **51**(6), 1486-1493.
doi:10.1111/1365-2664.12323

Friend, G. R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* **65**(2), 99-114.

Fox, B. J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* **63**, 1332-1341.

Gardner, M. G., Hugall, A. F., Donnellan, S. C., Hutchinson, M. N., and Foster, R. (2008). Molecular systematics of social skinks: phylogeny and taxonomy of the *Egernia* group (Reptilia: Scincidae). *Zoological Journal of the Linnean Society* **154**(4), 781-794.

- Gibson, D. (1994). Predation by feral cats, *Felis catus*, on the rufous hare-wallaby, *Lagorchestes hirsutus*, in the Tanami Desert. *Australian Mammalogy* **17**(5), 103-107.
- Gill, A. M. (2000). *Fire-pulses in the Heart of Australia: Fire Regimes and Fire Management in Central Australia*. CSIRO Centre for Plant Biodiversity Research. (Environment: Canberra.)
- Gill, A. M. (1975). Fire and the Australian flora: a review. *Australian Forestry* **38**(1), 4-25.
- Gill, A. M., and Ingwersen, F. (1976). Growth of *Xanthorrhoea Australis* R.Br. in relation to fire. *Journal of Applied Ecology* **13**, 195-203.
- Gorissen, S., Mallinson, J., Greenlees, M., and Shine, R. (2014). The impact of fire regimes on populations of an endangered lizard in montane south-eastern Australia. *Austral Ecology* **40**(2), 170-177. doi:10.1111/aec.12190.
- Greenville, A. C., Dickman, C. R., Wardle, G. M., and Letnic, M. (2009). The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. *International Journal of Wildland Fire* **18**, 631–639. doi:10.1071/WF08093.
- Greenville, A. C., Wardle, G. M., Nguyen, V., & Dickman, C. R. (2016). Spatial and temporal synchrony in reptile population dynamics in variable environments. *Oecologia* **182**(2), 475-485.
- Griffen, G. F. (1984). Hummock Grasslands. In *Management of Australian Rangelands* (Eds GN Harrington, AD Wilson and MD Young.) pp. 271-284. (CSIRO Publishing: Melbourne.)

- Griffen, G. F., Price, N. F., and Portlock, H. F. (1983). Wildfire in central Australian rangelands, 1970-1980. *Journal of Environmental Management* **17**, 311-323.
- Griffin, G. F., and Friedel, M. H. (1985). Discontinuous change in central Australia: some implications of major ecological events for land management. *Journal of Arid Environments* **9**, 63–80.
- Hardman, B., Moro, D., and Calver, M. (2016). Direct evidence implicates feral cat predation as the primary cause of failure of a mammal reintroduction programme. *Ecological Management & Restoration* **17**(2), 152-158.
- Haslem, A., Kelly, L. T., Nimmo, D. G., Watson, S. J., Kenny, S. A., Taylor, R. S., Avitabile, S. C., Callister, K. E., Spence-Bailey, L. M., and Clarke, M. F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* **48**, 247–256.
doi:10.1111/j.1365-2664.2010.01906.x.
- Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Pérez, H. J. Á., and Garland, T. (2009). Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London B: Biological Sciences* **276**(1664), 1939-1948.
- Huey, R. B., Losos, J. B., and Moritz, C. (2010). Are lizards toast? *Science* **328**(5980), 832-833.
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., and Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behavior, physiology and adaptation. *Phil. Trans. R. Soc. B* **367**(1596), 1665-1679.

Huey, R. B., Buckley, L. B., and Du, W. (2018). Biological buffers and the impacts of climate change. *Integrative zoology* **13**, 349-354.

Hughes, L. (2003). Climate change and Australia: trends, projections and impacts. *Austral Ecology* **28**(4), 423-443.

Jarman, P. (1986). *The red fox—an exotic, large predator*. The Ecology of Exotic Animals and Plants: Some Animal Case Histories. (Wiley: Brisbane.) 43-61.

Johnson, C. (2006). 'Australia's Mammal Extinctions: a 50,000 Year History.' (Cambridge University Press: Cambridge, UK.)

Jones, R. (1969). Fire-stick farming. *Australian Natural History* **16**, 224–228.

Kearney, M. R. (2013). Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters* **16**, 1470–1479. doi:10.1111/ele.12192.

Kearney, M., Shine, R., and Porter, W. P. (2009). The potential for behavioural thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proceedings of the National Academy of Sciences, USA* **106**, 3835–3840. doi:10.1073/pnas.0808913106.

Kelly, L. T., Nimmo, D. G., Spence-Bailey, L. M., Haslem, A., Watson, S. J., Clarke, M. F., and Bennett, A. F. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity & Distributions* **17**, 462–473. doi:10.1111/j.1472-4642.2011.00754.x.

Kershaw, A. P., Clark, J. S., Gill, A. M., and D'Costa, D. M. (2002). A history of fire in Australia. In *Flammable Australia: the Fire Regimes and Biodiversity of a*

Continent. (Eds R. A. Bradstock, J. E. Williams and A. M. Gill.) pp. 3–25.

(Cambridge University Press: Cambridge, UK.)

Kimber, R. (1983). Black lightning: Aborigines and fire in central Australia and the Western Desert. *Archaeology in Oceania* **18**, 38–45.

Kolb, A., and Diekmann, M. (2005). Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* **19**(3), 929-938.

Körtner, G., Pavey, C. R., and Geiser, F. (2007). Spatial ecology of the mulgara in arid Australia: impact of fire history on home range size and burrow use. *Journal of Zoology* **273**, 350–357. doi:10.1111/j.1469-7998.2007.00334.x.

Langlands, P. R., Brennan, K. E. C., and Pearson, D. J. (2006). Spiders, spinifex, rainfall and fire: long-term changes in an arid spider assemblage. *Journal of Arid Environments* **67**, 36–59. doi:10.1016/j.jaridenv.2006.01.018.

Latz, P. K., and Griffin, G. F. (1978). Changes in Aboriginal land management in relation to fire and food plants in central Australia. In *The Nutrition of Aborigines in Relation to the Ecosystems of Central Australia*. (Eds B. S. Hetzel and H. J. Frith.) pp. 77–85. (CSIRO: Melbourne.)

Legge, S., Murphy, B. P., McGregor, H., Woinarski, J. C. Z., Augusteyn, J., Ballard, G., and Baseler, M. *et al.* (2017). Enumerating a continental-scale threat: How many feral cats are in Australia? *Biological Conservation* **206**, 293-303.

Lenoir, J., and Svenning, J. C. (2015). Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography* **38**(1), 15–28. doi: 10.1111/ecog.00967.

Letnic, M., and Dickman, C. R. (2006). Boom means bust: interactions between the El Niño/southern oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation* **15**, 3847–3880.
doi:10.1007/s10531-005-0601-2.

Letnic, M., Dickman, C. R., Tischler, M. K., Tamayo, B., and Beh, C. L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* **59**, 85–114.
doi:10.1016/j.jaridenv.2004.01.014.

Letnic, M. (2003). The effects of experimental patch burning and rainfall on small mammals in the Simpson Desert, Queensland. *Wildlife Research* **30**(6), 547-563.

Letnic, M., Tischler, M., and Gordon, C. (2013). Desert small mammal responses to wildfire and predation in the aftermath of a La Niña driven resource pulse. *Austral Ecology* **38**(7), 841-849.

Letnic, M., Tamayo, B., and Dickman, C. R. (2005). The responses of mammals to La Nina (El Nino southern oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy* **86**, 689–703. doi:10.1644/1545-1542(2005)086[0689:TROMTL]2.0.CO;2.

Letnic, M., and Dickman, C. R. (2010). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews* **85**(3), 501-521.

Letnic, M., and Dickman, C. R. (2005). The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. *Austral Ecology* **30**(1), 24-39.

Lindenmayer, D. B., Wood, J. T., MacGregor, C., Michael, D. R., Cunningham, R. B., Crane, M., Montague-Drake, R., Brown, D., Muntz, R., and Driscoll, D. A. (2008). How predictable are reptile responses to wildfire? *Oikos* **117**, 1086–1097.
doi:10.1111/j.0030-1299.2008.16683.x

Long, K. (2009). Burrowing bandicoots—an adaptation to life in a fire-prone environment? *Australian Mammalogy* **31**(1), 57-59.

Losos, J. B. (1987). Postures of the military dragon (*Ctenophorus isolepis*) in relation to substrate temperature. *Amphibia-Reptilia* **8**(4), 419-423.

McAlpin, S. (2001). *A Recovery Plan for the Great Desert Skink (Egernia kintorei)*. (Arid Lands Environment Centre: Alice Springs, NT.)

McAlpin, S. (2011). *Social structure and mating systems of the great desert skink, Liopholis kintorei*. M.Sc. Thesis. (Macquarie University: Sydney.)

McAlpin, S., Duckett, P., and Stow, A. (2011). Lizards cooperatively tunnel to construct a long-term home for family members. *PLoS ONE* **6**, e19041.
doi:10.1371/journal.pone.0019041.

McDonald, P. J., Stewart, A., Schubert, A. T., Nano, C. E., Dickman, C. R., and Luck, G. W. (2016). Fire and grass cover influence occupancy patterns of rare rodents and feral cats in a mountain refuge: implications for management. *Wildlife Research* **43**(2), 121-129.

- McKenzie, N. L., Burbidge, A. A., Baynes, A., Brereton, R. N., Dickman, C. R., Gordon, G., Gibson, L. A., Menkhorst, P. W., Robinson, A. C., Williams, M. R., and Woinarski, J. C. Z. (2007). Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* **34**(4), 597-611.
- Marlon, J. R., Bartlein, P. J., Carcaillet, C., Gavin, D. G., Harrison, S. P., Higuera, P. E. et al. (2008). Climate and human influences on global biomass burning over the past two millennia. *Nature Geoscience* **1**, 697-701.
- Marlow, N. J., Thomas, N. D., Williams, A. A., Macmahon, B., Lawson, J., Hitchen, Y., ... and Berry, O. (2015). Cats (*Felis catus*) are more abundant and are the dominant predator of woylies (*Bettongia penicillata*) after sustained fox (*Vulpes vulpes*) control. *Australian Journal of Zoology* **63**(1), 18-27.
- Masters, P. (1993). The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. *Wildlife Research* **20**(6), 803-813.
- Masters, P. (1996). The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildlife Research* **23**, 39–47. doi:10.1071/WR9960039.
- Moseby, K. E., Hill, B. M., and Read, J. L. (2009). Arid Recovery—A comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof enclosure in arid South Australia. *Austral Ecology* **34**(2), 156-169.

- Moseby, K. E., Read, J. L., Paton, D. C., Copley, P., Hill, B. M., and Crisp, H. A. (2011). Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation* **144**(12), 2863-2872.
- Moseby, K. E., Peacock, D. E., and Read, J. L. (2015). Catastrophic cat predation: a call for predator profiling in wildlife protection programs. *Biological Conservation* **191**, 331-340.
- Nano, C. E. M., Clake, P. J., and Pavey, C. R. (2012). Fire regimes in arid hummock grasslands and *Acacia* shrublands. In *Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world*. (Ed. R. Bradstock, R. Williams and A. Gill.) pp. 195-214. (CSIRO Publishing: Melbourne.)
- Nielsen, T. P., & Bull, C. M. (2016). Impact of foxes digging for the pygmy bluetongue lizard (*Tiliqua adelaidensis*). *Transactions of the Royal Society of South Australia* **140**(2), 228-233.
- Nimmo, D., Kelly, L. T., Spence-Bailey, L. M., Watson, S. J., Haslem, A., White, J. G., and Bennett, A. F. (2012). Predicting the century-long post-fire responses of reptiles. *Global Ecology and Biogeography* **21**(11), 1062-1073.
- Nimmo, D. G., Kelly, L. T., Spence-Bailey, L. M., Watson, S. J., Taylor, R. S., Clarke, M. F., and Bennett, A. F. (2013). Fire mosaics and reptile conservation in a fire-prone region. *Conservation Biology* **27**(2), 345-353.
- Noble, I. R., and Slatyer, R. O. (1981). Concepts and models of succession in vascular plant communities subject to recurrent fire. In *Conference on Fire and the Environment*.

Australian Biota, Canberra (Australia), 9 Oct 1978. Australian Academy of Science.

Ofori, B. Y., Stow, A. J., Baumgartner, J. B., and Beaumont, L. J. (2017). Influence of adaptive capacity on the outcome of climate change vulnerability assessment. *Scientific reports*, **7**(1), 12979.

Paltridge, R., Gibson, D., and Edwards, G. (1997). Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research* **24**, 67–76. doi:10.1071/WR96023.

Paltridge, R. (2002). The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* **29**, 389–403. doi:10.1071/WR00010.

Parks and Wildlife Service Tasmania, <http://www.parks.tas.gov.au/> [Accessed 2014].

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**, 637-669.

Pastro, L. A., Dickman, C. R., and Letnic, M. (2011). Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. *Ecological Applications* **21**(8), 3238-3253.

Pastro, L. A., Dickman, C. R., and Letnic, M. (2013). Effects of wildfire, rainfall and region on desert lizard assemblages: the importance of multi-scale processes. *Oecologia* **173**, 603–614. doi:10.1007/s00442-013-2642-7.

Pausas, J. (2009). A burning story: the role of fire in the history of life. *BioScience* **7**, 593-601.

- Pausas, J. G., and Keeley, J. E. (2009). A burning story: the role of fire in the history of life. *Bioscience* **59**, 593–601. doi:10.1525/bio.2009.59.7.10
- Payne, S. J. (1991). ‘Burning Bush: a fire history of Australia.’ (University of Washington Press: Seattle, WA.)
- Pearre, S., Maass, R., and Maass, R. (1998). Trends in the prey size-based trophic niches of feral and house cats *Felis catus* L. *Mammal Review* **28**(3), 125-139.
- Pearson, D., Davies, P., Carnegie, N., and Ward, J. (2001). The Great Desert Skink (*Egernia kintorei*) in Western Australia: distribution, reproduction and ethno-zoological observations. *Herpetofauna* **31**(1), 64-68.
- Pianka, E. R. (1969). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* **50**, 498–502. doi:10.2307/1933908.
- Pianka, E. (1992). Disturbance, spatial heterogeneity, and biotic diversity: fire succession in arid Australia. *Research & Exploration* **8**, 352–371.
- Pianka, E. R. (1996). Long-term changes in lizard assemblages in the Great Victoria Desert. In *Long-term Studies of Vertebrate Communities*. (Eds M. L. Cody and J. A. Smallwood.) pp. 191–215. (Academic Press: New York.)
- Pianka, E. R., and Goodyear, S. E. (2012). Lizard responses to wildfire in arid interior Australia: Long-term experimental data and commonalities with other studies. *Austral Ecology* **37**, 1–11. doi:10.1111/j.1442-9993.2010.02234.x.

- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., ... and Duarte, C. M. (2013). Global imprint of climate change on marine life. *Nature Climate Change* **3**(10), 919. doi: 10.1038/nclimate1958.
- Quinn, G. P., and Keough, M. J. (2002). *Experimental Design and Data Analysis for Biologists*. (Cambridge University Press: Cambridge, UK.)
- R Development Core Team (2011). *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing: Vienna. Available at <http://www.R-project.org/>. [Accessed 21st January 2014]
- Read, J., and Bowen, Z. (2001). Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research* **28**(2), 195-203.
- Read, J. L., & Scoleri, V. (2015). Ecological implications of reptile mesopredator release in arid South Australia. *Journal of Herpetology* **49**(1), 64-69.
- Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S., and Wright, I. W. (2000). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* **27**(3), 223-235.
- Saxon, E. C. (1983). Mapping the habitats of rare animals in the Tanami wildlife sanctuary (central Australia): an application of satellite imagery. *Biological Conservation* **27**, 243–257. doi:10.1016/0006-3207(83)90021-6.
- Saxon, E. C. (1984). *Anticipating the inevitable: a patch-burn strategy for fire management at Uluru (Ayers Rock–Mt Olga) National Park*. (CSIRO Division of Wildlife and Rangelands Research, CSIRO: Alice Springs, NT.)

Schubert, A. T. (2014). *Does fire or productivity drive relative bark thickness from desert to savanna in northern Australia?* M. Sc. Thesis. (Charles Darwin University: Darwin.)

Sinervo, B., Mendez-De-La-Cruz, F., Miles D.B. et al. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894-899.

Southgate, R., and Masters, P. (1996). Fluctuations of rodent populations in response to rainfall and fire in a central Australian hummock grassland dominated by *Plectrachne schinzii*. *Wildlife Research* **23**(3), 289-303.

Stevenson, J. S., and Hope, G. (2005). A comparison of late Quaternary forest changes in New Caledonia and northeastern Australia. *Quaternary Research* **64**, 372-383.

Stokeld, D., Fisher, A., Gentles, T., Hill, B. M., Woinarski, J. C., Young, S., and Gillespie, G. R. (2018). Rapid increase of Australian tropical savanna reptile abundance following exclusion of feral cats. *Biological Conservation* **225**, 213-221.

Storr, G. M. (1968). Revision of the *Egernia whitei* species-group (Lacertilia: Scincidae). *Journal of the Royal Society of Western Australia* **51**, 51-62.

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, K. R., Dulvy, K. N., Longino, J. T., and Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences* **111**, 5610-5615.

Sutherland, D. R., Glen, A. S., & Paul, J. (2010). Could controlling mammalian carnivores lead to mesopredator release of carnivorous reptiles? *Proceedings of*

the Royal Society of London B: Biological Sciences, Online,

doi:10.1098/rspb.2010.2103

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., and Hughes, L. (2004). Extinction risk from climate change. *Nature* **427**(6970), 145-148.

Triggs, B., Brunner, H., and Cullen, J. M. (1984). The food of fox, dog and cat in Croajingolong National Park, south-eastern Victoria. *Wildlife Research* **11**(3), 491-499.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, **348**(6234), 571-573.

Webb, J. K., and Shine, R. (2008). Differential effects of a severe wildfire on survival of sympatric snakes. *The Journal of Wildlife Management* **72**, 1394–1398.
doi:10.2193/2007-515.

Whelan, R. J., Rodgerson L., Dickman, C. R., and Southerland, E.F. (2002). Critical life cycles of plants and animals: developing a process-based understanding of population change in fire-prone landscapes. In *Flammable Australia: The fire regimes and Biodiversity of a Continent*. (Eds R.A. Bradstock, J.E. Williams, and A.M. Gill.) pp. 94-124. (Cambridge University Press, Cambridge: UK.)

Wilson, S. (2012). ‘Australian lizards: a natural history.’ (CSIRO Publishing.)

Wright, B. R., Latz, P. K., and Zuur, A. F. (2016). Fire severity mediates seedling recruitment patterns in slender mulga (*Acacia aptaneura*). *Plant Ecology* **217**(6), 789-800.

Woinarski, J. C. Z. (1999). Fire and Australian birds: a review. In *Australia's Biodiversity – Responses to Fire: Plants, Birds and Invertebrates*. (Eds J. C. Z. Woinarski, A. York and A. M. Gill.) pp. 55–180. (Environment Australia: Canberra.)

Woinarski, J. C. Z. (2007). *Lost from our Landscape: Threatened Species of the Northern Territory*. (Department of Natural Resources, Environment and The Arts, Palmerston: NT.)

Woinarski, J. C. Z. (2015). Critical-weight-range marsupials in northern Australia are declining: a commentary on Fisher *et al.* (2014). 'The current decline of tropical marsupials in Australia: is history repeating?' *Global Ecology and Biogeography* **24**, 118–122. doi:10.1111/geb.12165

Woinarski, J., Burbidge, A., and Harrison, P. (2014). *Action Plan for Australian Mammals 2012*. (CSIRO Publishing: Melbourne.)

Woinarski, J. C. Z., Murphy, B. P., Palmer, R., Legge, S. M., Dickman, C. R., Doherty, T. S., ... and Stokeld, D. (2018). How many reptiles are killed by cats in Australia? *Wildlife Research* **45**, 247-266.

Woinarski, J. C., South, S. L., Drummond, P., Johnston, G. R., and Nankivell, A. (2018). The diet of the feral cat (*Felis catus*), red fox (*Vulpes vulpes*) and dog (*Canis familiaris*) over a three-year period at Witchelina Reserve, in arid South Australia. *Australian Mammalogy* **40**, 204-213.

Vaarzon-Morel, P., and Gabrys, K. (2009). Fire on the horizon: contemporary Aboriginal burning issues in the Tanami Desert, central Australia. *GeoJournal* **74**(5), 465-476.

CHAPTER 2

STUDY SITE



Vast semi-saline spinifex sandplains—typical *Liopholis kintorei* habitat within Newhaven Wildlife Sanctuary (J. Schofield).

Newhaven Wildlife Sanctuary

Location

This research was conducted at Newhaven Wildlife Sanctuary (Newhaven) which lies within the Great Sandy Desert Bioregion, 350 km north-west of Alice Springs in the Northern Territory. Newhaven is owned and managed for conservation by the Australian Wildlife Conservancy.

Newhaven sits within the eastern extent of the Great Sandy Desert Bioregion, which itself is nestled between the Burt Plain and the McDonnell Ranges Bioregions (Fig. 2.1). Newhaven is surrounded by Aboriginal land: Yunkanjini Aboriginal Land Trust to the north and west, Haast Bluff Aboriginal Land Trust to the south and the Ngalurrtju Aboriginal Land Trust to the east.



Fig. 2.1 The location of Newhaven Wildlife Sanctuary within the Great Sandy Desert Bioregion in relation to the Tanami, Burt Plain and MacDonnell Ranges Bioregions.

Vegetation description

Newhaven is largely dominated by vast spinifex sand plains. A large ephemeral salt lake, Lake Bennett—also locally known as Yunkanjini—lies centrally within the property and a series of smaller reticulated ephemeral saltwater lakes are dotted across the landscape to the east (Young *et al.* 1995). These ephemeral salt lakes are contained within a large semi-saline spinifex sandplain dominated by soft spinifex *Triodia pungens*. The lakes and semi-saline spinifex sandplains are bounded to the south by woodlands of witchetty bush (*Acacia kempeana*), mulga (*Acacia aptaptaneura*) and ghost gum (*Corymbia aparrerinja*), which grow on shallow soils over calcrete. Within the northern part of the property a series of broken quartzite ranges rise to an elevation of 800 m. An extensive dune field dominated by hard spinifex *Triodia basedowii* spans the property's southern boundary. The north-west of the property is principally hard spinifex sand plains with a mixed acacia overstory. These sand plains are interspersed with patches of mulga woodland, blue mallee sand plains and open salt bush flats (Latz *et al.* 2003).

Climate

Newhaven's climate is arid tropical, with an average mean summer temperature of 35.9 °C, an average mean winter temperature of 7.5 °C, and with daily extremes ranging from -2 to 46 °C (Latz *et al.* 2003; Bureau of Meteorology 2014). The annual mean rainfall for the property over the past 51 years is 332.4 mm with the median being slightly lower at 321.3 mm (Bureau of Meteorology 2014) (Fig. 2.2). Rainfall is most common within the summer months, however high levels of spatial and temporal

variability in rainfall characterise the region. Decadal scale cycles of El Niño-driven, below average rainfall periods are unpredictably broken by flooding rainfall events. This pattern of drought followed by flooding rains is considered normal (Stafford-Smith and Morton 1990).

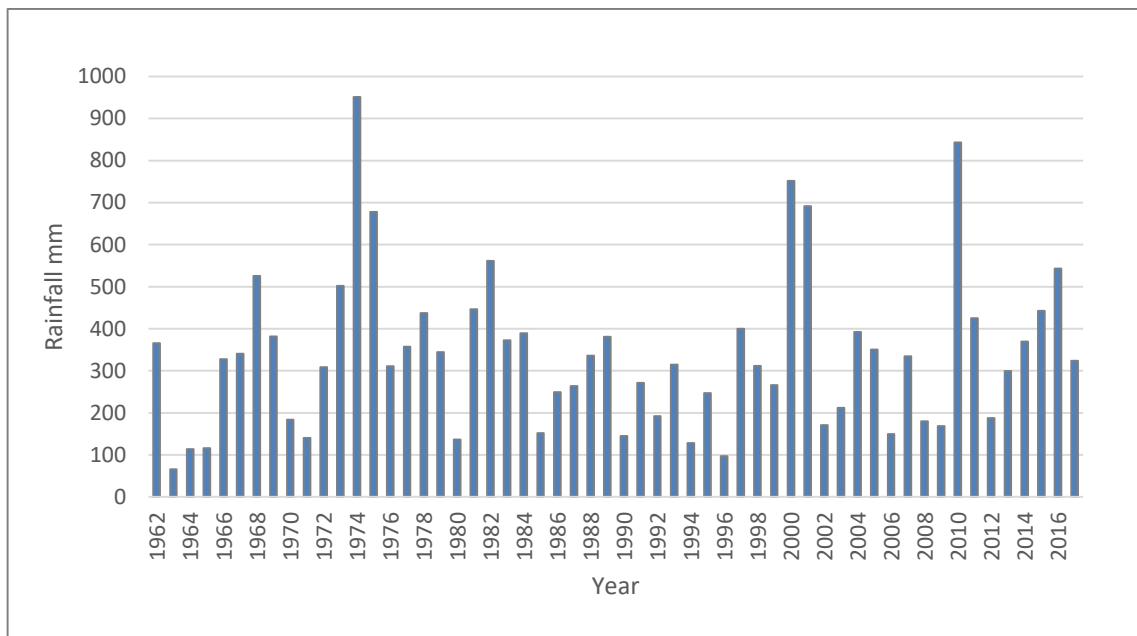


Fig. 2.2 Annual rainfall recorded at Newhaven Wildlife Sanctuary from 1962 to 2015 (Bureau of Meteorology 2017).

Focal study site

A 75 ha focal study site was defined within the semi-saline spinifex sand plain (Fig. 2.3), where an extensive population of *L. kintorei* was identified as being locally abundant. It was here that experimental burns were conducted. These sand plains are associated with ephemeral drainage lines and are characterised by the presence of: (1) the fast-growing stoloniferous form of the soft spinifex *Triodia pungens*; (2) small clusters of the

inland tea-tree *Melaleuca glomerata*, and; (3) the perennial daisy *Pluchea ferdinandi meulleri* (McAlpin 2001). This vegetation community typifies *L. kintorei* habitat on Newhaven.

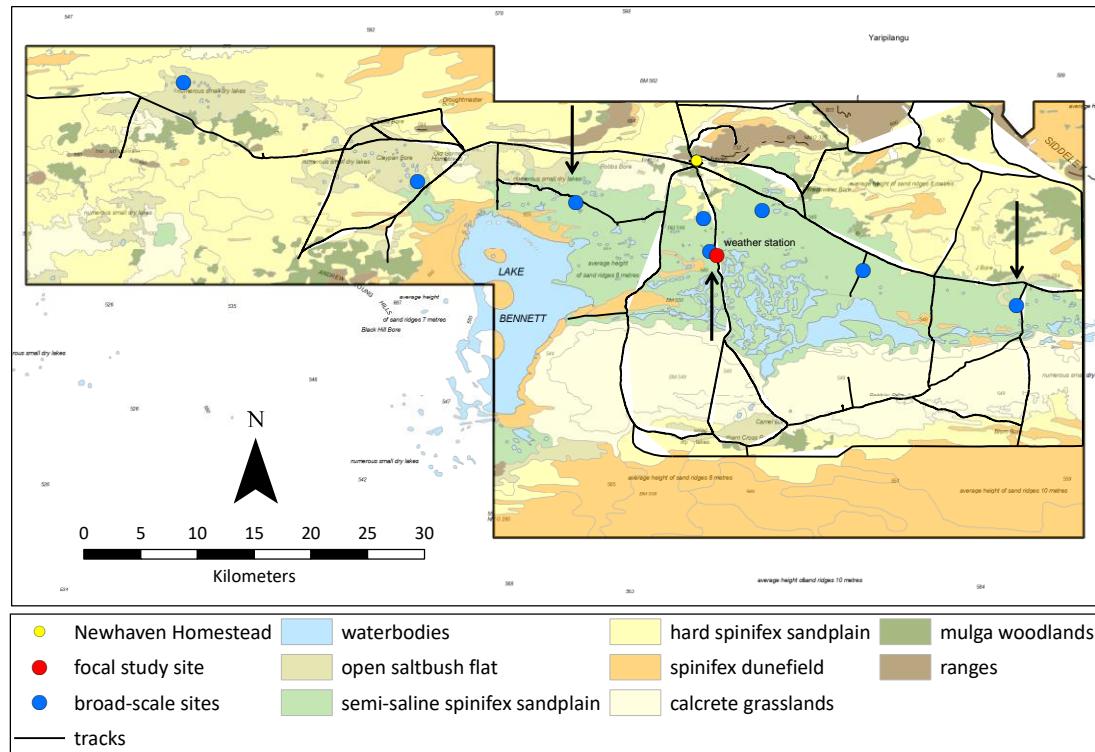


Fig. 2.3 Topographical features, major vegetation communities on Newhaven Wildlife Sanctuary and the location of the broad-scale sites and the focal study site. The arrows indicate the broad-scale sites where predator scats were collected.

Focal study site vegetation composition

Semi-saline spinifex sandplains are a widespread vegetation community on Newhaven, occupying 13% of the property (Latz *et al.* 2003). This community is complex with plant

species finely reflecting subtle changes in sand depth, texture and salinity. The vegetation is typically dominated by *Hakea leucoptera*, *Melaleuca glomerata* and the sub-shrub *Pluchea ferdinandi-mulleri* over hummock grass *Triodia pungens* (the stoloniferous growth form).

When the adjacent land system is sandy, *Triodia pungens* dominates with the overstory consisting of scattered *Grevillea striata*, *Templetonia egena*, *Acacia ligulata*, *Stylobasium spathulatum* and the sub-shrub daisy *Pluchea ferdinandi-mulleri* (Latz et al. 2003). If the adjacent land system is either saltbush dominated, or is a limestone ridge, the dominant spinifex becomes *Triodia salina* (Latz et al. 2003). Where the sand is deeper thickets of *Acacia jennera* with *Grevillea juncifolia* and *Stylobasium spathulatum* are common over *Triodia pungens* and shallow sands support the rare shrub *Daviesia eremaea* over *Cyperus blakei*, *Fimbristylis dichotoma* and *Eragrostis speciosa* (Latz et al. 2003).

Freshwater and semi-saline lakes are also a common feature of the property. These ephemeral waterbodies vary considerably in size, depth and salinity and are often fringed by inland tea-tree, *Melaleuca glomerata*, with the lake beds supporting either *Cyperus* species if salinity is low, or *Tecticornia* and *Halosarcia* species if salinity is high (Latz et al. 2003).

The focal study site is bordered to the north by a sand dune supporting desert oak *Allocasuarina decaisneana* over spinifex *Triodia schinzii* and to the south by a semi-saline lake (Fig. 2.4). The semi-saline spinifex sandplain continues to the east and west of the study site. A small semi-saline lake fringed by inland tea-tree is situated centrally

within the study site. Deeper sand supports *Acacia jennera* overstory in the northern and southern parts of the study site.



Fig. 2.4 The focal study site looking north to a sand dune supporting desert oak *Allocasuarina decaisneana* over spinifex *Triodia schinzii*. The soft spinifex *Triodia pungens* dominates the vegetation cover in the fore ground.

Focal study site fire history

The fire regime prevailing within the arid zone prior to European settlement was manipulated by Aboriginal people. This regime consisted of numerous, mostly small-scale fires, lit at various times throughout the year (Burrows *et al.* 2006). The results of this management created a heterogeneous landscape consisting of a variety of post-fire vegetation ages. With the movement of Aboriginal people from their traditional lands

and thus the cessation of traditional burning practices, fire patterns shifted towards infrequent, broad scale intensive fires (Latz and Paltridge 2006).

A comprehensive fire history exists for Newhaven Sanctuary where the season and extent of fire events have been recorded since 1976 (Fig. 2.5). Over the past 43 years the focal study site has been burnt twice—once during the summer of 1982–83 and again 22 years later during the summer of 2004–05 (Latz and Paltridge 2006).

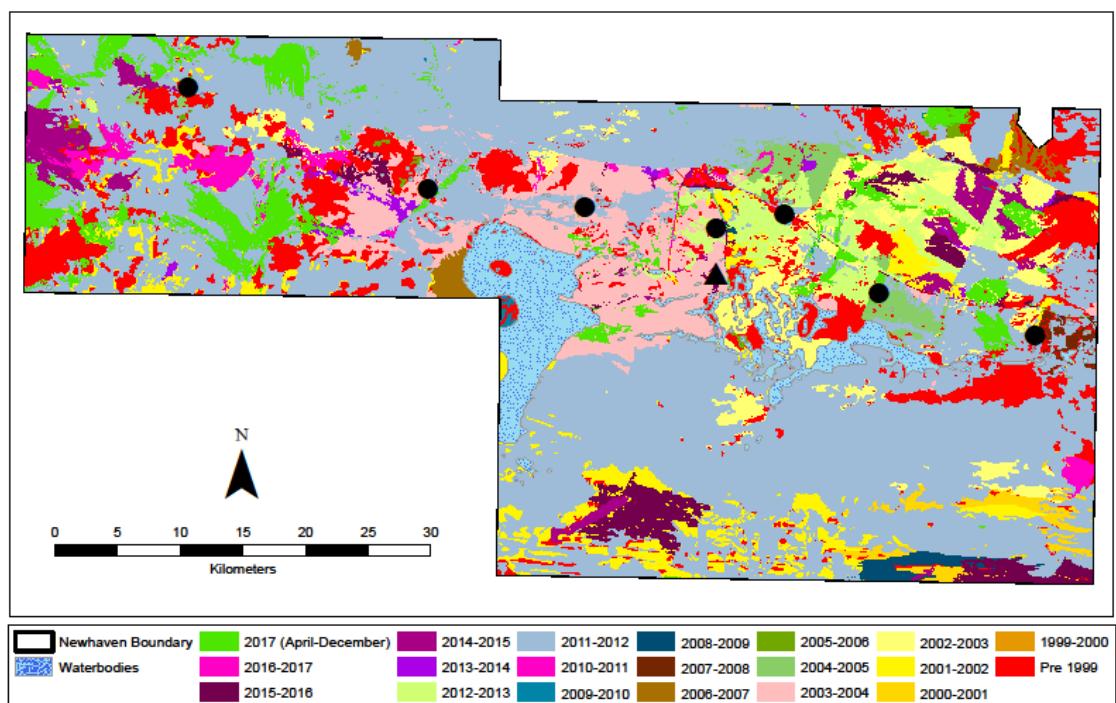


Fig. 2.5 The fire history, showing the extent of annual burns, on Newhaven Wildlife Sanctuary between 1976 and 2017. The location of the focal study site (closed triangle) and the broad-scale study sites (closed circles) are indicated (AWC 2018).

References

- Bureau of Meteorology (2017). *Climate Data Online*. Available from:
<http://www.bom.gov.au/jsp/ncc/cdio/weatherData>. [accessed January 2018].
- Burrows, N. D., Burbidge, A. A., Fuller, P. J., and Behn, G. (2006). Evidence of altered fire regimes in the Western Desert region of Australia. *Conservation Science Western Australia* **5**, 14–26.
- Latz, P., Paltridge, R., and Holmes, J. (2003). *Vegetation Survey of Newhaven Reserve (2003)*. A report prepared for Birds Australia by Desert Wildlife Services, Alice Springs.
- Latz, P., and Paltridge, R. (2006). *Fire Management Strategy for Newhaven Reserve 2006–2011*. A report prepared for Birds Australia by Desert Wildlife Services, Alice Springs.
- McAlpin, S. (2001). *A Recovery Plan for the Great Desert Skink (Egernia kintorei)*. (Arid Lands Environment Centre: Alice Springs, NT.)
- Stafford-Smith, D. M., and Morton, S. R. (1990). A framework for the ecology of arid Australia. *Journal of Arid Environments* **18**(3), 255-278.
- Young, D. N., Edgoose, C. J., Blake, D. H., and Shaw, R. D. (1995). *Mount Doreen SF 52-12 Explanatory Notes. 1:250,000 Geological Series*. (Northern Territory Geological Survey.)

CHAPTER 3

IS FIRE A THREATENING PROCESS FOR *LIOPHOLIS KINTOREI*—A NATIONALLY LISTED THREATENED SKINK?



An active *Liopholis kintorei* burrow-system where a prescribed burn was conducted
(D. Moore).

The following chapter has been published in the journal *Wildlife Research*. Publication details are: Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow A. (2015). Is fire a threatening process for *Liopholis kintorei*, a nationally listed threatened skink? *Wildlife Research* **42**(3) 207-216. <https://doi.org/10.1071/WR14227>.

Abstract

Context. Prescribed burning is widely adopted as a conservation-management tool, with priorities largely being the protection of fire-sensitive plant communities, threatened fauna habitat and minimising the risk and impacts of broad-scale wildfire. However, an improved understanding of the ecological mechanisms that underpin species responses to fire will assist the development and refinement of prescribed-burning practice.

Aims. To examine the effect of fire on burrow-system occupancy and breeding success at different spatial and temporal scales for a threatened skink, *Liopholis kintorei*.

Methods. Experimental burns simulating different fire types (clean burn, patchy burn and no burn) were conducted at 30 *L. kintorei* burrow systems that were selected from within a 75 ha focal study area. Burrow-system occupancy was monitored daily for one month, then monthly for an additional three months. Breeding success was assessed once at all 30 burrow systems. Eight additional 1-km² sites within *L. kintorei* habitat that had experienced some degree of fire two years earlier were selected from across Newhaven Wildlife Sanctuary. Burrow-system occupancy and breeding success of *L. kintorei* at these sites was assessed once.

Key Results. There was no significant effect of fire on burrow-system occupancy one month after experimental burns; however, burrow-system occupancy was significantly higher at unburnt sites four months after experimental burns and two years post-fire. Breeding success was significantly higher at unburnt sites than at clean-burnt and patchy-burnt sites.

Conclusions. Fire adversely affects *L. kintorei*, as demonstrated by a higher proportion of unoccupied burrow systems and fewer successful breeding events post-fire, particularly when all ground cover is lost.

Implications. Because fire is an inevitable and natural process within arid-zone spinifex grasslands, the primary habitat for *L. kintorei*, we recommend prescribed-burning practices that aim to maximise ground cover by reducing the frequency, intensity and size of fires. More specifically, we recommend fire exclusion from key sites within distinct localities where *L. kintorei* is known to be locally abundant. Depending on the size of these key sites, there may also be a need to construct strategic fire breaks within sites to ensure that any unwanted ignitions do not result in the loss of all vegetation cover.

Introduction

Fire has been a major influence on Australian environments from as early as the Tertiary (Kershaw *et al.* 2002; Mooney *et al.* 2012). Plants have evolved adaptations in response to fire and fire frequency shapes the distribution of plant communities that are specialised to particular fire regimes (Kershaw *et al.* 2002; Pausas and Keeley 2009; Bowman *et al.* 2012). For thousands of years before European occupation,

Aboriginal people used fire extensively to sustain interrelated cultural and political values along with sustaining resource requirements (Kimber 1983; Griffin and Friedel 1985; Payne 1991; Bowman *et al.* 2012). Traditional Aboriginal fire regimes resulted in a fine mosaic of vegetation patches at various successional stages of post-fire regeneration (Latz and Griffin 1978; Saxon 1984). European settlement of Australia has led to Aboriginal people abandoning or modifying their traditional use of fire (Latz and Griffin 1978; Kimber 1983; Griffin and Friedel 1985; Burrows *et al.* 2006). Within remote arid Australia, this cessation of landscape-scale mosaic burning has dramatically changed the seasonality, size and spacing of burnt patches (Griffin and Friedel 1985; Gill 2000). Fire regimes within unmanaged landscapes have shifted towards infrequent, severe and broad-scale wild-fire events that result in vast tracks of homogenous habitat (Latz and Griffin 1978; Saxon 1983; Griffin and Friedel 1985; Burbidge and McKenzie 1989; Morton 1990; Burrows *et al.* 2006; Edwards and Allan 2009). Depending on the amount of rainfall following a fire, vegetation cover in areas as large as 5000 km² could potentially remain low for long periods, reducing the availability and diversity of habitats and the resources they contain (Edwards and Allan 2009).

It has been suggested that the loss of medium-sized mammal species from arid and semi-arid Australia has been a consequence of these changed fire regimes, coupled with the introduction and subsequent establishment of introduced predators, namely, the feral cat and European red fox (Bolton and Latz 1978; Saxon 1983; Burbidge and McKenzie 1989; Morton 1990; Woinarski *et al.* 2014). In central Australia alone, 16 native mammal species are extinct with many other species, including

reptiles, declining in distribution and/or density (Burbidge and McKenzie 1989;

Paltridge *et al.* 1997; Environment Australia 2018; Woinarski *et al.* 2014).

It is now well established that, in arid and semi-arid Australia, the distribution and abundance of species is associated with fire history and inappropriate fire regimes are recognised as a continuing threat (Bolton and Latz 1978; Saxon 1983; Burbidge and McKenzie 1989; Morton 1990; Woinarski *et al.* 2014). The ecological effects of a fire event are influenced by a range of multi-scale processes such as climate, fire history, habitat characteristics, resource distribution, grazing history and predator pressure (Pastore *et al.* 2013). For this reason, it is often difficult to disentangle the effect of altered fire regimes from other environmental factors. Today, there is an increasing effort to investigate and understand the mechanisms that explain the effect of fire on biodiversity and how this knowledge can be applied to better achieve conservation outcomes.

The arid zone of Australia supports the world's richest reptile assemblages (Pianka 1969; Morton and James 1988). It is thought that many arid-zone lizard species are fire specialists, reaching their peak population densities only when post-fire habitats have regenerated to the required seral stage (Pianka 1992). Despite many studies supporting the habitat-accommodation model of succession, there remains uncertainty around how closely lizard species follow the expected post-fire recovery trajectory (Driscoll and Henderson 2008; Nimmo *et al.* 2012; Pianka and Goodyear 2012; Pastore *et al.* 2013). In many cases, reptiles appear to show a clear successional response to fire that is driven by vegetation succession (Masters 1996; Pianka 1996; Letnic *et al.* 2004). Fire-succession cycles generate heterogeneity in habitats, both

spatially and temporally, with each habitat being more suitable for a particular assemblage of species (Pianka 1996; Pianka and Goodyear 2012). Recent studies have also suggested that rainfall is a dominant factor driving lizard responses to fire and have shown no evidence of post-fire lizard succession, instead suggesting that a range of factors including food availability, predator pressure and grazing history all contribute to abundance and assemblages of lizard species (Pastro *et al.* 2013).

As prescribed burning becomes an increasingly important conservation land-management tool, it is imperative that land managers understand the effect of fire, and more importantly, fire type, on species persistence. Fires can vary in intensity and scale such that high-intensity fires may result in a complete burn, leaving little remaining vegetation cover, whereas lower-intensity fires may leave patches of unburnt vegetation. Whereas space-for-time studies of fire impacts are important approaches for understanding the ecological effects of fire, manipulative experimental approaches are powerful tools for more explicitly determining the causal linkages between fire and abundance (Haslem *et al.* 2011; Kelly *et al.* 2011). There have been very few manipulative experiments or broad-scale studies investigating the effects of different fire types on species persistence conducted in hummock grasslands of arid Australia (Masters 1996; Pianka *et al.* 2012).

Here we employ two approaches, namely, a manipulative field experimental approach and a ‘natural experiment’ approach, to explore the effect of fire type on a burrowing arid-zone reptile, the great desert skink, *Liopholis kintorei*. Specifically, we examine the effect of fire on burrow-system occupancy and breeding success.

Liopholis kintorei is a long-lived, obligate burrower that constructs and maintains a

complex burrow system (Chapple 2003; McAlpin *et al.* 2011). The burrow system is continuously occupied by a single family for an average of four years; however, observations have recorded a burrow system being continually occupied for 10 years (McAlpin 2011). *Liopholis kintorei* has a distribution confined to fire-prone arid environments of the western deserts of Australia. Several potential threatening processes have been identified as being the likely cause of *L. kintorei* population declines, including habitat alteration caused by changes in recent fire regimes (McAlpin 2001; Woinarski 2007). Burrow systems presumably offer protection from the direct effects of fire and, being ectothermic, reptiles are well suited to surviving without regular food. Consequently, we do not have a priori expectation on the impact of fire type on burrow occupancy or breeding success in this species.

Materials and methods

The study was conducted at Newhaven Wildlife Sanctuary in central Australia, Northern Territory (22.72°S, 131.17°E; Fig. 3.1). Experimental burns were conducted during October 2013 at 30 *L. kintorei* burrows that were selected from within a 75 ha focal study area where *L. kintorei* was known to be locally abundant. The effect of fire on *L. kintorei* occupancy was monitored daily for one month and monthly for up to four months post-fire.

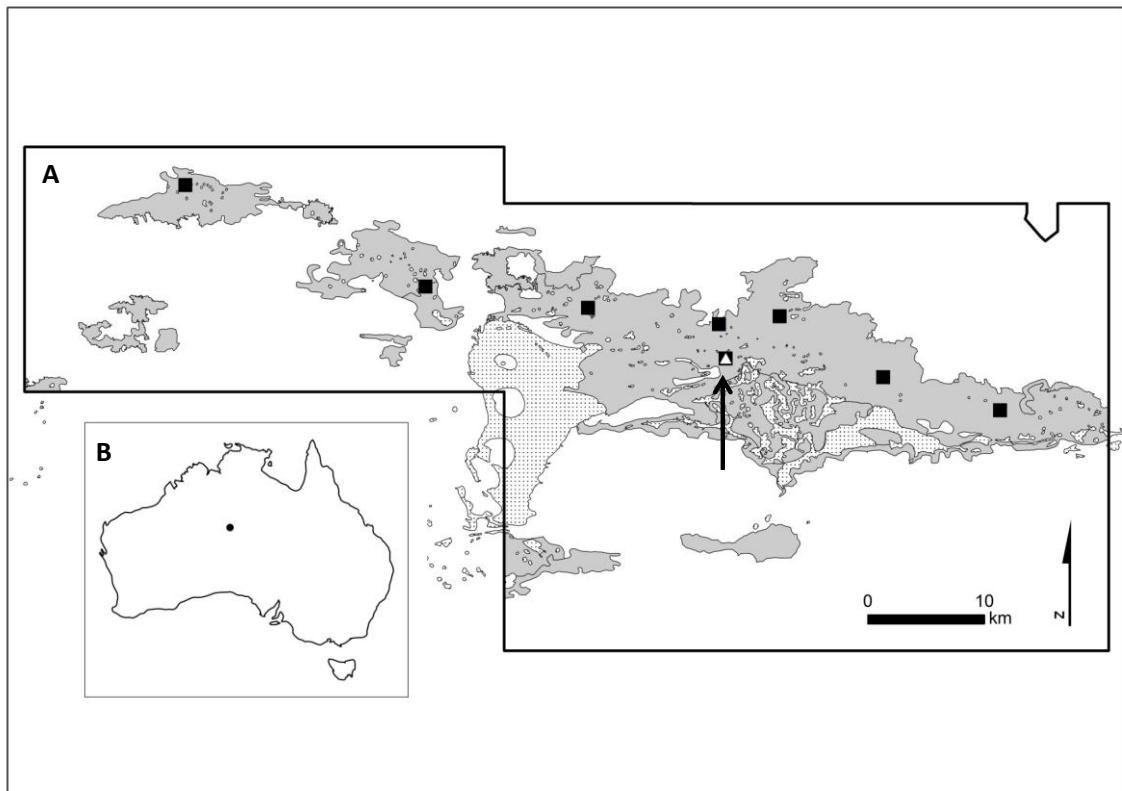


Fig. 3.1 (a) Newhaven Wildlife Sanctuary, showing the location of the eight broad-scale 1-km² sites (closed squares). The arrow indicates the location of the focal study area (open triangle). The shaded grey areas indicate potential *Liopholis kintorei* habitat and the hatched areas indicate ephemeral lakes. (b) The inset map shows the location of Newhaven Wildlife Sanctuary within Australia.

Breeding success was assessed once at the end of the summer season in early March 2014. Eight additional sites were selected where populations of *L. kintorei* had previously been recorded on Newhaven Wildlife Sanctuary. A proportion (0.05–0.95) of six of these sites had been burnt during 2011, and two remained unburnt, providing

an additional ‘natural experiment’ on the effect of fire on *L. kintorei* burrow occupancy and breeding success approximately two years post-fire.

Selecting locations for experimental burns

The 75 ha study area was systematically searched for *L. kintorei* burrow systems by walking transects spaced 10 m apart. A burrow system can contain up to 20 entrances leading into an interconnected network of tunnels (McAlpin *et al.* 2011). The coordinates of each *L. kintorei* burrow system located were recorded using a GPS. Each *L. kintorei* burrow system was assessed for current occupancy by evaluating tracks, scats within the latrine or diggings within the burrow (burrow maintenance). Each burrow system was categorised as ‘unoccupied’, where no fresh tracks, scats or burrow-maintenance activity was observed at the burrow, ‘occupied by a group of individuals’, where fresh adult and subadult tracks and/or fresh scats of different sizes within the latrine and fresh sign of burrow maintenance observed, or ‘occupied by a single individual’, where fresh tracks of only one adult or subadult skink and/or fresh scats of only one-sized individual and no burrow maintenance activity was observed.

We identified 104 *L. kintorei* burrow systems located within the focal study site. Thirty burrow systems that were categorised as being occupied by a group of individuals were chosen for the experimental burns. It was assumed that burrow systems that were occupied by a group of individuals had previously been a successful breeding burrow (McAlpin *et al.* 2011) and were more likely to remain occupied throughout the coming summer.

Experimental-burn sites

Burrow systems for each experimental-burn treatment were selected at random. A visual appraisal of the locations of treatment sites within the focal study area confirmed that particular treatments were not clustered and had a reasonably even spread. The extent of the burrow system was determined by locating every burrow entrance. Approximately 10 m was then measured from the outer-most burrow entrances to define the burn area (the experimental burn area was as large as practically possible so that a controlled prescribed burn was achieved). A cleared line ~1.5 m in width was then created around the burrow system by manually removing all of the vegetation (Fig. 3.2). This cleared line had two purposes; it would initially be used to help contain the experimental burns and then prepared to be used as a tracking surface to monitor *L. kintorei* activity.

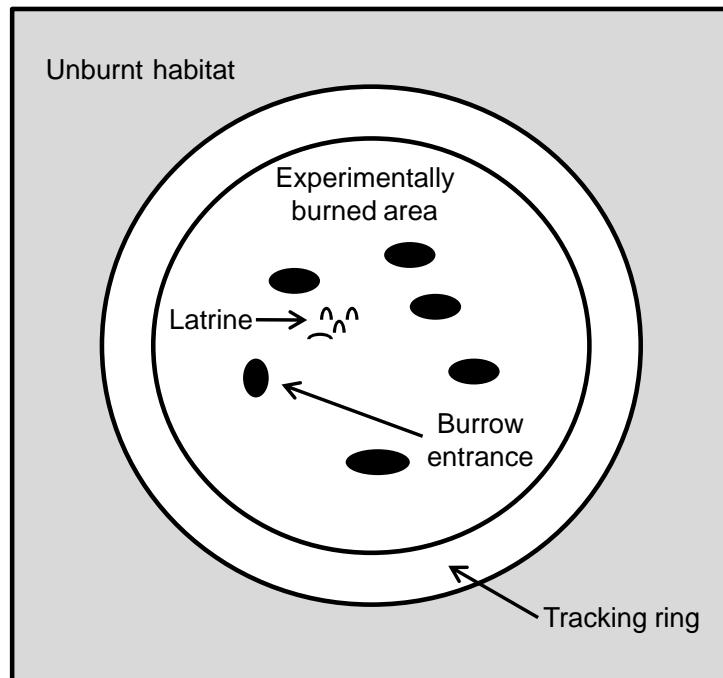


Fig. 3.2 A schematic of a *Liopholis kintorei* burrow system, the tracking ring and the experimental-burn area (not to scale).

The following three fire treatments were applied, with 10 replicates each: (1) clean burn – all ground cover over the *L. kintorei* burrow system was burnt within the experimental burn zone; (2) patchy burn – 30–40% of ground cover was left unburnt within the experimental burn zone; the vegetation covering one to two burrow entrances was burnt and the latrine remained unburnt; and (3) no burn – no experimental burn was conducted.

After the experimental burn was conducted, the tracking ring was swept to remove all tracks and prepare the surface for tracking. The experimental burns took place over a six-day period, with three to four burrow systems being burnt each day. Tracking at each burrow system began the morning of the day following the burn. A 1.5 m cleared line was also created and prepared as a tracking surface around the 10 burrow systems that would remain unburnt. As a procedural control, the fire unit used to put the experimental burns out was parked at the burrow system and water was sprayed over the burrow to simulate a level of disturbance similar to that experienced by the other burrow systems. Tracking began at all of the control sites the day following the last experimental burn.

Ground-cover assessment

The ground cover of vegetation less than 0.5 m in height that was located within the experimental burn zone was visually estimated at each of the 30 *L. kintorei* burrow systems before the experimental burns were conducted. This was achieved by dividing

each burn site into quarters, estimating the cover within each quarter and then amalgamating the data into a single estimate per site. A visual-assessment aid was used at each site; this aid provided a visual representation of various amounts of cover, ensuring that a consistent estimate was achieved among sites. A photo of each burrow system was taken before and after each experimental burn.

Recording burrow-system occupancy

Burrow occupancy was assessed daily between 0700 hours and 0900 hours, starting the morning after the experimental burn was conducted at a given burrow system. Each burrow system was assessed for *L. kintorei* occupancy on at least 24 consecutive mornings and at most 30 consecutive mornings (apart from one morning when it rained).

Burrow activity was assessed in the following three ways: (1) the perimeter of the tracking ring was walked and all *L. kintorei* tracks were recorded and, where possible, the direction of travel was determined; (2) each burrow entrance was surveyed for *L. kintorei* tracks (adult, subadult and/or juvenile), and fresh signs were recorded; and (3) the latrine was searched for the presence of fresh scats. For scats to be recorded as fresh, they needed to be black, shiny, soft and moist.

All *L. kintorei* tracks on the tracking ring and at the burrow entrances were removed daily by sweeping them away with a soft broom. A burrow system was recorded as occupied if fresh *L. kintorei* tracks were detected at a burrow entrance. A burrow system was considered unoccupied if no *L. kintorei* sign (i.e. no fresh sign) was recorded for three consecutive days. Burrow-system occupancy was assessed an

additional two times over a three-month period. Initially, one month and then again approximately four months after daily tracking had ceased.

Recording breeding success at experimental-burn sites

Liopholis kintorei is known to mate during September through to October (D. Moore, pers. obs.; McAlpin 2011), with the first juveniles being born ~10–11 weeks later, in November through to late January (McAlpin 2011). Breeding success at all 30 *L. kintorei* burrow systems was assessed in mid-March 2014. Breeding success was confirmed if juvenile scats were observed in the communal latrine. The scats of individual skinks within their first year of growth are easily identified by their size; they are ~10–20 mm in length (D. Moore, pers. obs.). Adult scats range in length, varying between 20 and 40 mm.

Broad-scale analysis of the effect of fire on burrow-system occupancy and breeding success

Eight 1-km² sites were established across Newhaven where *L. kintorei* had previously been recorded. Each site consisted of 11 transects, 500 m in length and situated at 200 m intervals, along the 2 km-wide site. GPS coordinates for either end of each of the 11 transects per site were determined using ArcMap (ArcGIS version 9.3.1, Esri, Redlands, California, USA) and navigated to in the field. The pre-defined transects were searched on foot, scanning ~5 m either side of the transect line for *L. kintorei* burrow systems. These sites were surveyed in early March 2014 over a two week period. Each burrow system we located was assessed for occupancy and all occupied burrow systems were assessed for breeding success as per the method outlined

above. Each burrow system located was also assigned a fire-type category that represented one of the three main vegetation-cover states that remained (~10 m either side the burrow system) immediately around the burrow system after the last fire event that affected the burrow systems, as follows: (1) clean burn, where all cover was removed from a single fire event within the past 2 years; (2) patchy burn, where some cover, up to 40%, had been removed from a single fire event within the past two years, or the burrow system was located within one metre of a burnt edge, or the burrow system was located within a small patch of unburnt spinifex surrounded by spinifex that had been burnt within the past two years; or (3) no burn, where no cover was removed by a fire event within the past two years.

Analysis

The unit of replication was the burrow system at all sites (experimental-burn focal study site and eight 1 km² broad-scale natural-experiment sites). We analysed the experimental burn burrow-system occupancy data by using a chi-square test to compare the deviance of logistic regression models including all treatments, compared with models with only the controls. Pearson's chi-square test (Quinn and Keough 2002) was used to examine the effect of fire type on burrow-system occupancy within the broad-scale natural experiment.

The Fisher's exact test (Quinn and Keough 2002) was used to explore the effect of fire type on breeding success. Breeding-success data from the experimental burn sites included data from burrow systems that had become unoccupied over the four-month period after experimental burns. In this case, all 30 burrow systems were

categorised as ‘occupied by a group of individuals’ and had an assumed equal chance of breeding success. In contrast, breeding-success data from the natural experiment excluded unoccupied burrow systems because we had no prior knowledge of their occupancy pre-fire.

Analysis was performed using R version 3.0.2. (R Development Core Team 2011).

Results

Ground-cover assessment of experimental-burn sites

Ground cover across all 30 burrow systems ranged from 50% to 75% before the experimental burns (Fig. 3.3, Table S3.1, available as Supplementary Material for this paper). The perennial hummock grass *Triodia pungens* was the dominant species at 22 burrow systems. The shrub *Melaleuca glomerata* was the dominant species at two burrow systems and these two species co-dominated at six burrows systems. Prior to experimental burning, there was no significant difference in vegetation cover among treatment sites (Kruskal–Wallis rank-sum test, d.f. = 2, $P = 0.67$, $\chi^2 = 0.80$). After the experimental burns were conducted there was a significant difference in ground cover when clean burn and patchy burn fire types were compared with no burn (Kruskal–Wallis rank-sum test, d.f. = 2, $P = < 0.001$, $\chi^2 = 27.24$; d.f. = 1, $P = < 0.001$, $\chi^2 = 16.44$, respectively).

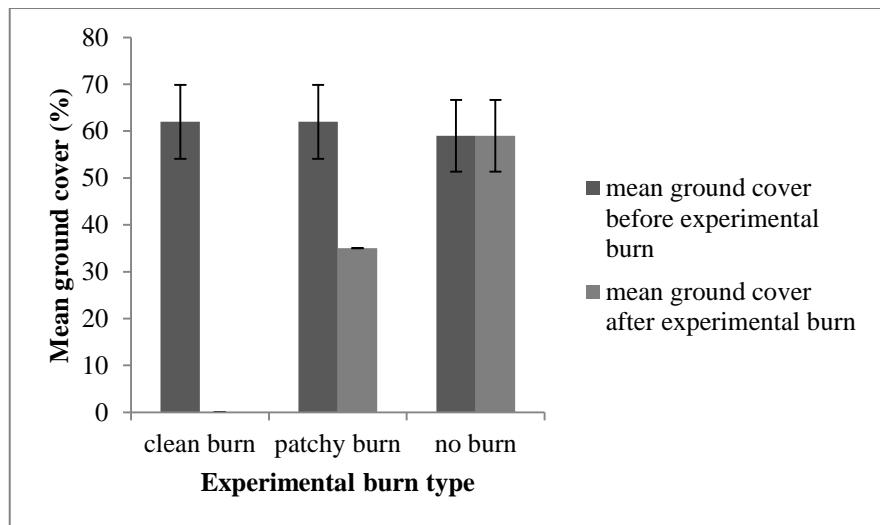


Fig. 3.3 The estimated mean ground cover at each *Liopholis kintorei* burrow system before and after experimental burns across experimental-burn type: (a) clean burn, (b) patchy burn and (c) no burn. Error bars denote standard deviations.

Burrow occupancy at experimental-burn sites

There was no effect of fire type on burrow-system occupancy one month after experimental burns; all 30 *L. kintorei* burrow systems remained occupied regardless of fire treatment (Fig. 3.4, Table S3.2). However, four months after the experimental burns, the burrow-system occupancy differed across experimental burn types. In all, 20% of burrows that were treated with a patchy burn became unoccupied and more than half of the burrow systems that were burnt clean became unoccupied. There was a significant difference in burrow-system occupancy when no-burn and clean-burn fire types were compared ($D_{df} = 2, P = 0.003$); however, there was no significant difference in burrow-system occupancy when no-burn and patchy-burn fire types were compared ($D_{df} = 1, P = 0.08$).

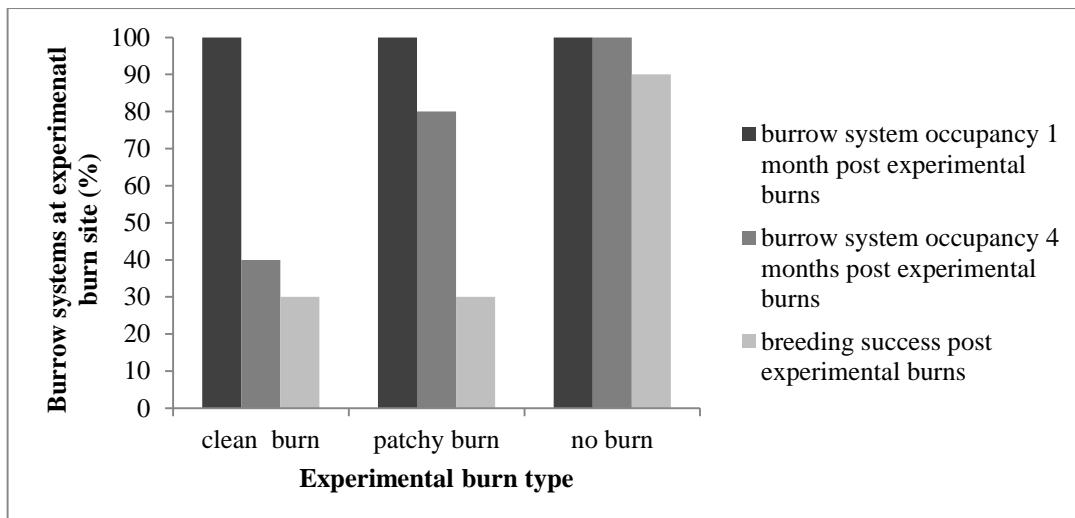


Fig. 3.4 The percentage of *Liopholis kintorei* burrow systems from the experimental-burn site that remained occupied one month and four months after the experimental burns were conducted, and the percentage of occupied and unoccupied *L. kintorei* burrow systems from the experimental-burn site where breeding success over the summer of 2013–2014 was confirmed after the experimental burns were conducted.

Breeding success at experimental-burn sites

Breeding success differed markedly between burrow systems that were not burnt and those that were treated experimentally with fire (Fig. 3.4, Table S3.3, available as Supplementary Material for this paper). In all, 90% of burrow systems that remained unburnt had evidence of breeding success, compared with only 30% that were burnt clean or in a patchy way. Breeding success was significantly higher at sites that were unburnt than at sites with the patchy-burn and clean-burn fire types ($P = 0.02$, Fisher's exact test).

Broad-scale burrow occupancy and breeding success

A total of 60 km of transect was systematically walked searching for *L. kintorei* burrow systems. In all, 114 *L. kintorei* burrow systems were recorded from eight 1-km² sites across Newhaven.

The effect of fire on burrow-system occupancy at a larger scale reflected the results that were found from the experiment. There was a significant effect of fire on burrow-system occupancy when unburnt habitat was compared with both patchy- and clean-burned habitat (Fig. 3.5, Table S3.4, available as Supplementary Material for this paper; $\chi^2 = 14.8$, d.f. = 2, $P < 0.001$). Of the 78 occupied burrow systems located, 84% were in unburnt habitat, compared with just 8% in both patchy- and clean-burn fire types. There was no difference detected in burrow-system occupancy when clean-burn and patchy-burn fire types were compared ($\chi^2 = 1.9$, d.f. = 1, $P = 0.2$).

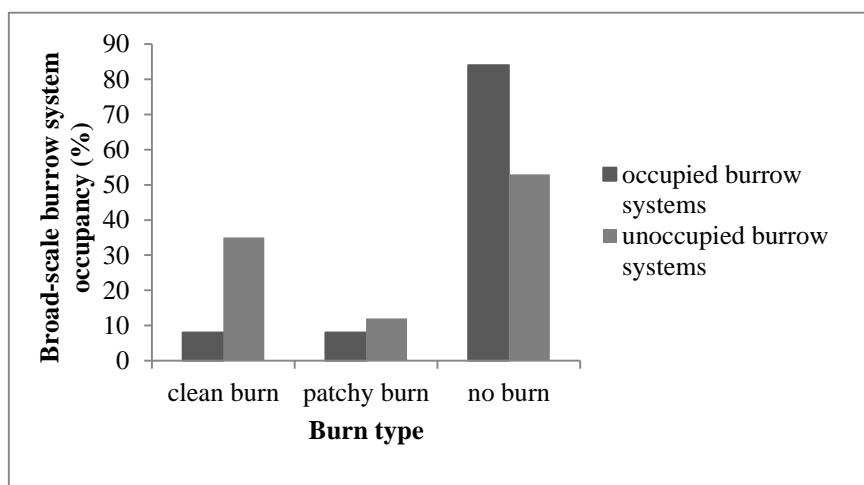


Fig. 3.5 The percentage occurrence of occupied and unoccupied *Liopholis kintorei* burrow systems across burn type two years after fire.

Our broad-scale survey of breeding success across burn types showed a pattern similar to that in the manipulative field experiment, with disproportionately higher breeding success in the unburnt sites (Fig. 3.6, Table S4; $P = 0.02$, Fisher's exact test). No occupied burrow systems within clean-burned habitat had successful breeding evidence. In all, 67% and 56% of occupied burrows systems had evidence of breeding within patchy-burned habitat and unburnt habitat, respectively. In contrast to the manipulative field experiment, there was no effect of fire on breeding success when patchy burn was compared with no-burn fire type.

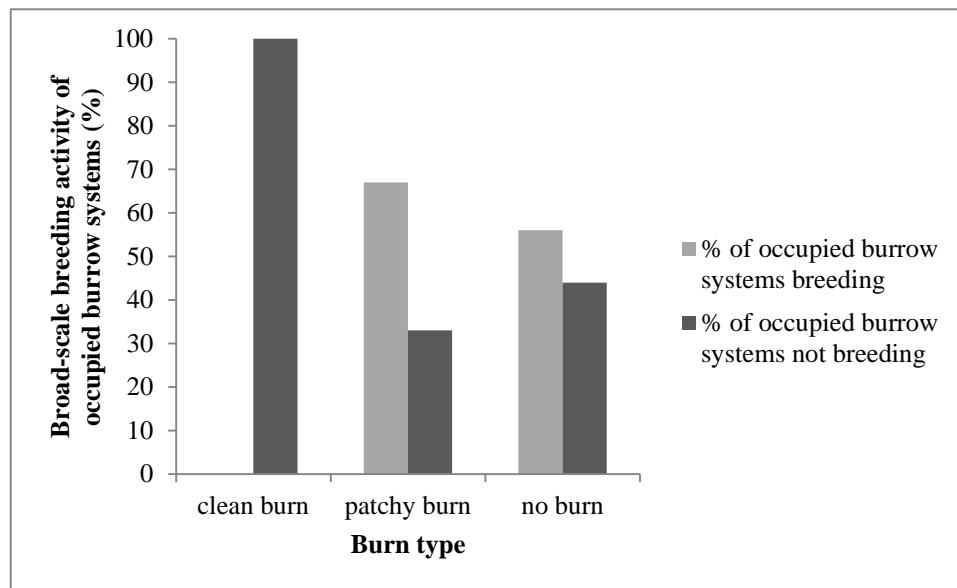


Fig. 3.6 The percentage of burrow systems that were occupied where breeding success during the summer of 2013–2014 was detected across burn type two years after fire.

Discussion

Our study uniquely employed two approaches, namely, a manipulative field-experimental approach and an examination of a naturally occurring situation, to

explore the effect of fire type on burrow-system occupancy and breeding success of an endangered arid-zone skink *L. kintorei*. The manipulative field experiment allowed us to investigate more closely how fire may be influencing the observed patterns of burrow-system occupancy within the broader landscape.

Our broad-scale burrow-system survey indicated that burrow-system occupancy and breeding success were highest within unburnt habitat. This pattern was also reflected in the manipulative field experiment. The results of our manipulative field experiment showed that fire type had no immediate or short-term effect on *L. kintorei* burrow-system occupancy. All 20 burrow systems treated with fire remained occupied for at least one month after the experimental burns were conducted and breeding success was detected at six of these burrow systems four months after experimental burns. This result suggests that the effect of fire is not an immediately direct one owing to burn injury or voluntary migration from the area. Instead, over a period of four months or more, the presence of a burn and the type of burn significantly influenced burrow-system occupancy, with occupancy being at its lowest at sites that had been clean burned.

Although the effect of fire on burrow-system occupancy was lessened by patchy burns in the manipulative field experiment, it is important to note that the experiments produced very little variability in the level of ground cover remaining (30–40%) immediately around the burrow system and, in all cases, these burns occurred within unburnt habitat. However, broader-scale fires will introduce substantially more variability. This is reflected by our broad-scale survey where the impact of patchy burns ranged from the majority of ground cover being removed from an extensive

area around some burrow systems, to others remaining more-or-less unburnt. The varying degree and the spatial nature of the ground cover remaining after a fire event may greatly influence burrow-system occupancy and breeding success. Therefore, it is critical to consider the ecological significance of the ‘patchiness’ of ground cover remaining within *L. kintorei* habitat after a fire.

Our observations of breeding success varied between the manipulative field experiment and the broad-scale survey. The broad-scale survey indicated that the breeding success at occupied burrow systems was similar between patchy burn and unburnt habitat. In contrast, the manipulative field experiment indicated that breeding success at occupied burrow systems was similar between a patchy-burn and clean-burn habitat. However, in both cases, the greatest number of burrow systems where breeding success was detected was in unburnt habitat. Breeding success can be reduced significantly at several burrow systems by very few successful predation attempts. For example, male *L. kintorei* are known to be polygamous, fathering offspring of different females residing within several different burrow systems within close proximity (McAlpin *et al.* 2011). During the mating season, male skinks move from burrow system to burrow system in search of females to mate with. Over this period, male skinks are already at a greater risk of predation, with this risk increasing further within habitats that afford no ground cover for shelter. The loss of just one male to predation may have a large impact on the breeding success of numerous burrow systems.

Numerous factors resulting from the effects of fire may be interacting over time to influence burrow-system occupancy and breeding success of *L. kintorei*. Such

factors may include temperature-based activity restriction from fire-induced changes to the vegetation structure, a decrease in food availability, and an increased risk of predation caused by the removal of vegetation cover. We now consider each of these possibilities in turn.

Temperature-based activity restriction

Being ectotherms, lizards are ultimately restricted in their use of their environment by their thermoregulatory requirements. For many reptile species, thermoregulation is achieved by exploiting temperature differences available within a habitat, such as those produced by shade from vegetation or burrows (Cowles and Bogert 1994). Shade availability will become increasingly critical within the warmer regions of Australia for the survival of diurnal ectotherms (Kearney 2009 *et al.*; Kearney 2013).

Liopholis kintorei is mostly nocturnal; therefore, it does not rely on shade to thermoregulate, because it is less likely to encounter stressfully high body temperatures during its normal activity periods at night. It constructs deep (up to 800 mm), complex burrow systems that offer a broad gradient of thermal conditions (D. Moore, unpubl. data). It uses its burrow system during the day and night to attain its thermoregulation requirements. Although it is unknown how the removal of vegetation cover by fire, and, therefore, shade, affects the thermal conditions available within a *L. kintorei* burrow system, we suggest that given the depth and humidity of the burrow system, the required thermal conditions would remain available regardless of the extent of ground-cover loss after a fire event. The results of our manipulative experiment confirmed that *L. kintorei* is indeed able to persist at its

burrow system after fire and does not disperse into unburnt habitats because all 20 burrow systems treated with experimental burns remained occupied for at least one month.

A decrease in food resource availability

Limited data exist on the distribution and abundance of arid-zone invertebrates and the factors that may be influencing this are largely unknown (Langlands *et al.* 2006); however, there are a few notable exceptions. A study conducted by Letnic *et al.* (2004) within the Simpson Desert of Australia showed that termite biomass was greatest at recently burned (<1 year) sites and there was no significant difference in arthropod and ant biomass at sites of differing post-fire regeneration age; however, the biomass of many arthropods was correlated with rainfall. A long-term study within the Great Victoria Desert of Australia focusing on spiders also reported that rainfall appeared to be the dominant driving force behind spider species richness, assemblages and abundance (Langlands *et al.* 2006).

The feeding behaviour and diet of *L. kintorei* varies depending on food availability. *Liopholis kintorei* is known to both forage away from its burrow (observed up to 150 m) in search of food and also opportunistically ambush potential prey from the burrow entrance (McAlpin 2011). The species is omnivorous, feeding predominantly on harvester termites of the genus *Drepanotermes* (McAlpin 2011). Termites have evolved with strategies that enable them to persist during periods when food availability is scarce, such as, during times of drought or after fire.

Drepanotermes termites harvest large quantities of plant material to obtain cellulose

during favourable periods, which are then utilised during periods of food shortages (Anderson 2005). Harvester termites of the genus *Drepanotermes* are common within *L. kintorei* habitat at Newhaven (D. Moore, pers. obs.) and the post-fire survival strategies of these termites are likely to ensure a secure, protein-rich diet for *L. kintorei*, irrespective of habitat or environmental conditions. Consequently, burrow occupancy and breeding success are unlikely to be influenced by fire because of a decrease in food resource availability.

An increased risk of predation caused by the removal of cover

Numerous native and introduced species, including brush-tailed mulgara (*Dasyurus blythii*), sand goanna (*Varanus gouldii*), woma python (*Aspidites ramsayi*), dingo (*Canis dingo*), feral cat (*Felis catus*), and European red fox (*Vulpes vulpes*), have been identified as being potential predators of *L. kintorei* (McAlpin 2001, 2011). Limited data exists confirming these species as predators or on the extent of the possible predation impact caused by these species.

The success of predators may be influenced by the removal of vegetation cover through fire. It has been suggested that processes threatening small mammals within arid Australia may be acute following periods of high rainfall when the risk of broad-scale wildlife (hence, broad-scale removal of vegetation cover) is greatest and predators are abundant (Paltridge 2002; Letnic *et al.* 2005; Letnic and Dickman 2006). For example, a study conducted by Körtner *et al.* (2007) in central Australia on the brush-tailed mulgara, a small carnivorous marsupial that occupies a small home range, identified that this species typically survives a fire event by sheltering within its

burrow and then persisting within regenerating habitat. However, subsequent population declines were observed and were attributed to introduced predators within the recently burnt habitat. In this case, the fire event did not directly drive the observed population decline; however, the indirect impact of fire, i.e. reduced vegetation cover, presumably increased the risk of predation by introduced predators. With the removal of vegetation cover predation risk is likely to increase because prey items are more exposed. Such processes have been shown to be as threatening for reptiles as they are for small mammals (Fenner and Bull 2007; Webb and Shine 2008; Gorissen *et al.* 2014). A study conducted by Fenner and Bull (2007) on the effect of fire on the endangered pygmy bluetongue, *Tiliqua adelaidensis*, confirmed that although no adult lizards were directly killed by the fire, there was a significant reduction in activity and foraging behaviour when compared with lizards at an unburnt site. It was concluded that lizards may perceive a greater threat from exposure in a habitat where no vegetation cover remains. Similarly, a 16-year-long mark–recapture study investigating the effect of wildfire on the survival of two sympatric snakes showed that the difference in foraging mode between the two snakes may have attributed to the detected difference in survival rates. Wildfire did not affect the survival of the species that ambushed their prey and spent long periods within retreat sites, whereas the snake species that actively foraged on the ground experienced significant declines in survival. This higher foraging activity within a post-fire open burnt habitat may have increased the vulnerability to avian predation (Webb and Shine 2008).

Although the complexity of a *L. kintorei* burrow system and the size of each burrow opening provide a degree of protection from predators, the removal of ground

cover within their habitat may leave *L. kintorei* susceptible to greater predation pressure when foraging widely, basking, when subadults are dispersing or when adult males are searching for adult females during the breeding season.

Feral cats have recently been identified as being a significant predator of *L. kintorei* within spinifex grasslands (Moore *et al.* 2017). A recent study looking at the hunting ecology of feral cats showed that 26% of hunting events in which prey were in a grass tussock or a rocky refuge were successful, whereas in open areas, the kill rate increased significantly to 84% (McGregor 2014). Feral cats may also have the ability to become specialist predators, learning to hunt particular prey effectively. For example, two separate mala (*Lagorchestes hirsutus*), reintroduction programs that were attempted in the late 1980s and early 1990s within Tanami desert of Australia failed because of cats (Gibson 1994). It was suspected that individual large feral cats learnt how to hunt mala effectively and then specialised on killing them until the small populations became extinct (Johnson 2006). As *L. kintorei* exhibits strong burrow fidelity and burrows are often tightly clustered within the landscape, it is plausible that individual feral cats may become familiar with the locations of occupied *L. kintorei* burrow systems and focus their hunting efforts at these locations, becoming, over time, specialist hunters of *L. kintorei*. This hunting efficiency may also be influenced by recent fire events whereby feral cats focus on burrow systems within open burnt habitats.

Conclusions

The present study has demonstrated that *L. kintorei* is adversely affected by fire within spinifex grasslands, and this is most likely due to an indirect impact on predation levels. The increased effectiveness of hunting by mammalian predators at occupied burrow systems within open burnt habitat following a fire is likely to be a key threatening process for this species. Fire is an inevitable and natural process within arid-zone spinifex grasslands. Within unmanaged fire-prone landscapes, fire events are characterised as broad-scale and intense. Such events are often associated with above-average rainfall periods that support elevated predator populations. Therefore, we recommend prescribed-burning practices that aim to maximise ground cover within *L. kintorei* habitat by reducing the frequency, intensity and size of fires. More specifically, we recommend fire exclusion from key sites within distinct localities where *L. kintorei* is known to be locally abundant. Depending on the size of these key sites, there may also be the need to implement a fire risk-management strategy within sites, such as fire breaks, to ensure that any unwanted ignitions do not result in the loss of all vegetation cover. This management recommendation aims to reduce the incidence of ground-cover loss caused by fire within key sites, while maintaining suitable habitat over more extensive areas.

As the use of fire becomes more widely adopted as a conservation land-management tool, understanding the ecological mechanisms that underpin species declines is critical for the development and refinement of appropriate prescribed-burning practices (Allan and Southgate 2002; Greenville *et al.* 2009; Driscoll *et al.*

2010; Murphy *et al.* 2010; Woinarski 2014). Although autecological studies focusing on fire-related conservation issues provide specific information for targeted fire management (Woinarski 1999, 2014), they remain rare within the fire-ecology field. Our results highlighted the value of manipulative field research in exploring plausible mechanisms behind threatening processes and support the need for further research on the effect of burning practices on endangered species in arid Australia.

References

- Allan, G. E., and Southgate, R. I. (2002). Fire regimes in the spinifex landscapes of Australia. In 'Flammable Australia: The Fire Regimes and Biodiversity of a Continent'. (Eds R. A. Bradstock, J. E. Williams and A. M. Gill.) pp. 145–176. (Cambridge University Press: Cambridge, UK.)
- Andersen, A. N. (2005). 'Termites of Northern Australia.' (Barker Souvenirs: Alice Springs, NT.)
- Bolton, B. L., and Latz, P. K. (1978). The western hare-wallaby *Lagorchestes hirsutus* (Gould) (Macropodidae), in the Tanami Desert. *Wildlife Research* **5**, 285–293.
doi:10.1071/WR9780285.
- Bowman, D., Murphy, B. P., Burrows, G. E., and Crisp, M. D. (2012). Fire regimes and the evolution of the Australian biota. In 'Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World'. (Eds R. Bradstock, R. Williams and A. Gill.) pp. 3–25. (CSIRO Publishing: Melbourne.)

Burbidge, A. A., and McKenzie, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**, 143–198. doi:10.1016/0006-3207(89)90009-8.

Burrows, N. D., Burbidge, A. A., Fuller, P. J., and Behn, G. (2006). Evidence of altered fire regimes in the Western Desert region of Australia. *Conservation Science Western Australia* **5**, 14–26.

Chapple, D. G. (2003). Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monograph* **17**, 145–180. doi:10.1655/0733-1347(2003)017[0145:ELABIT]2.0.CO;2.

Cowles, R. B., and Bogert, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* **83**, 263–296.

Driscoll, D. A., and Henderson, M. K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* **141**, 460–471. doi:10.1016/j.biocon.2007.10.016.

Driscoll, D. A., Lindenmayer, D. B., Bennett, A. F., Bode, M., Bradstock, R. A., Cary, G. J., Clarke, M. F., Dexter, N., Fensham, R., and Friend, G. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* **143**, 1928–1939. doi:10.1016/j.biocon.2010.05.026.

Edwards, G. P., and Allan, G. E. (2009). Desert Fire: fire and regional land management in the arid landscape of Australia. Desert Knowledge CRC Report No. 37. (Desert Knowledge Cooperative Research Centre: Alice Springs, NT.)

Environment Australia (2018). 'EPBC Act List of Threatened Fauna.' Available at <http://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=fauna>. [Accessed 25 November 2018]

Fenner, A. L., and Bull, C. M. (2007). Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *Journal of Zoology* **272**, 444–450.
doi:10.1111/j.1469-7998.2007.00287.x.

Gibson, D. (1994). Predation by feral cats, *Felis catus*, on the rofous hare-wallaby, *Lagorchestes hirsutus*, in the Tanami Desert. *Australian Mammalogy* **17**, 5.

Gill, A. M. (2000). 'Fire-pulses in the Heart of Australia: Fire Regimes and Fire Management in Central Australia.' CSIRO Centre for Plant Biodiversity Research. (Environment: Canberra.)

Gorissen, S., Mallinson, J., Greenlees, M., and Shine, R. (2014). The impact of fire regimes on populations of an endangered lizard in montane south-eastern Australia. *Austral Ecology*. doi:10.1111/aec.12190.

Greenville, A. C., Dickman, C. R., Wardle, G. M., and Letnic, M. (2009). The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. *International Journal of Wildland Fire* **18**, 631–639. doi:10.1071/WF08093.

- Griffin, G. F., and Friedel, M. H. (1985). Discontinuous change in central Australia: some implications of major ecological events for land management. *Journal of Arid Environments* **9**, 63–80.
- Haslem, A., Kelly, L. T., Nimmo, D. G., Watson, S. J., Kenny, S. A., Taylor, R. S., Avitabile, S. C., Callister, K. E., Spence-Bailey, L. M., and Clarke, M. F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* **48**, 247–256. doi:10.1111/j.1365-2664.2010.01906.x.
- Johnson, C. (2006). ‘Australia’s Mammal Extinctions: a 50 000 Year History.’ (Cambridge University Press: Cambridge, UK.)
- Kearney, M. R. (2013). Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters* **16**, 1470–1479. doi:10.1111/ele.12192.
- Kearney, M., Shine, R., and Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer ‘cold-blooded’ animals against climate warming. *Proceedings of the National Academy of Sciences, USA* **106**, 3835–3840. doi:10.1073/pnas.0808913106.
- Kelly, L. T., Nimmo, D. G., Spence-Bailey, L. M., Haslem, A., Watson, S. J., Clarke, M. F., and Bennett, A. F. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity & Distributions* **17**, 462–473. doi:10.1111/j.1472-4642.2011.00754.x.
- Kershaw, A. P., Clark, J. S., Gill, A. M., and D’Costa, D. M. (2002). A history of fire in Australia. In ‘Flammable Australia: the Fire Regimes and Biodiversity of a Continent’.

(Eds R. A. Bradstock, J. E. Williams and A. M. Gill.) pp. 3–25. (Cambridge University Press: Cambridge, UK.)

Kimber, R. (1983). Black lightning: Aborigines and fire in central Australia and the Western Desert. *Archaeology in Oceania* **18**, 38–45.

Körtner, G., Pavey, C. R., and Geiser, F. (2007). Spatial ecology of the mulgara in arid Australia: impact of fire history on home range size and burrow use. *Journal of Zoology* **273**, 350–357. doi:10.1111/j.1469-7998.2007.00334.x.

Langlands, P. R., Brennan, K. E. C., and Pearson, D. J. (2006). Spiders, spinifex, rainfall and fire: long-term changes in an arid spider assemblage. *Journal of Arid Environments* **67**, 36–59. doi:10.1016/j.jaridenv.2006.01.018.

Latz, P. K., and Griffin, G. F. (1978). Changes in Aboriginal land management in relation to fire and food plants in central Australia. In 'The Nutrition of Aborigines in Relation to the Ecosystems of Central Australia'. (Eds B. S. Hetzel and H. J. Frith.) pp. 77–85. (CSIRO: Melbourne.)

Letnic, M., and Dickman, C. R. (2006). Boom means bust: interactions between the El Niño/southern oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation* **15**, 3847–3880. doi:10.1007/s10531-005-0601-2.

Letnic, M., Dickman, C. R., Tischler, M. K., Tamayo, B., and Beh, C. L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* **59**, 85–114. doi:10.1016/j.jaridenv.2004.01.014.

- Letnic, M., Tamayo, B., and Dickman, C. R. (2005). The responses of mammals to La Nina (El Nino southern oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy* **86**, 689–703. doi:10.1644/1545-1542(2005)086[0689:TROMTL]2.0.CO;2.
- Masters, P. (1996). The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildlife Research* **23**, 39–47. doi:10.1071/WR9960039.
- McAlpin, S. (2001). 'A Recovery Plan for the Great Desert Skink (*Egernia kintorei*).' (Arid Lands Environment Centre: Alice Springs, NT.)
- McAlpin, S. (2011). Social structure and mating systems of the great desert skink, *Liopholis kintorei*. M.Sc. Thesis. (Macquarie University: Sydney.)
- McAlpin, S., Duckett, P., and Stow, A. (2011). Lizards cooperatively tunnel to construct a long-term home for family members. *PLoS ONE* **6**, e19041. doi:10.1371/journal.pone.0019041.
- McGregor, H. (2014). Density, movements and hunting of feral cats in relation to fire and grazing in northern Australia. Ph.D. Thesis. (University of Tasmania: Hobart.)
- Mooney, S. D., Harrison, S. P., Bartlein, P. J., and Stevenson, J. (2012). The prehistory of fire in Australia. In 'Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World'. (Eds R. Bradstock, R. Williams and A. Gill.) pp. 3–25. (CSIRO: Melbourne.)

- Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. (2017). Feeling the pressure at home: predator activity at the burrow entrance of an endangered arid-zone skink. *Austral Ecology*. doi: 10.1111/aec.12547.
- Morton, S. R. (1990). The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. In 'Proceedings of the Ecological Society of Australia'. pp. 201–213. (CSIRO: Melbourne.)
- Morton, S. R., and James, C. D. (1988). The diversity and abundance of lizards in arid Australia: a new hypothesis. *American Naturalist* **132**, 237–256.
doi:10.1086/284847.
- Murphy, S. A., Legge, S. M., Heathcote, J., and Mulder, E. (2010). The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). *Wildlife Research* **37**, 145–155.
doi:10.1071/WR09007.
- Nimmo, D., Kelly, L. T., Spence-Bailey, L. M., Watson, S. J., Haslem, A., White, J. G., Clarke, M. F., and Bennett, A. F. (2012). Predicting the century-long post-fire responses of reptiles. *Global Ecology and Biogeography* **21**, 1062–1073.
doi:10.1111/j.1466-8238.2011.00747.x.
- Paltridge, R. (2002). The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* **29**, 389–403.
doi:10.1071/WR00010.
- Paltridge, R., Gibson, D., and Edwards, G. (1997). Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research* **24**, 67–76. doi:10.1071/WR96023.

- Pastro, L. A., Dickman, C. R., and Letnic, M. (2013). Effects of wildfire, rainfall and region on desert lizard assemblages: the importance of multi-scale processes. *Oecologia* **173**, 603–614. doi:10.1007/s00442-013-2642-7.
- Pausas, J. G., and Keeley, J. E. (2009). A burning story: the role of fire in the history of life. *Bioscience* **59**, 593–601. doi:10.1525/bio.2009.59.7.10
- Payne, S. J. (1991). ‘Burning Bush: a fire History of Australia.’ (University of Washington Press: Seattle, WA.)
- Pianka, E. R. (1969). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* **50**, 498–502. doi:10.2307/1933908.
- Pianka, E. (1992). Disturbance, spatial heterogeneity, and biotic diversity: fire succession in arid Australia. *Research & Exploration* **8**, 352–371.
- Pianka, E. R. (1996). Long-term changes in lizard assemblages in the Great Victoria Desert. In ‘Long-term Studies of Vertebrate Communities’. (Eds M. L. Cody and J. A. Smallwood.) pp. 191–215. (Academic Press: New York.)
- Pianka, E. R., and Goodyear, S. E. (2012). Lizard responses to wildfire in arid interior Australia: Long-term experimental data and commonalities with other studies. *Austral Ecology* **37**, 1–11. doi:10.1111/j.1442-9993.2010.02234.x.
- Quinn, G. P., and Keough, M. J. (2002). ‘Experimental Design and Data Analysis for Biologists.’ (Cambridge University Press: Cambridge, UK.)

R Development Core Team (2011). 'R: a Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna.) Available at <http://www.R-project.org/>. [Accessed 21st January 2014]

Saxon, E. C. (1983). Mapping the habitats of rare animals in the Tanami wildlife sanctuary (central Australia): an application of satellite imagery. *Biological Conservation* **27**, 243–257. doi:10.1016/0006-3207(83)90021-6.

Saxon, E. C. (1984). Anticipating the inevitable: a patch-burn strategy for fire management at Uluru (Ayers Rock–Mt Olga) National Park. CSIOR Division of Wildlife and Rangelands Research (CSIRO: Alice Springs, NT.)

Webb, J. K., and Shine, R. (2008). Differential effects of an intense wildfire on survival of sympatric snakes. *The Journal of Wildlife Management* **72**, 1394–1398. doi:10.2193/2007-515.

Woinarski, J. C. Z. (1999). Fire and Australian birds: a review. In 'Australia's Biodiversity – Responses to Fire: Plants, Birds and Invertebrates'. (Eds J. C. Z. Woinarski, A. York and A. M. Gill.) pp. 55–180. (Environment Australia: Canberra.)

Woinarski, J. C. Z. (2007). 'Lost from our Landscape: Threatened Species of the Northern Territory.' (Department of Natural Resources, Environment and The Arts: Palmerston, NT.)

Woinarski, J. C. Z. (2014). Critical-weight-range marsupials in northern Australia are declining: a commentary on Fisher *et al.* (2014). 'The current decline of tropical marsupials in Australia: is history repeating?' *Global Ecology and Biogeography* **24**, 118–122. doi:10.1111/geb.12165.

Woinarski, J., Burbidge, A., and Harrison, P. (2014). 'Action Plan for Australian Mammals 2012.' (CSIRO Publishing: Melbourne.)

Supplementary material

Table S3.1 The estimated mean ground cover at each *Liopholis kintorei* burrow system before and after experimental burns across experimental burn type
: a. clean burn; b. patchy burn, and; c. no burn.

Treatment	Mean ground cover before experimental burns (%)	Mean ground cover after experimental burns (%)
Clean burn	62	0
Patchy burn	62	35
No burn	59	59

Table S3.2 The number of *Liopholis kintorei* burrow systems that were sampled under different fire treatments (*n*) and the percentage of *Liopholis kintorei* burrow systems that remained occupied at least one month and four months post experimental burns.

Treatment	<i>n</i>	Occupancy one month post experimental burn (%)	Occupancy four months post experimental burn (%)
Clean burn	10	100	40
Patchy burn	10	100	80
No burn	10	100	100

Table S3.3 The percentage of occupied and unoccupied *Liopholis kintorei* burrow systems from the experimental burn site where breeding success over the summer of 2013/2014 was confirmed after the experimental burns were conducted.

Treatment	<i>n</i>	Breeding activity
		(%)
Clean burn	10	30
Patchy burn	10	30
No burn	10	90

Table S3.4 The number (*n*) and percentage occurrence of occupied and unoccupied *Liopholis kintorei* burrow systems across burn type two years after fire and the percentage of occupied burrow systems where breeding success during the summer of 2013/2014 was detected.

Burn category	<i>n</i>	Occupied (%)	Unoccupied (%)	Breeding success confirmed at occupied burrow systems (%)
Clean burn	18	8	35	0
Patchy burn	10	8	12	67
No burn	75	84	53	56

CHAPTER 4

FEELING THE PRESSURE AT HOME: PREDATOR ACTIVITY AT THE BURROW SYSTEM ENTRANCE OF AN ENDANGERED ARID ZONE SKINK



Fresh feral cat tracks at an entrance of a *Liopholis kintorei* burrow-system (D. Moore).

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Abstract

Habitat modification and invasive species are among the most important contemporary drivers of biodiversity loss. These two threatening processes are often studied independently and few studies have focused on how they interact to influence species declines. Here we assess the predation pressure placed on the threatened great desert skink (*Liopholis kintorei*) and how this interacts with fire-induced habitat modifications. We collected daily track data of potential predators for one month at 30 great desert skink burrow-systems where vegetation cover varied significantly after experimental burns. We used these data to evaluate potential predation pressure at the burrow-system and assess whether fire influenced predator pressure. We supplemented this analysis by documenting predation via the inspection of large mammalian predator scats collected from great desert skink habitat. The level of feral cat activity at burrow-system entrances was significantly higher than that of any other potential predator, however fire had no effect on the visitation rates of feral cats, dingoes or large snakes to great desert skink burrow-systems. The remains of great desert skink were found significantly more frequently in feral cat scats, compared to fox and dingo scats. We provide the first direct evidence that feral cats are a significant predator for great desert skink, thus supporting the hypothesis that feral cat predation is a key threatening process. Feral cat activity was not influenced by small-scale

experimental burns; however, this does not preclude an effect of larger scale fires and we recommend further research exploring this possible interaction.

Introduction

Habitat modification and invasive species are the most important contemporary drivers of biodiversity loss (Purvis *et al.* 2000; Didham *et al.* 2007; Fisher and Lindenmayer 2007; Brook *et al.* 2008; Doherty *et al.* 2015). However, these two threatening processes are often studied independently rather than as drivers that interact synergistically; few studies have focused on their possible interactions, and indirect effects on species declines that may occur as a result of these interactions (Hobbs 2001; Didham *et al.* 2005; Didham *et al.* 2007; Brook *et al.* 2008; Chalfoun and Martin 2009; Conner *et al.* 2011; McGregor *et al.* 2014; Hradsky *et al.* 2017).

Predator-prey relationships are likely to be strongly influenced by the interaction between habitat modification and invasive species. Variability in vegetation structure influences the outcome of predator-prey interactions because predation risk and hunting success can be affected by attributes of the habitat occupied by both predator and prey (Moreno *et al.* 1996; Janssen *et al.* 2007; Chalfoun *et al.* 2009; Conner *et al.* 2011; McDonald *et al.* 2016; Hradsky *et al.* 2017). For example, an experiment investigating the short-term effects of a prescribed fire on the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) and their native mammalian prey in south-eastern Australia found that under pre-fire conditions invasive predators were more likely to occur at sites with an open understory, whereas most small- and medium-sized native mammals were positively associated with understory cover. Fire reduced understory cover by more than 80%, and resulted in a five-fold increase in the

occurrence of invasive predators and the relative consumption of medium-sized native mammals by foxes doubled (Hradsky *et al.* 2017). Many invasive species take opportunistic advantage of habitat modification and therefore increase their overall impact within these habitats (Didham *et al.* 2005; Janssen *et al.* 2007; McDonald *et al.* 2016; McGregor *et al.* 2014; Hradsky *et al.* 2017). In many cases structurally complex habitats have been shown to decrease predation risk by providing refuges or shelter for prey, reducing encounter rates between predator and prey, hindering foraging activity of predators and reducing predator kill rate success (Fischer and Lindenmayer 2007; Janssen *et al.* 2007; Robinson *et al.* 2013; McGregor *et al.* 2014; Hradsky *et al.* 2017). A study conducted in northern Australia by McGregor *et al.* (2014) on the interactive effects between habitat modification and potential predator pressure found that modifications of habitat produced by grazing, and particular fire types, have strong effects on feral cat movement behaviour. Specifically, they showed that feral cats selected areas with low grass cover and that severe fires and grazing created habitat conditions that are favoured by feral cats, increasing predator pressure on prey species.

In recent history, Australia has suffered the greatest loss of native vertebrate species of any continent (Johnson 2006). Diagnosing possible threatening processes associated with native species population declines, and understanding the underlying mechanisms and interactive effects driving these declines, is critical to the delivery of appropriate and effective conservation management (Hobbs 2001; Norris 2004; Didham *et al.* 2007; Brook *et al.* 2008). In Australia, predation by introduced mammalian predators and habitat loss and/or modification are widely considered to be the key threats contributing to this

significant national loss of species (Gibbons *et al.* 2000; Johnson 2006; Woinarski *et al.* 2007; Wilson 2012; Frank *et al.* 2014; Woinarski *et al.* 2014).

In Australia, it will often be necessary to consider key threatening processes in the context of changed fire regimes. Since as early as the Tertiary, fire has been recognised as a major influence shaping Australian environments (Kershaw *et al.* 2002; Mooney *et al.* 2012) and it continues to be one of the largest drivers of habitat modification. For thousands of years prior to European occupation much of Australia's environments were being shaped by traditional Aboriginal burning practices, which resulted in a fine mosaic of vegetation patches at various stages of post-fire recovery (Latz and Griffin 1978; Kimber 1983; Saxon 1984; Griffin and Friedel 1985; Payne 1991; Bowman *et al.* 2012). Traditional Aboriginal fire regimes across Australia were abandoned or modified post European settlement (Latz and Griffin 1978; Kimber 1983; Griffin and Friedel 1985; Burrows *et al.* 2006). This cessation of landscape-scale anthropomorphic burning has seen a shift towards infrequent, severe and broad-scale wild-fire events that result in vast tracts of modified habitat (Latz and Griffin 1978; Burbidge and McKenzie 1989; Morton 1990; Gill 2000; Allan and Southgate 2002; Burrows *et al.* 2006; Edwards and Allan 2009). Within these highly modified environments, invasive predators have the potential to threaten native fauna with extinction (Hobbs 2001).

The great desert skink (*Liopholis kintorei*) is an internationally listed vulnerable species with a distribution confined to fire-prone arid environments of the western deserts of Australia (McAlpin 2001; IUCN 2016). This distribution overlaps with introduced mammalian predators, most notably feral cats and European red fox (Dickman 1996; Strahan and Van Dyck 2006). The known range of this species has contracted and localised population declines and extinctions have been documented (McAlpin 2001). Habitat modification

caused by changes in recent fire regimes and increased predation by introduced mammalian predators have been previously identified as likely causes of great desert skink population declines (McAlpin 2001; Cadenhead *et al.* 2015; Moore *et al.* 2015).

The influence of fire on great desert skink populations has been investigated at different spatial scales. At a relatively small scale, fire was found to have a negative impact on occupancy rates at great desert skinks burrow-systems, along with rates of breeding success (Moore *et al.* 2015). At a larger spatial scale, fire regime was identified as a major determinant of great desert skink viability, with an increase in fire size and frequency predicted to drive populations to extinction (Cadenhead *et al.* 2015). However, in each of these studies, the mechanism by which fire is related to reduced burrow-system occupancy rates and the predicted local extinctions remained unclear.

Here we present the results of an observational study built opportunistically around a prior experimental burn study that focused on great desert skink burrow system occupancy and breeding success post fire conducted on Newhaven Wildlife Sanctuary (Moore *et al.* 2015). We aim to investigate the ecological mechanisms that underpin great desert skinks response to fire by determining: 1) the magnitude of predation on great desert skink by large mammalian predators generally across the sanctuary; 2) the level of potential predator pressure that exists at great desert skink burrow-systems, and; 3) if predator pressure was influenced by the presence and type of fire.

Materials and methods

Study site

The study was conducted at Newhaven Wildlife Sanctuary in central Australia, Northern Territory (22.72°S, 131.17°E; Fig. 4.1). This property is managed for conservation by the Australian Wildlife Conservancy. Newhaven Wildlife Sanctuary has the largest known population of great desert skink, and here their preferred habitat is semi-saline spinifex sandplain (Latz *et al.* 2003). This community is typically dominated by needlewood (*Hakea leucoptera*), inland tea-tree (*Melaleuca glomerata*) and the sub-shrub *Pluchea ferdinandii-mulleri* over hummock grass *Triodia pungens* (the stoloniferous growth form; Latz *et al.* 2003).

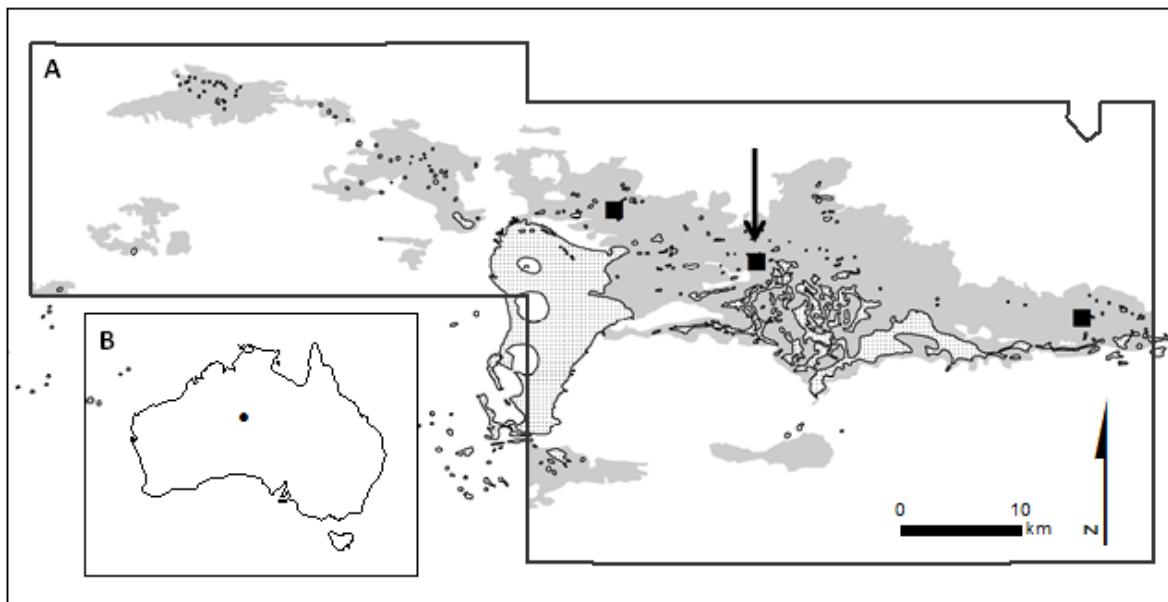


Fig. 4.1 Newhaven Wildlife Sanctuary (A) showing the location of the three 1 km² sites from which predator scats were collected (closed squares). The arrow indicates the location of the study site at which predator tracking was performed. The shaded grey areas indicate potential great desert skink habitat and the hatched areas and small irregular shaped black areas indicate ephemeral lakes. The inset map (B) shows the location of Newhaven Wildlife Sanctuary within Australia.

Study species

The great desert skink grows to approximately 200 mm snout-vent length, can weigh up to 350 g, and is endemic to arid Australia (McAlpin 2001; Chapple 2003). It is an obligate burrower that constructs and maintains a complex burrow-system with multiple openings and interconnecting tunnels that can be up to 80 cm in depth. Burrows can be occupied continuously for up to seven years and house close relatives, often consisting of the two parents and two age cohorts of their offspring (McAlpin *et al.* 2011; Dennison 2015). It is

crepuscular and nocturnal, spending the majority of its surface activity time at the burrow entrance and rarely foraging far from its burrow-system (Moore *et al.* in review).

Fire induced habitat modification at great desert skink burrow-systems and potential predator activity

Within a 75 ha focal study site, 30 burrow-systems were selected for a study on the impacts of fire on persistence of great desert skinks (see Moore *et al.* 2015 for detail). Three fire type treatments (with 10 replicates of each) were applied to an area approximately 0.25 ha. This was the size required for the burn treatment to cover the extent of a single burrow system. The three fire treatments were: 1. clean burn—all ground cover was burnt within the experimental burn zone; 2. patchy burn—30% - 40% of ground cover was left unburnt within the experimental burn zone and the vegetation covering one to two burrow entrances was burnt and the latrine remained unburnt, and; 3. no burn—no experimental burn was conducted (Moore *et al.* 2015). The proportion of ground cover that remained at the burrow-systems after the experimental burns differed significantly when clean-burn and patchy-burn fire types were compared with no burn (Moore *et al.* 2015).

The cleared line that was created manually around each of the 30 burrow-systems to help contain the experimental burns provided an excellent tracking surface to systematically monitor potential predator activity at each burrow-system. We used these cleared lines, (herein referred to as tracking ring/s), approximately 1.5 m in width, and the range of vegetation cover resulting from the experimental burns, to opportunistically collect data on potential predator visitation to the burrow-systems.

The following ground dwelling species, known to occur at Newhaven, were considered potential predators for great desert skink: feral cat, European red fox, dingo (*Canis dingo*), brush-tailed mulgara (*Dasyurus blythii*), woma python (*Aspidites ramsayi*), Stimson's python (*Antaresia stimsoni orientalis*), mulga snake (*Pseudechis australis*) and Mengden's brown snake (*Pseudonaja mengdeni*). Due to the difficulty in distinguishing between the tracks of mulga snake, Mengden's brown snake and the woma python, all snake tracks greater than 2 cm in width were categorised as "large snake". Although sand goanna could plausibly prey on juvenile great desert skink, we do not consider them a predator of this species. Goannas are strictly diurnal and forage at relatively high body temperatures, therefore they could only hunt great desert skink when it is inactive underground. In addition, the size and shape of great desert skink burrow-systems would usually preclude entry of adult sand goannas and restrict access to deep chambers within the burrow-system.

The day prior to tracking, the tracking ring was swept with a broom to remove all previous signs of animals and to create an even surface. In addition, all tracks (footprints) within 0.5 m of each burrow entrance were removed by sweeping. Potential great desert skink predators were detected by walking the tracking ring created around the burrow-system and searching for predator tracks. In addition, searches were made for predator tracks within 0.5 m of all entrances to each burrow. For consistency, only one of us (DM) made the tracking observations. Tracking took place between 7 am and 9 am when the sun was high enough to reach the surface of the ground but low enough to create shadows, therefore making tracks more obvious and keeping detection of tracks between burrow-systems equal. Potential predator tracks at each of the 30 burrow-systems were recorded

daily for approximately one month beginning the day after the experimental burns were conducted. All tracks found on the tracking ring and at the burrow entrances were removed daily by sweeping.

Tracking was conducted during summer months (November and December) when great desert skink are active. Below average rainfall was recorded in the 12 months period to when scats were collected and conditions throughout the tracking period were dry.

Potential predator scat collection and dietary analysis

Feral cat, dingo and fox scats were collected over a fourteen-month period (September 2013 to December 2014) from three 1 km² sites, separated by a minimum of 10 km. All sites were known to be inhabited by great desert skink, one of which included the focal study site (Fig. 4.1). On at least four occasions each of these sites was searched for predator scats.

Scats were placed into paper bags and transferred to the laboratory where they were placed in nylon bags and soaked in hot water for a minimum of 12 hours and then washed through a regular cycle in a domestic washing machine. Scats were then air-dried in the nylon bags. Scat contents were sorted under a dissecting microscope to determine the presence of great desert skink which could be distinguished from blue-tongue lizards and other reptiles by their distinctive claws and jaw bones (the claws of the great desert skink are sharper, longer and more slender than the blue-tongue which has shorter, broader and blunter claws. The jaw is also quite distinct—the great desert skink has many narrow, sharp, evenly sized teeth whereas blue-tongues have only half as many teeth and they are much thicker, blunter and variable in size along the length of the jaw).

Analysis

The Kruskal-Wallis rank sum test (Quinn and Keough 2002) was used to compare predator activity levels at burrow-system entrances and to test for effects of the presence and type of fire on predator activity at great desert skink burrow-systems. A detection bias may have occurred as a result of the variation in vegetation cover across sampled sites post experimental burns. To account for this possibility, if a significant result was found when examining the predator occurrence at a burrow-system entrance, we also analysed observation data from the tracking rings, where detectability across all thirty sites was equal.

Pearson's Chi-square test (Quinn and Keough 2002) was used to detect any significant difference in predation on great desert skink when examining the predator scat data. All analyses were performed using R version 3.0.2. (R Development Core Team 2011).

Results

Potential predator pressure at the burrow-system and the effect of fire on predator activity

Over the 4 week tracking period, 511 tracking surveys were conducted. From the seven potential predators identified, three species were recorded visiting great desert skink burrow-systems during the four weeks of intensive tracking. Two were native predators—dingoes, and large snakes as well as feral cats (Fig. 4.2). The level of feral cat activity at a burrow-system entrance (within 50 cm of at least one entrance to a burrow-system) was significantly higher than that of any other potential predator (Kruskal-Wallis rank sum test; $df = 3; P < 0.001, \chi^2 = 45.6$). Feral cat tracks were detected at a burrow-system entrance on

12.5% of the 511 track surveys, dingoes were only detected twice (0.39%) and large snakes were recorded on 1.2% of tracking surveys (Fig. 4.2). No European red fox or brush-tailed mulgara tracks were detected at burrow-systems, however tracks from each of these species were observed elsewhere (within 20 m of a tracking ring) within the focal study site.

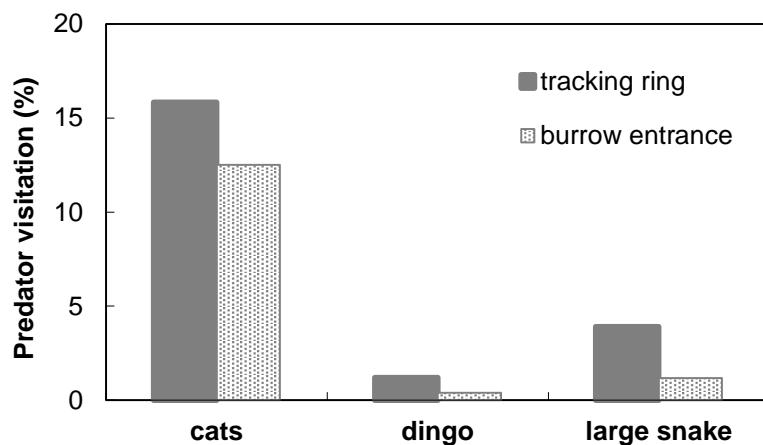


Fig. 4.2 The percentage occurrence of tracking surveys where predator tracks were detected at a great desert skink burrow-system entrance or on the tracking ring, irrespective of burn type.

There was no significant effect of the presence, or type, of fire on the frequency of cat, dingo and large snake visitations to a great desert skink burrow-system entrance. Feral cat activity at great desert skink burrow-system entrances was relatively high across all burrow-systems irrespective of burn type, with visitation ranging from 11.3% at clean burned sites to 14.6% at unburnt sites (Fig. 4.3). This equates to a burrow-system being visited by a cat every 7-9 days.

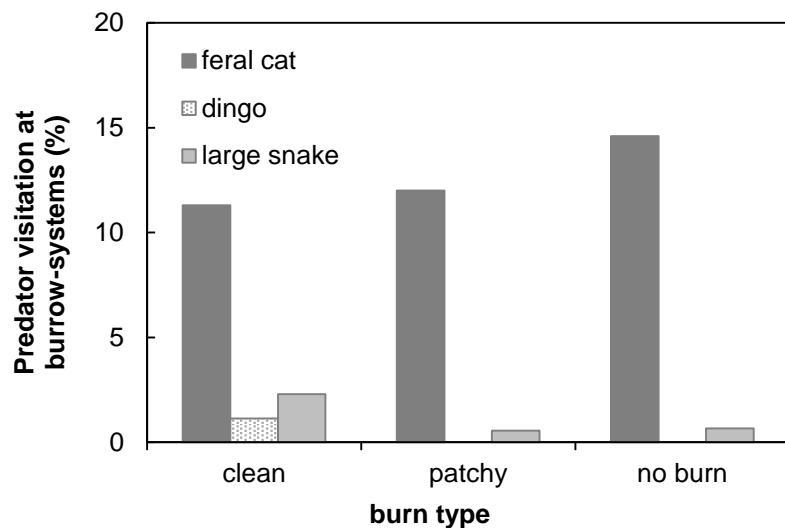


Fig. 4.3 The frequency of occurrence of feral cat, dingo and large snake tracks at great desert skink burrows across three burn types.

Large mammalian predator diet analysis

Over a 14-month period, 121 large mammalian predator scats were collected (39 feral cat, 65 dingo and 17 fox) from three 1 km² sites. The remains of great desert skink were confirmed in 49% of feral cat scats, 18% of fox scats and 14% of dingo scats (Fig. 4.4). The frequency of great desert skink remains occurring in feral cat scats was significantly higher than in fox and dingo scats (Pearson's Chi-squared test; $\chi^2 = 16.2$, d.f. = 2, $P < 0.001$).

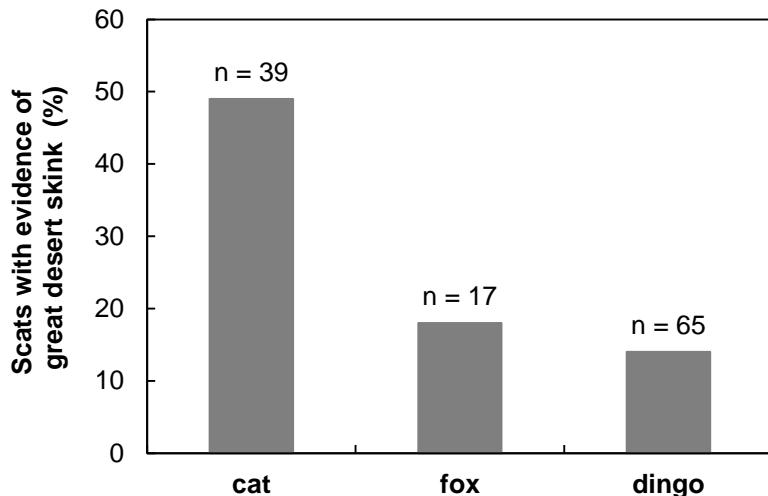


Fig. 4.4 The percentage of feral cat, European red fox and dingo scats that contained the remains of great desert skink. The number of scats sampled per predator, 'n', is also indicated.

Discussion

Relative predator impact on great desert skink

Results of this study strongly indicate that feral cats are the most significant predator of the nationally threatened great desert skink within semi-saline sand plains on Newhaven. Feral cats were the most frequently recorded predator at great desert skink burrow-systems and they had a significantly higher frequency of occurrence of great desert skink remains in their diets than dingo and European red fox. These results are consistent with the general conclusion in the literature that feral cats are a significant threat to Australian native fauna (Frank *et al.* 2014; McGregor *et al.* 2014; Woinarski *et al.* 2014).

The results of our tracking survey, in particular, highlight the increased predation pressure placed on this species by feral cats. Predator pressure, in this instance, refers to the pressure that might be experienced by an individual skinks or a family group inhabiting a

burrow-system caused by the presence of a predator at the burrow-system. During the four-week intensive tracking period we determined that a great desert skink burrow-system would be visited by a predator once every 7 days. If feral cats were removed from the ecosystem, this predator visitation would be reduced to once every 67 days.

Several aspects of the behaviour of some native species have been identified as likely to increase their susceptibility to feral cat predation. These include being nocturnal, of colonial habit, utilising terrestrial areas and/or exhibiting conspicuous behaviour (Dickman 1996). Great desert skink shows each of these traits—they are a crepuscular and nocturnal skink that spend a large proportion of their active time basking and hunting from a burrow-system entrance. In addition, they construct, maintain and occupy a family burrow-system for an average of four years (McAlpin *et al* 2011; Moore *et al.* in review). It is plausible that, because great desert skink burrow-systems are often tightly clustered and are a static feature within the landscape, individual feral cats may learn the locations of these burrow-systems and become specialist hunters of great desert skink. This specialisation is likely to magnify the impact of feral cat predation, in contrast to the impact caused by opportunistic hunting alone. Other studies have suggested that specialisation of hunting by feral cats has led to the local extirpation of native mammal species including the mala (*Lagorchestes hirsutus*) within the Tanami desert of Australia (Gibson 1994) and a captive colony of long-haired rat (*Rattus villosissimus*) within northern Australia (Frank *et al.* 2014). On average three or four of the 30 burrows-systems monitored during this study were visited by a feral cat each day, and we observed the footprints of an individual feral cat or cats travelling directly from one active burrow-system to another, investigating numerous burrow entrances along the way, in a systematic and predictable manner. It is thus possible that a

particular individual or individuals were targeting great desert skink in their hunting and concentrating their efforts on micro-habitats where prey capture is most likely.

Despite regular dingo activity along roads traversing and adjacent to the focal study site, dingo tracks were rarely detected at great desert skink burrow systems. In contrast to feral cat behaviour at a burrow-system, on the two occasions that dingo sign was observed at burrow-systems, the tracks indicated that the dingo walked directly over the burrow-system with no apparent change in direction or pace of travel. Despite this observation at the burrow-system, great desert skink still formed a relatively high proportion of dingo diet with 14 % of dingo scats containing the remains of this species. Although an analysis of 12,000 dingo scats over a 20 year period found that, across most of Australia, medium-sized mammals are the preferred prey of dingoes (Corbett 2001), within arid environments reptiles have been found to be a dominant part of the dingo diet (Paltridge 2002; Newsome *et al.* 2014). In support of this, we found that 62.5% of scats contained reptile remains (25% goanna, 21% skink exclusive of great desert skink; 10% dragon, 1.5% snake, 3% other reptile) compared with 15% of scats that contained the remains of mammals. This result may be influenced by the collection of scats during summer months only and prevailing environmental conditions. Below average annual rainfall was recorded at the study site in 2013 (299.5mm; 12 months prior to the collection of scats) possibly reducing the numbers of small mammals available during the study period. Additionally, seasonal conditions are known to influence dingo diet in central Australia, where mammals form a larger part of dingo diets in the winter months when many reptile species are hibernating, and reptiles forming the majority of dingo diet in the summer months (Newsome *et al.* 2014).

Large snake tracks were observed at great desert skink burrow-systems, particularly after rain or when relative humidity was high. Although our tracking method was unable to distinguish between large diurnal elapids (Mengden's brown snake and mulga snake) and nocturnal pythons (woma python and Stimpson's python), we did directly observe a woma python to be a predator of great desert skink at the study site. Large diurnal elapids may be attracted to great desert skink burrow-systems for shelter or if led there by other hunting opportunities, including small mammalian prey, however, it remains unconfirmed if these species prey on great desert skink.

Effect of fire on predation pressure at burrow-systems

The experimental burns, though at a small scale in the immediate vicinity of the burrow-system, are ecologically significant because previous studies have shown that this species spends approximately 67% of its surface activity time at the burrow entrance (Moore *et al.* in review). Our results did not show a significant effect of fire on the frequency of feral cat visitation to great desert skink burrow-systems. This is in contrast to a study from northern Australia that recorded cats travelling large distances to target their hunting in recently burnt habitat (McGregor *et al.* 2014). Our findings do not preclude feral cats targeting a recently burnt habitat following a more extensive wildfire, but in the current study the small area (approx. 0.25ha) of habitat modified by each experimental burn does not appear to have been sufficient to alter feral cat hunting preferences at great desert skink burrow-systems.

Regardless of how often feral cats visit a particular burrow-system, it is likely that their hunting success per visit is significantly influenced by the extent of vegetation cover at

burrows. Feral cats usually detect prey by sight or sound—species that are conspicuous within an open burnt landscape are therefore at high risk of predation as the hunting efficiency of the feral cat increases under these conditions (Dickman 1996; McGregor 2014). It is thus plausible that a synergistic effect exists between habitat modification caused by fire and predation pressure whereby the effectiveness of cat hunting increases with the removal of vegetation cover following severefire. This could explain the results of a concurrent study that found that, although great desert skink can initially persist in their burrow-system after fire, most burrow-systems become unoccupied between 1 and 4 months after the fire occurred (Moore *et al.* 2015). With no evidence that animals are dispersing from burnt burrow-systems, an alternative explanation for the disappearance of great desert skink from burnt sites is increased vulnerability to predation. If extirpations of individuals, or family groups, from burnt burrow-systems are driven by predation, the present study has revealed that cats are the main predator involved.

Conclusions

Predation by feral cats and inappropriate fire regimes have been recognised as key threats to extant Australian terrestrial mammals (Woinarski *et al.* 2014). These threats are potentially as critical for Australian terrestrial reptiles as they are for mammals, especially burrow constructing species with high burrow fidelity. Although, our results did not detect an increased presence of feral cats at fire-affected great desert skink burrow-systems, our data identified feral cats as their most significant predator, supporting the need for ongoing feral cat management at locations with vulnerable populations. Conservation management of great desert skink would benefit from further research that gains an understanding of

predation pressure imposed by feral cats in habitat subjected to landscape-scale habitat modification caused by fire.

References

- Allan, G. E., and Southgate, R. I. (2002). Fire regimes in the spinifex landscapes of Australia. In 'Flammable Australia: The Fire Regimes and Biodiversity of a Continent'. (Eds. R. A. Bradstock, J. E. Williams and A. M. Gill.) pp. 145-176. (Cambridge University Press: Cambridge.)
- Bowman, D., Murphy, B. P., Burrows, G. E., and Crisp, M. D. (2012). Fire regimes and the evolution of the Australian biota. In 'Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world'. (Eds. R. Bradstock, R. Williams and A. Gill.) pp. 3-25. (CSIRO Publishing: Melbourne.)
- Brook, B. W., Sodhi, N. S., and Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**, 453-460.
- Burbidge, A. A., and McKenzie, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**, 143-198.
- Burrows, N. D., Burbidge, A. A., Fulle, P. J., and Behn, G. (2006). Evidence of altered fire regimes in the Western Desert region of Australia. *Conservation Science Western Australia* **5**, 14-26.
- Cadenhead, N. C. R., Kearney, M. R., Moore, D., McAlpin, S., and Wintle, B. A. (2015). Climate and fire scenario uncertainty dominate the evaluation of options for conserving the Great Desert Skink. *Conservation Letters* **9**, 181-190.

Chalfoun, A. D., and Martin, T. E. (2009). Habitat structure mediates predation risk for sedentary prey: tests of alternative hypotheses. *Journal of Animal Ecology* **78**, 497-503.

Chapple, D. G. (2003). Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs* **17**, 145-180.

Conner, L. M., Castleberry, S. B., and Derrick, A. M. (2011). Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. *The Journal of Wildlife Management* **75**(4), 938-944.

Corbett, L. K. (1995). 'Dingo in Australia and Asia.' (J. B. Books: Marleston.)

Dennison, S. (2015). *Social organisation and population genetics of the threatened great desert skink, Liopholis kintorei*. Ph. D. Thesis. (Macquarie University: Sydney.)

Dickman, C. R. (1996). *Overview of the impacts of feral cats on Australian native fauna. Australian Nature Conservation Agency Report*. (Australian Nature Conservation Agency: Canberra.)

Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., and Gemmell, N. J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution* **20**, 470-474.

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., and Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution* **22**, 489-496.

Edwards, G. P., and Allan, G. E. (2009). Desert Fire: fire and regional land management in the arid landscape of Australia. Desert Knowledge CRC Report No. 37. (Desert Knowledge Cooperative Research Centre: Alice Springs.)

Doherty, T. S., Dickman, C. R., Nimmo, D. G., and Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation* **190**, 60-68.

Fischer, J., and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**, 265-280.

Frank, A. S., Johnson, C. N., Potts, J. M., Fisher, A., Lawes, M. J., Woinarski, J. C. Z., Tuft, K., Radford, I. J., Gordon ,I. J., Collis, M. A., and Legge, S. (2014). Evidence that feral cats cause local extirpation of small mammals in Australia's tropical savannas. *Journal of Applied Ecology* **51**, 1486-1493.

Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., and Winne, C. T. (2000). The global decline of reptiles, déjà vu amphibians reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *BioScience* **50**, 653-666.

Gibson, D. (1994). Predation by feral cats, *Felis catus*, on the rufous hare-wallaby, *Lagorchestes hirsutus*, in the Tanami Desert. *Australian Mammalogy* **17**, 5.

Gill, A. M. (2000). *Fire-pulses in the heart of Australia: fire regimes and fire management in central Australia*. CSIRO Centre for Plant Biodiversity Research. (Environment: Canberra.)

- Griffin, G. F., and Friedel, M. H. (1985). Discontinuous change in central Australia: some implications of major ecological events for land management. *Journal of Arid Environments* **9**, 63-80.
- Hradsky, B. A., Mildwaters, C., Ritchie, E. G., Christie, F., and Di Stefano, J. (2017). Responses of invasive predators and native prey to a prescribed forest fire. *Journal of Mammalogy* **98**(3), 835-847.
- Hobbs, R. J. (2001). Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conservation Biology* **15**, 1522-1528.
- IUCN (2016). *The IUCN Red List of Threatened Species. Version 2016-2*.
<<http://www.iucnredlist.org>>. [accessed 04 September 2016].
- Janssen, A., Sabelis, M. W., Magalhães, S., Montserrat, M., and Van der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology* **88**(11), 2713-2719.
- Johnson, C. (2006). *Australia's mammal extinctions: A 50,000 year history*. (Cambridge University Press: New York.)
- Kimber, R. (1983). Black lightning: Aborigines and fire in central Australia and the Western Desert. *Archaeology in Oceania* **18**, 38-45.
- Kershaw, A. P., Clark, J. S., Gill, A. M., and D'Costa, D. M. (2002). A history of fire in Australia. In 'Flammable Australia: The Fire regimes and Biodiversity of a Continent'. (Eds. R. A. Bradstock, J. E. Williams and A. M. Gill.) pp. 3-25. (Cambridge University Press: Cambridge.)
- Latz, P., Paltridge, R., and Holmes, J. (2003). *Vegetation survey of Newhaven Reserve*. A report prepared for Birds Australia. (Desert Wildlife Services: Alice Springs.)

Latz, P. K., and Griffin, G. F. (1978). Changes in Aboriginal land management in relation to fire and food plants in central Australia. In 'The Nutrition of Aborigines in Relation to the Ecosystems of Central Australia'. (Eds. B. S. Hetzel and H. J. Frith.) pp. 77-85. (CSIRO: Melbourne.)

McAlpin, S. (2001). *A Recovery Plan for the Great Desert Skink (Egernia kintorei)*. Arid Lands Environment Centre. (Arid Lands Environment Centre: Alice Springs.)

McAlpin, S., Duckett, P., and Stow A. (2011). Lizards cooperatively tunnel to construct a long-term home for family members. *PLoS one* **6**, e19041.

McDonald, P. J., Stewart, A., Schubert, A. T., Nano, C. E. M., Dickman, C. R., and Luck, G. W. (2016). Fire and grass cover influence occupancy patterns of rare rodents and feral cats in a mountain refuge: implications for management. *Wildlife Research* **42**, 121-129.

McGregor, H. (2014). *Density, movements and hunting of feral cats in relation to fire and grazing in northern Australia*. PhD Thesis. (University of Tasmania: Hobart.)

McGregor, H. W., Legge, S., Jones, M. E., and Johnson, C. N. (2014). Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS one* **9**, e109097.

Mooney, S. D., Harrison, S. P., Bartlein, P. J., and Stevenson, J. (2012). The prehistory of fire in Australia. In 'Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world'. (Eds. R. Bradstock, R. Williams and A. Gill.) pp. 3-25. (CSIRO: Melbourne.)

Moore, D., Kearney, M.R., Paltridge, R., McAlpin, S., and Stow, A. (2015). Is fire a threatening process for *Liopholis kintorei*, a nationally listed threatened skink? *Wildlife Research* **42**, 207-216.

Moreno, S., Delibes, M., and Villafuerte, R. (1996). Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. *Canadian Journal of Zoology* **74**, 1656-1660.

Morton, S. R. (1990). The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. In 'Proceedings of the Ecological Society of Australia'. pp. 201-213. (CSIRO: Melbourne.)

Newsome, T.M., Ballard, G.A., Fleming, P.J., van de Ven, R., Story, G.L., and Dickman, C.R. (2014). Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia* **175**(1), 139-150.

Norris, K. (2004). Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology* **41**, 413-426.

Paltridge, R. (2002). The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* **29**, 389-403.

Payne, S. J. (1991). *Burning Bush: A fire history of Australia*. (University of Washington Press: Seattle.)

Purvis, A., Jones, K. E., and Mace, G. M. (2000). Extinction. *BioEssays* **22**, 1123-1133.

Quinn, G. P., and Keough, M. J. (2002). *Design and data analysis for biologists*. (Cambridge University Press: Cambridge.)

R Development Core Team (2011). R: A language and environment for statistical computing.

R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL

<http://www.R-project.org/>.

Robinson, N. M., Leonard, S. W., Ritchie, E. G., Bassett, M., Chia, E. K., Buckingham, S., Gibb, H., Bennett, A. F., and Clarke, M. F. (2013). Refuges for fauna in fire-prone landscapes: their ecological function and importance. *Journal of Applied Ecology* **50** (6), 1321-1329.

Saxon, E. C. (1984). *Anticipating the inevitable: a patch-burn strategy for fire management at Uluru (Ayers Rock-Mt Olga) National Park*. CSIRO Division of Wildlife and Rangelands Research. (CSIRO: Alice Springs.)

Strahan, R., and Van Dyck, S. (3rd Ed.) (2006). 'Mammals of Australia.' (Reed New Holland: Sydney.)

Wilson, S. K. (2012). 'Australian lizards: a natural history.' (CSIRO Publishing: Collingwood.)

Woinarski, J. C. Z., Pavey, C., Kerrigan, R., Cowie, I., and Ward, S. (2007). *Lost from our landscape: threatened species of the Northern Territory*. (Department of Natural Resources, Environment and The Arts: Palmerston.)

Woinarski, J., Burbidge, A., and Harrison, P. (2014). *Action Plan for Australian Mammals 2012*. (CSIRO Publishing: Collingwood.)

CHAPTER 5

UNDER THE WEATHER? THE DIRECT EFFECTS OF CLIMATE WARMING ON A THREATENED DESERT LIZARD ARE MEDIATED BY THEIR ACTIVITY PHASE AND BURROW SYSTEM



Steve McAlpin at a large basking mound at the entrance of a *Liopholis kintorei* burrow-system on Newhaven Wildlife Sanctuary (D. Moore).

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Abstract

- (1) For ectotherms such as lizards, the importance of behavioural thermoregulation in avoiding thermal extremes is well established and is increasingly acknowledged in modern studies of climate warming and its impacts. Less appreciated and understood are the buffering roles of retreat sites and the activity phase, in part because of logistical challenges of studying below-ground activity. Burrowing and nocturnal activity are key behavioural adaptations that have enabled a diverse range of reptiles to survive extreme environmental temperatures within hot desert regions. Yet, the direct impact of recent global warming on activity potential has been hypothesised to have caused extinctions in desert lizards, including the Australian arid zone skink *Liopholis kintorei*.
- (2) We test the relevance of this hypothesis through a detailed characterisation of the above- and below-ground thermal and hydric microclimates available to, and used by, *Liopholis kintorei*.
- (3) We integrate operative temperatures with observed body temperatures to construct daily activity budgets, including the inference of subterranean behaviour. We then

assess the likelihood that contemporary and future local extinctions in this species, and those of similar burrowing habits, could be explained by the direct effects of warming on its activity budget and exposure to thermal extremes.

- (4) We found that *Liopholis kintorei* spent only 4% of its time active on the surface, primarily at dusk, and that overall potential surface activity will be increased, not restricted, with climate warming. The burrow system provides an exceptional buffer to current and future maximum extremes of temperature (≈ 40 °C reduction from potential surface temperatures), and desiccation (burrows near 100% humidity). Therefore, any climate warming impacts on this species are likely to be indirect.
- (5) Our findings reflect the general buffering capacity of underground microclimates, therefore our conclusions for *Liopholis kintorei* are more generally applicable to nocturnal and crepuscular ectotherms, and highlight the need to consider the buffering properties of retreat sites and activity phases when forecasting climate change impacts.

Introduction

Reptiles and other ectotherms have a well-defined temperature range where their performance is optimal (Cowles and Bogert 1944; Bogert 1949; reviewed in Huey 1982). Increasing environmental temperatures through climate warming have thus been predicted to result in localised extinctions through exposure to stressful body temperatures (and through constrictions of the activity budget (Deutsch *et al.* 2008; Huey *et al.* 2009; Sinervo *et al.* 2010).

The use of buffering retreat sites has enabled a diverse range of reptiles to thrive in thermally extreme environments such as deserts (Cowles and Bogert 1944; Heatwole 1970; Pianka 1969; Pianka 1986; Heatwole and Taylor 1987; Roger 2008). Retreat sites are generally microclimates that offer thermal and/or hydric relief from unfavourable environmental conditions. Common retreat sites include sheltering in the shade of vegetation, under bark, under leaf litter or within a burrow. For lizards living in such regions where the risk of overheating or desiccation is high, time sequestered within retreat sites may amount to a large proportion of each day (Huey 1982; Huey *et al.* 1989; Kerr *et al.* 2004). The thermal and hydric properties of retreat sites may therefore substantially impact on the physiological performance and development of an individual (Dawson 1975; Huey and Slatkin 1976; Huey 1982; Lynch and Gabriel 1987). In desert environments, where deep shade is rare and vegetation is sparse, burrow construction is common and provides a cool retreat during the day when surface temperatures are unfavourably hot (Heatwole 1970; Huey *et al.* 1989). Burrows may also permit the maintenance of higher body temperatures at night or during cooler days (Heatwole and Taylor 1987; Hertz 1992; Sunday *et al.* 2014).

A burrowing habit in conjunction with a crepuscular (active during dawn and dusk) and or nocturnal activity phase, provides even greater buffering from climate extremes than burrowing alone. Nocturnal lizards often retain ancestrally high thermal preferences and activity is typically limited by low rather than high temperatures (Pianka and Pianka 1976; Autumn *et al.*, 1999), while burrows and other retreat sites can provide thermoregulatory opportunities during the day (Bustard, 1967; Dial, 1978; Webb and Shine 1998; Kearney *et al.* 2000). Recent research has highlighted that most reptiles would be unable to survive the warmest potential body temperatures within exposed habitats, and that a reliance on

behaviours and or habitats that provide a buffer to current and potential increases in extreme operative temperatures is therefore critical (Huey *et al.* 2009; Kearney *et al.* 2009; Huey *et al.* 2010; Scheffers *et al.* 2014; Sunday *et al.* 2014; Grimm-Seyfarth *et al.* 2017).

Predictive models are frequently relied upon to generate broad-scale conclusions around the extinction risks for ectotherms caused by climate warming (e.g. Thomas *et al.* 2003; Deutsch *et al.* 2007; Huey *et al.* 2009; Sinervo *et al.* 2010). However, key factors such as thermoregulatory capacity, microclimate variability and the use of refuge sites are often overlooked (Buckley 2013; Kearney 2013; Sunday *et al.* 2014; Briscoe *et al.* 2016). Recent research (Sinervo *et al.* 2010) argued that climate warming is driving population extinctions of lizards across the globe and that 20% of all lizard species may be extinct by 2080. This research proposed a mechanism for global lizard population extinction under climate warming where activity periods are restricted due to elevated field body temperatures. This activity restriction model, derived from studies of diurnal Mexican *Sceloporus* lizards, was used to predict recent population extinctions in additional lizards globally, irrespective of activity phase. Sinervo *et al.*'s predictions included our study species, the great desert skink *Liopholis kintorei*; an internationally listed vulnerable species (Stirling and Zietz 1893; IUCN 2016). The relevance of restricted activity periods for *L. kintorei*, and therefore possibly other species, is questionable given that field observations point to a crepuscular and nocturnal activity phase in this species (McAlpin 2001; Pearson *et al.* 2001).

Here we aim to further understand the potential role of climate warming as a threatening process for non-diurnal lizards living in extreme desert environments, by investigating the thermal constraints for *L. kintorei*. This species was chosen as a case study species because it is known to be a crepuscular and nocturnal lizard, and constructs and

maintains a deep burrow-system. Specifically, we assess if the reported local extinctions for *L. kintorei* could be explained by a restriction of activity period due to an increase in field body temperatures. We then assess the potential for future activity restrictions under a climate warming scenario. In addition, we evaluate the extent to which the burrow system constructed by *L. kintorei* provides a buffer against current extreme maximum temperatures and those predicted by future climate warming.

To achieve these objectives, we characterised the thermal surface environment within *L. kintorei* habitat and the thermal and hydric conditions of their burrow systems. We concurrently collected field body temperatures from adult *L. kintorei*. We use these three temperature datasets to infer the location of the skink within the burrow system or on the surface, thereby indirectly deriving daily activity budgets and determining their activity phase. Finally, we consider a climate warming scenario and estimate: 1) current and future potential activity times within four micro-habitats by calculating the total hours observed within the voluntary foraging body temperature limits ($27.1\text{ }^{\circ}\text{C} - 37.6\text{ }^{\circ}\text{C}$) at dawn, dusk, day and night, and; 2) current and future thermal stress levels experienced within the burrow system by comparing thermal tolerance limits (maximum body temperature) to burrow system temperatures at various depths.

Materials and methods

Study species and site

Liopholis kintorei is a large (200 mm snout to vent length, up to 350 g), long-lived skink. It is restricted to sandy and gravelly habitats within the western desert regions of Australia (McAlpin 2001; Chapple 2003). It is an obligate burrower that constructs and maintains a

deep (up to 80 cm) and complex burrow system. The burrows are occupied by family groups of close relatives, often consisting of an adult pair and two age cohorts of individuals (McAlpin *et al.* 2011; Dennison 2015). No field datum exists to determine their primary activity phase, however, limited field observations suggest a crepuscular and nocturnal habit during warmer months, with a period of hibernation during the winter months (McAlpin, 2001; Chapple 2003).

Our study was conducted at Newhaven Wildlife Sanctuary in central Australia, Northern Territory (22.72°S, 131.17°E; Fig. 5.1). This property is managed for conservation by the Australian Wildlife Conservancy (AWC). On Newhaven, *L. kintorei*'s preferred habitat is semi-saline spinifex sandplains, a typically homogenous vegetation community dominated by hummock grass *Triodia pungens*. This study was conducted at a 75 ha study site where *L. kintorei* was known to be locally abundant.

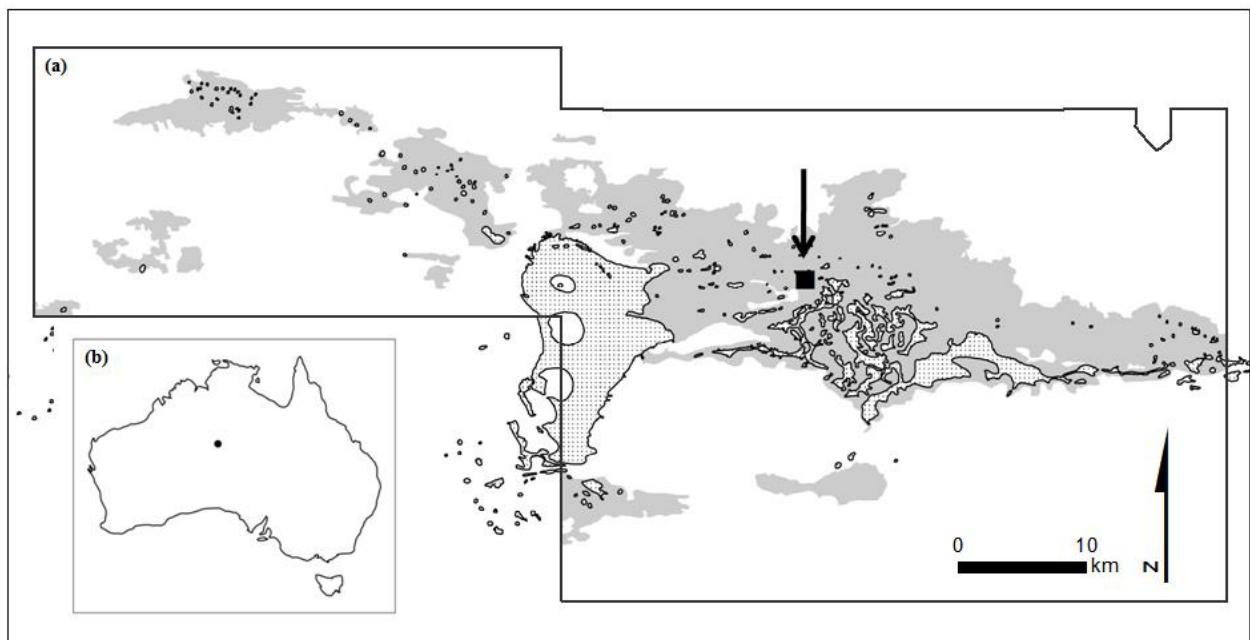


Fig. 5.1 Newhaven Wildlife Sanctuary (a) showing the location of the 75 ha study site (closed square). The shaded grey areas indicate potential *Liopholis kintorei* habitat and the hatched areas indicate ephemeral salt lakes. The inset map (b) shows the location of Newhaven Wildlife Sanctuary within Australia.

Newhaven's climate is arid tropical, with annual air temperatures ranging from -2 to 46 °C (measured at 1.2 m from the ground) and highly variable annual rainfall (range 66 to 951 mm in the last 50 years) falling mainly in the summer (Stafford-Smith and Morton 1990; Latz *et al.* 2003; Bureau of Meteorology 2016).

Local weather data

Local weather conditions were recorded using an automated weather station (WeatherHawk, Campbell Scientific, Inc.) installed at the study site. Air temperature, relative humidity, wind speed and direction, solar radiation and rainfall were recorded at high resolution (every 10 minutes; 1.2 m above the ground) for a 12-month period.

Measuring the operative thermal environment

The available above-ground thermal environment within *L. kintorei* habitat was measured using physical models (herein referred to as copper models) to estimate operative environmental temperatures (T_e ; Bakken and Gates 1975; Bakken 1992; Grant and Dunham 1988; Shine and Kearney 2001; Bakken and Angilletta 2014). Operative temperatures are the body temperatures an organism would reach if exposed to a particular environment long enough to attain a thermal steady state (Bakken and Gates 1975). Two sizes (210 x 40 mm and 139 x 20 mm, length x diameter) of thin-walled (1 mm) copper pipe were used to represent adult and sub-adult *L. kintorei*, respectively. Temperature sensitive data-loggers

(Maxim Thermochron iButton DS1922L) were inserted into each length of copper pipe. The data-loggers were seated in a piece of thin polystyrene to ensure each data-logger sat centrally in the pipe. In an attempt to match the absorptivity of the copper pipe and *L. kintorei* as closely as possible, copper pipes (which were already orange in colour) were capped with plastic end-caps and painted an orange colour similar to the dorsal colour of *L. kintorei*.

We sampled the three dominant surface microhabitats within the semi-saline spinifex sandplain: 1) fully shaded, where copper models were placed under a large (~1 m diameter) hummock of soft spinifex *Triodia pungens*; 2) partially shaded, where copper models were placed under a small (~30 cm diameter) hummock of soft spinifex *Triodia pungens*, and; 3) exposed, where copper models were centred within a 2 m² area of cleared vegetation exposed to full sun. A large and small copper model (see description above) were placed within each of the three microhabitats at six randomly chosen locations within the study site. Each copper model was orientated east-west to maximise exposure to the sun, placed on the surface of the sand with the top of the data-logger facing upwards, and set to record the temperature (°C; accuracy ± 0.5 °C) every 30 minutes for a 12-month period—October 2013 to September 2014.

Measuring temperature and humidity within the burrow system

Six occupied *L. kintorei* burrow systems were selected randomly from the study site. The temperature (°C; accuracy ± 0.5 °C) and relative humidity (%; accuracy ± 0.5 %) of each burrow system was recorded at 30-minute intervals for a 12-month period—October 2013 to September 2014. Temperature and humidity data-loggers (Maxim Thermochron iButton DS1923) were taped onto a 2 – 4 m length of high tensile wire and placed down an active

burrow entrance (a small hole was cut into the tape to expose the humidity sensor of the data-logger). Data-loggers were attached to the wire approximately 10 cm from the burrow entrance (shallow), at the mid-point of the wire (mid) and at the base of the wire (deep).

Standardised sampling of temperature and relative humidity at a variety of depths across the burrow system was difficult because the construction of each burrow system varied; the actual depths of data-loggers were therefore unknown. We compared sub-surface soil temperature taken simultaneously from the study site to infer the approximate depth of each data-logger within the burrow system (see below). We thereby inferred that burrow system temperatures recorded from the burrow entrance were between 5 cm – 15 cm deep, those from the mid burrow system were 30 cm – 50 cm, and those from deep within the burrow were between 50 cm to 1 m. We converted relative humidity (%) to vapour density (kg m^{-3}) using the WETAIR subroutine of the NicheMapR package (R Core Team 2015; Kearney and Porter 2016), to assess the extent that relative humidity differences were driven by absolute water content of the air.

Measuring the temperature profile of soils within arid spinifex sandplains

The temperature profile of the soil substrate was measured at 6 randomly chosen locations within the study site. Temperatures ($^{\circ}\text{C}$, accuracy $\pm 0.5 ^{\circ}\text{C}$) were measured at the surface and at depths of 5, 15, 30, 50 and 100 cm. A 1.5 m length of plastic skirting was used to hold the data-loggers (Maxim Thermochron iButton DS1922L) at their pre-determined depths. Temperature data-loggers were covered with a single sheet of OPSITE film (Smith and Nephew) to provide an extra measure of water resistance. Each data-logger was fitted snugly into drilled holes and a layer of gaffer tape was then placed over the back. The exposed side

of the data-logger was sprayed with OPSITE before being buried. The front of each surface data-logger faced south and the vegetation was cleared around the data-loggers to create 2 m² area of bare earth that would be continuously exposed to the sun. The temperature was measured at 30-minute intervals for 12 months—October 2013 to September 2014.

*Measuring the field body temperatures of *Liopholis kintorei**

The distribution of *L. kintorei* field body temperature (T_b) was obtained by sampling twenty adult skinks (mean body mass: 217 g), each from a distinct burrow system. Adult skinks were trapped at their burrow system using Elliott traps (Elliott Scientific Equipment). Temperature data-loggers (Maxim Thermochron iButton DS1922L; accuracy ± 0.5 °C) and VHF transmitters were attached using *Hyperfix* (Smith and Nephew), a soft, flexible, breathable medical tape. The data-logger and VHF transmitter units had a combined weight of <7 grams, with the total dimensions being 30 x 17 x 5 (L / W / H, mm). The units were fitted laterally on the skink allowing for normal leg movement and so that the skinks could move freely within the burrow system. The surface of the data-logger was placed directly onto the skin of the lizard. Temperature was recorded at 15-minute intervals from September – December 2013. All skinks were located using a VHF receiver in mid-December, prior to when females give birth (McAlpin 2001), at which point the data-loggers and VHF transmitters units were removed.

Our approach uses skin temperature measurements as a proxy for core body temperature measurements. This is justified from a biophysical point of view when the ratio of external and internal resistance to heat flow (the Biot number) in a system under transient heat exchange is less than 0.1, in which case the system can be considered to be of

uniform temperature (Porter *et al.* 1973). Following the calculations of Porter *et al.* (1973) for a 217g lizard, one obtains a Biot number of exactly 0.1. Kerr *et al.* (2004) used the same data loggers to estimate body temperature of a larger lizard, *Tiliqua rugosa* (adult mass ~ 700g). They justified this using the findings of Chilton and Bull (1992), who compared internal (cloacal) temperature as measured remotely by thermistor-transmitters with spot measures of surface body temperature for 16 adult *T. rugosa* and obtained a mean difference of 0.5 °C (range -3.8 to 3.8 °C, across a body temperature range of 13.4 °C to 32.2 °C).

Very few records of T_b exist for *L. kintorei* — Pianka (1969) recorded a single field T_b value of 25.2 °C and Henzell (1972) reported a mean T_b of 33.6 °C under laboratory conditions. Due to the difficulties in obtaining individuals of this threatened species for laboratory observations, we assumed the critical thermal max (CT_{max}) for *L. kintorei* to be 43.1 °C by averaging existing published CT_{max} data for *Liopholis inornata* (42.8 °C; Heatwole and Taylor 1987) and unpublished CT_{max} data for *Liopholis slateri* (43.5 °C). Although these two species differ in body size, they are closely related to *L. kintorei* (Pianka Giles 1982) and therefore we have used this estimated value as a reference point on our plots.

Activity budget and activity phase

A series of individual time budgets were created where half-hourly mean surface operative temperatures, burrow entrance temperatures, sub-surface soil temperatures (used as a proxy for burrow system temperatures when inferring the location of the skinks within a burrow system; Fig. S1), and weather data (rainfall and solar radiation) were plotted against the T_b of an individual *L. kintorei* over a specified period. We developed an algorithm to

compute the absolute difference between each available temperature and the body temperature of the individual lizard, to identify the closest of the environmental temperatures to the lizard body temperature. This automated procedure faced ambiguities at sunrise and sunset when operative temperatures and burrow system temperatures were the same within any half hour period. The predictions were thus manually checked to judge the inferred location and activity state of each individual skink based on the state in the previous time intervals (Fig. S2). Activity states were: 1) active deep in burrow; 2) inactive deep in burrow; 3) active shallow in burrow; 4) inactive shallow in burrow; 5) at burrow entrance, or; 6) on the surface. Activity within the burrow was defined as a change in the depth of location within the burrow system across the half-hour time steps.

To define activity phase from T_b observations, we determined the dawn and dusk time periods based on solar radiation data collected from the remote weather station. We defined these periods as when solar radiation values were between 1-20 W m⁻² such that dawn and dusk occurred between the hours of 6.00 am and 7.00 am (1 hour), and 6.30 pm and 7.30 pm (1 hour), respectively. Accordingly, diurnal activity was defined as the hours between 7.00 am and 6.30 pm (11.5 hours) and nocturnal activity as the hours between 7.30 pm and 6.00 am (10.5 hours). Pearson's Chi-square test of independence was used to test for statistical independence between activity state and time of day (Quinn and Keough 2002). From these data we generated: 1) a mean activity budget; 2) individual activity budgets for 17 lizards, and; 3) daily activity budgets for 10 lizards (those with the most data overall) for a period of a week where most concurrent data were available.

Potential activity times and restrictions under current and future climatic conditions

We estimated monthly and annual proportions of thermally suitable time (i.e. within the range of observed surface body temperatures, 27.1 °C to 37.6 °C, based on our observed data for 2013) during the day, night, dawn and dusk where *L. kintorei* could be active on the surface (either within exposed or deeply shaded habitats), or the burrow system entrance (5 cm to 15cm deep). If conditions were thermally unsuitable (i.e. outside the observed T_b range), inactivity deep within the burrow system was assumed. We did not estimate the proportion of thermally suitable time at mid depths or deep within the burrow system because at these locations T_e never exceeded the voluntary maximum T_b (39.6 °C) of *L. kintorei* under current climatic conditions or future warming scenarios. We also excluded partly shaded surface conditions and focused the analysis on the extremes of T_e — exposed and deeply shaded. We then assessed how this activity potential would change under a projected climate change scenario for the site in 2070. We extracted monthly climate change scenario estimates of maximum air temperature from six climate models for our study site (see Briscoe *et al.* 2016, for details on the climate models used). Although an increased frequency of extreme high daily temperatures has been predicted for central Australia, we imposed an averaged, uniform increase in maximum air temperature of 2.8 °C in 2070, because there was little variation among the models or between months within models and there remains uncertainty around the nature of these extreme temperature events (Reisinger *et al.* 2014; Fig. S3). To predict future thermal stress levels, we added the defined increases in temperature to our operative temperature and burrow system temperature data.

Buffering effect of the burrow system

We demonstrated the current effectiveness of burrow systems to regulate *L. kintorei* body temperature by plotting the distribution of adult *L. kintorei* observed field body temperature against sub-surface soil temperatures ranging from 5 cm to 1 m (used as a proxy for burrow system temperatures), and against observed surface operative temperatures within exposed, partly shaded and deeply shaded micro-habitats. In addition, we quantified the frequency, intensity and duration of current and future levels of thermal stress experienced within the burrow system. We compared the observed upper thermal tolerance limit ($T_{vol.\max}$) of *L. kintorei*, derived from the activity budget analysis, to the minimum hourly maximum temperatures of the burrow system at three depths (deep, mid and burrow entrance) to calculate: 1) the percentage of a year T_e at a given location in the burrow exceeded $T_{vol.\max}$; 2) the maximum degrees above $T_{vol.\max}$, and; 3) the maximum consecutive hours above $T_{vol.\max}$. This allowed us to estimate the extent that the burrow system buffers this species from extreme temperatures under current and future climatic conditions.

Results

*Field body temperatures of *Liopholis kintorei**

We obtained data on the field T_b of 20 individual adult *L. kintorei* between early September and mid December 2013 (mid spring and early summer). Each individual was monitored between three and 50 days resulting in 33 504 T_b temperature data points. Three individual T_b samples were removed from analysis—one skink was preyed upon by a woma python

(*Aspidites ramsayi*) and two additional skinks exhibited no movement, suggesting the logger detached early on.

During the study period the minimum and maximum T_b recorded during all activity was 25.7 °C and 39.6 °C, respectively, and the mid 50% T_b ranged from 28.6 °C to 32.1 °C (Fig. 5.2). The minimum and maximum T_b recorded during surface activity was 27.1 °C and 37.6 °C respectively and the middle 50% T_b during surface activity ranged from 32.1°C to 34.6 °C (Fig. 5.2).

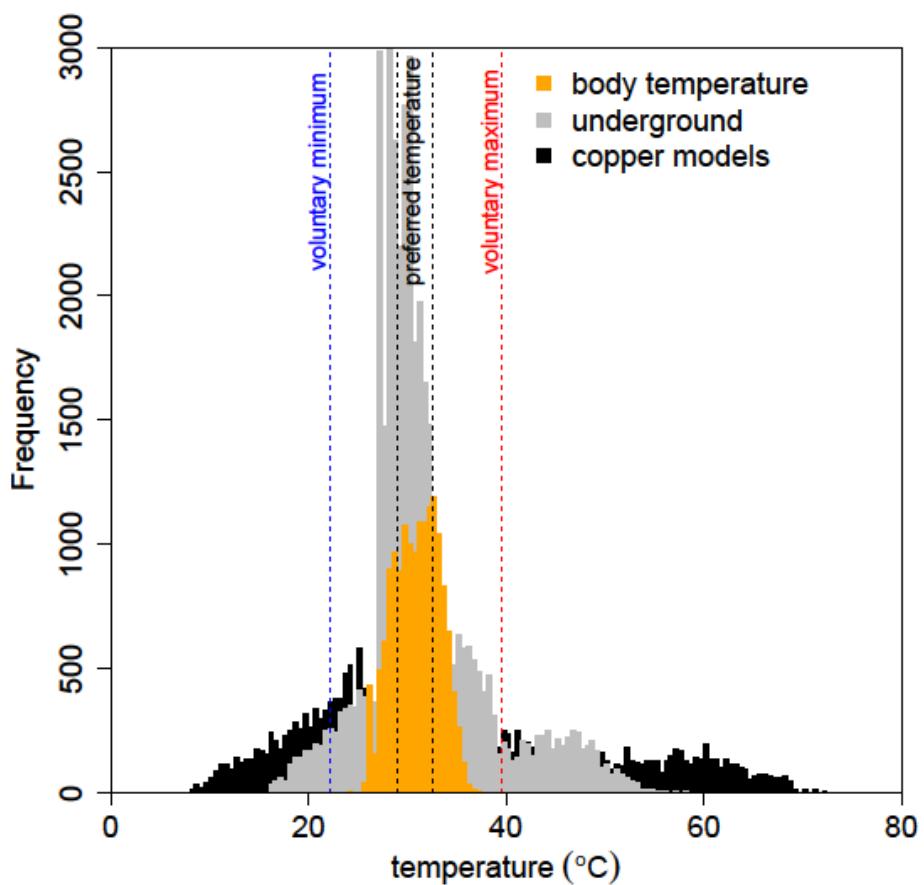


Fig. 5.2 The frequency distribution of observed field body temperatures of adult *Liopholis kintorei*, surface operative temperatures (copper models) and sub-surface soil profile temperatures.

Activity budget and activity phase

The number of days over which T_b was recorded varied in length for each individual skink — ranging between three and 50 days (Fig. S5.4). Among-individual activity varied, however, where observations were longer than 6 days, activity budgets showed consistent patterns of high proportions of inactivity within the burrow with relatively smaller amounts of activity at shallow depths within the burrow, at the entrance or on the surface. When surface activity was observed, the proportions were consistently higher during dusk (Fig. S5.4). Among-day activity varied substantially, with no evidence of synchrony in activity among individuals (Fig. S5.5).

Mean activity levels varied significantly across the different periods of the day ($\chi^2 = 941.2, df = 15, P < 0.001$; Fig. 5.3). *Liopholis kintorei* spent 4 % of their total observed activity time on the surface. The proportion of surface activity was significantly higher during the hours of dusk (31%) than during the dawn (0%), day (5%) or night (1%) ($\chi^2 = 148, df = 5, P < 0.001, \chi^2 = 963.4, df = 5, P < 0.001$ respectively). Only 8% of time was spent at the burrow entrance, with proportions similar during the day and night (47% and 49% respectively). A large proportion (88%) of time was spent sequestered within the burrow system where skinks appeared to be inactive for 82% of the time. Most time was spent deep within the burrow, at a depth ranging between 50 cm and 1 m (52%), and 35% of time was spent at shallower depths between 15 cm to 30cm.

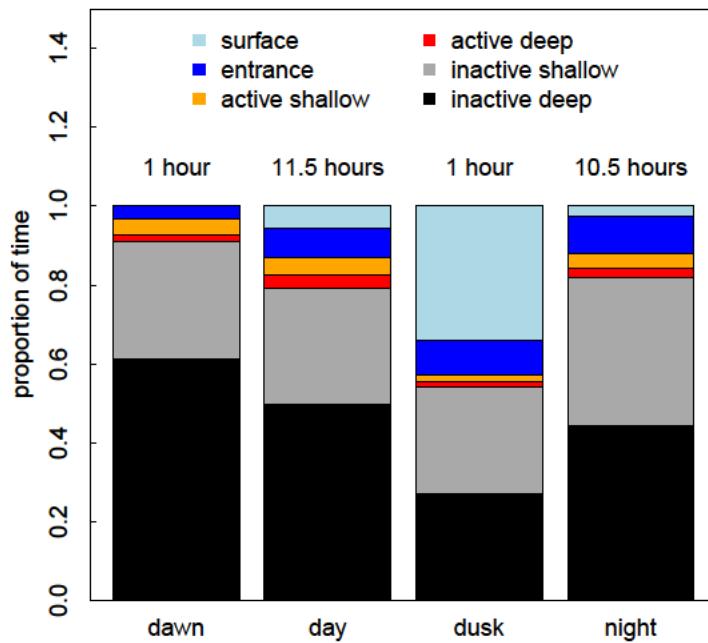


Fig. 5.3 The observed proportion of time an adult *L. kintorei* spends active or inactive within the burrow system, at a burrow entrance or on the surface. The number of hours that each period of the day comprised of is given above the bars.

Annual cycles of surface operative environmental temperatures within arid spinifex sandplains

Maximum T_e values reached 76 °C and 78 °C in exposed conditions for adult and juvenile lizards, respectively (Fig. 5.4a; Fig S5.6; Table S5.1). Deeply shaded habitats were cooler by 22 °C for adults and 24 °C for juvenile lizards. Minimum T_e values measured -3°C for adult and juvenile lizards in exposed conditions — surface conditions were 2 °C warmer in deeply shaded habitats (Fig 5.4a; Fig. S5.6; Table S5.1). High rainfall events, as observed in January, April and, to a lesser extent July, decreased T_e values across all levels of cover (Fig. 5.4a, Fig. S5.6).

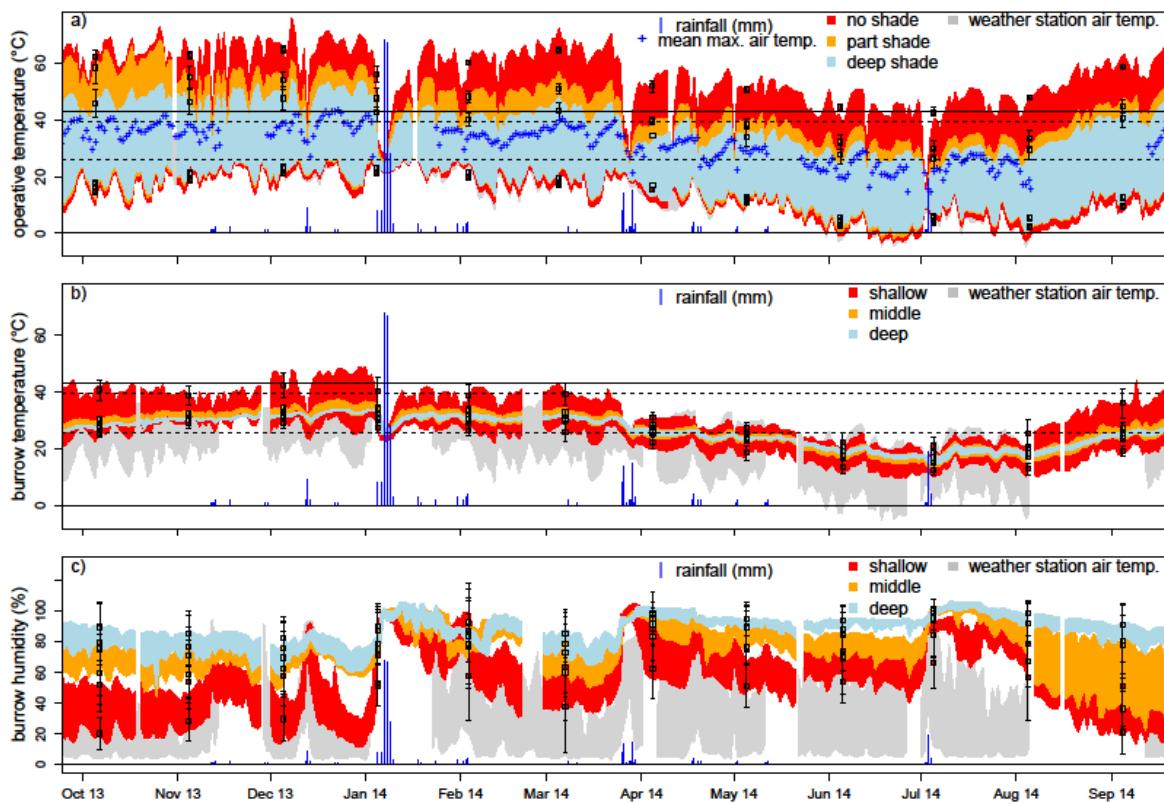


Fig. 5.4 Daily mean minimum and maximum surface operative temperatures for adult *L. kintorei* (a); daily mean minimum and maximum temperature within the burrow system (b), and daily mean minimum and maximum relative humidity within the burrow system (c). Monthly minimum and maximum means and standard deviation are denoted by the open squares and lines. *Liopholis kintorei* voluntary minimum and maximum field body temperatures are denoted by the dashed black lines with the critical thermal maximum indicated by the solid black line.

Annual cycles of temperature, relative humidity and vapour density of the burrow system

Burrow system minimum and maximum temperatures varied by month at all depths following a typical seasonal pattern. The highest monthly maximum temperatures were

recorded during the summer season (January and December) and reached as high as 34 °C deep in the burrow, 37 °C at mid depths, and 49 °C at the burrow entrance (Table S5.2). The lowest monthly minimum temperatures at all depths were recorded in July — temperatures dropped to 14 °C deep within the burrow system, 13 °C at mid depths and 9 °C at the burrow entrance. In some months, following rainfall, monthly maximum temperatures dropped substantially across all depths following an increase in soil moisture (Fig. 5.4b). In January, for example, temperature at all depths dropped dramatically after a six-day rainfall event where 178 mm of rain was recorded at the study site (Fig. 5.4b).

Maximum relative humidity occurred mostly deep within the burrow system with levels reducing towards the burrow entrance (Fig. 5.4c). However, there was a strong interaction between burrow system depth, month and humidity and, in some months, following rainfall, monthly maximum relative humidity levels were highest at the burrow surface (Fig. 5.4c; Table S5.3).

Vapour density values within the burrow system followed seasonal air temperature patterns with higher values within the summer months and lower values within the winter months (Fig. S5.7; Table S5.4). Vapour density correlated with atmospheric conditions, but was consistently higher within the burrow system at all depths (Fig. S5.7).

Potential activity times under current and future climatic conditions

The estimated proportion of time an adult *L. kintorei* could potentially spend active on the surface within exposed or shaded conditions was found to increase by 24% with a warming effect of 2.8 °C by 2070, with proportions changing notably at dawn (+11%) and at night (+28%; Fig. 5.5). During dusk, the primary activity phase period for *L. kintorei*, we estimated

that the amount of thermally suitable time available on the surface will decrease marginally by 2% (Fig. 5.5). As air temperatures increase, diurnal surface activity will be restricted, resulting in an increased proportion (16%) of time spent deep within the burrow system (Fig. 5.5).

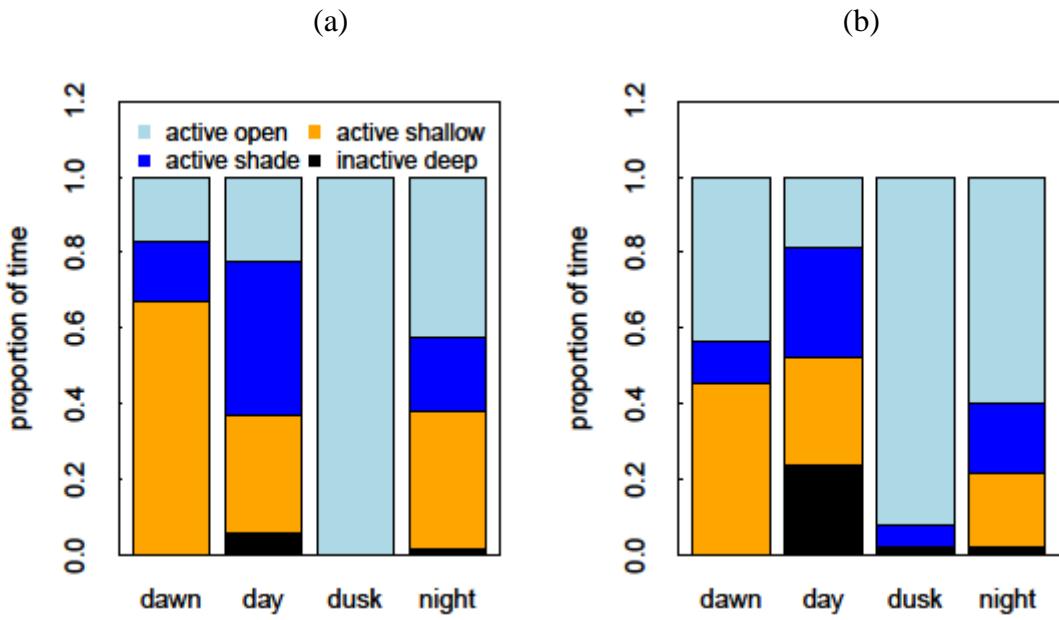


Fig. 5.5 The total estimated proportion of time in 2014 (a) and 2070 (b) during the day (11.5 h), night (10.5 h) dawn (1 h) or dusk (1 h), that an adult *L. kintorei* could potentially spend active on the surface, at a burrow entrance, or inactive deep within the burrow system.

When comparing present and future potential activity time across seasons, we predict potential surface activity (in exposed and shaded conditions) to increase across all seasons with a warming effect of 2.8 °C by 2070 (Fig. S5.8). A 40% increase is predicted during spring (September, October and November) and autumn (March, April and May). Potential surface activity (within exposed habitats) at dusk will become greater during the month of May —

under current climatic conditions, activity in this month is restricted to diurnal activity.

Similarly, the proportion of potential activity time in summer (December, January and February) is predicted to increase from 55% to 73%. Although potential activity time during the winter months (June, July and August) is predicted to increase from 14% to 20%, surface activity will remain restricted to the day (Fig. S5.8).

Buffering effects of the burrow system

The burrow system provides an exceptional buffer against maximum temperature extremes (Fig. 5.6). Hourly temperatures at mid and deep depths within the burrow system did not exceed the voluntary maximum T_b (39.6°C) of *L. kintorei* under current climatic conditions and future warming scenarios. The burrow entrance is more exposed to external atmospheric conditions, and measured temperatures exceeded the voluntary maximum T_b (Table 5.1). Under future climatic warming scenarios, we estimated that levels of thermal stress will increase at the burrow entrance, with burrow entrance activity being restricted by 3% by 2070 (Table 5.1).

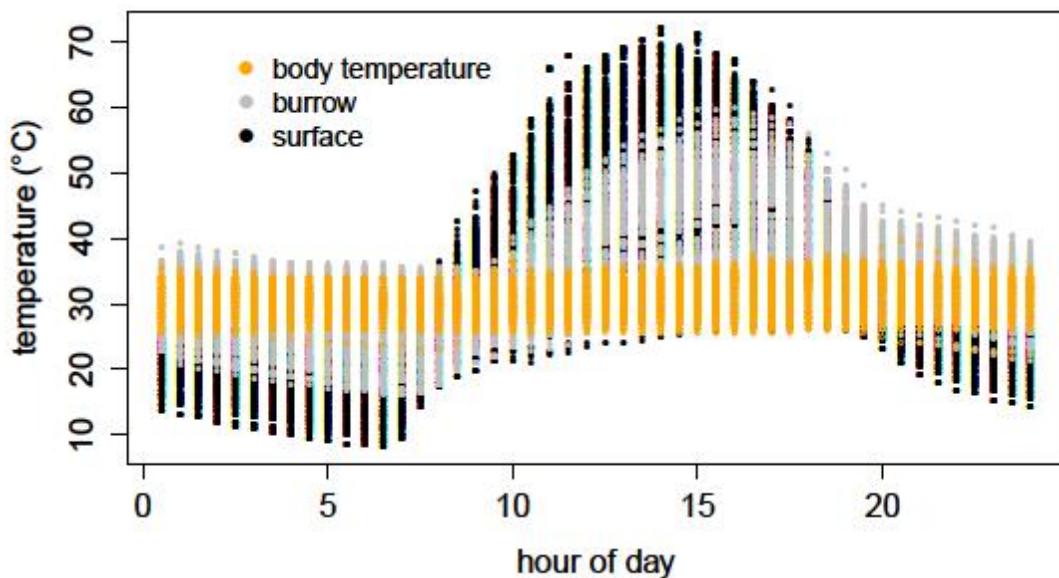


Fig. 5.6 The effectiveness of the burrow system to buffer individuals from temperature extremes is illustrated by observed hourly sub-surface temperatures (as a proxy for burrow system temperature), in comparison with observed surface temperatures.

Table 5.1 Contemporary and future thermal stress levels where the observed voluntary maximum field body temperature ($T_{vol.max}$) was greater than the burrow entrance operative temperature over a 12-month period.

Indicators of thermal stress at the burrow entrance	2013/2014	2070
Percentage of the year above $T_{vol.max}$	0.4	3
Maximum consecutive hours above $T_{vol.max}$	5	10
Maximum degree in any given hour above $T_{vol.max}$	2	5

Discussion

Although it is well established that lizard species are potentially vulnerable to the impacts of climate warming due to elevated field body temperatures (Grant and Dunhan 1988; Huey *et al.* 2009; Huey 2009; Sinervo *et al.* 2010; Sunday *et al.* 2014), it is critical that assessments of vulnerability to warming consider species-specific activity phase and the buffering potential of the microhabitats that a species uses (Scheffers *et al.* 2014). One of our aims was to test the hypothesis of Sinervo *et al.* (2010) that activity restriction through climate warming is generally a threatening process for lizards. We specifically considered *L. kintorei* in this context because it was a case study presented in Sinervo *et al.* (2010), but our findings will be relevant to many other taxa, particularly species with a nocturnal or crepuscular activity phase and/or that routinely make use of subterranean retreat sites.

Our data led us to reject the hypothesis that activity restriction due to increased field body temperatures caused the recent local extinctions of *L. kintorei*. First, above-ground temperature does not appear to be limiting surface activity in this species. Indeed, one of the most striking findings of our study is the very low level of surface and burrow entrance activity engaged in by *L. kintorei*, amounting to only 9% of their total activity budget despite 74% of time being thermally suitable. From the limited data available on lizard time budgets, many species, particularly sit-and-wait predators (Huey and Pianka 1981; Hertz *et al.* 1988), spend only a fraction (< 30%) of their potential activity period foraging actively, whereas active foragers spend a higher proportion of their potential activity period engaged in vigorous activity. Thus, it may not generally be true that potential activity time is a limiting factor for many lizards.

Second, our data indicate that *L. kintorei* is crepuscular (with similar proportions of diurnal and nocturnal surface activity observed), and we estimated that an increase in air temperature of 2.8 °C by 2070 will actually increase rather than decrease the total potential surface activity times during dawn and dusk. Seasonally, potential activity periods are predicted to increase, particularly in May (late autumn) and September (early spring), thus extending the active season (summer). An examination of individual activity budgets showed a substantial amount of asynchronous daily variation, with surface activity occurring sporadically, indicating that lizard activity patterns were largely independent of each other and thus not tied to particular environmental conditions (for example, all lizards emerging on warm nights). An increase in potential activity time associated with climate warming is likely to be true for most crepuscular or nocturnal lizards as suitable thermal conditions increase (Kearney 2013).

The dry weather conditions that prevailed over much of the study period may have influenced surface activity of the skinks. Relative humidity, rainfall and soil moisture content are expected to influence surface activity for two primary reasons. First, desiccation risk may restrict surface activity to wetter periods, as was demonstrated experimentally in the Gila Monster *Heloderma suspectum* (Davis and DeNardo 2009). Second, the primary food source for *L. kintorei* is harvester termites of the genus *Drepanopterus* (McAlpin 2011). These insects become active in very high numbers on the surface primarily from dusk to dawn during periods of high humidity, and swarming events occur after summer rainfall (Andersen 2005). During these times *L. kintorei* may spend more time on the surface at night foraging widely for this high protein food source.

Finally, our data clearly show that burrow systems provide an exceptional buffer to extremes of temperature and conditions of low humidity. Maximum burrow system temperatures measured during the study period at mid to deep depths (30 cm – 1m) remained within the estimated voluntary thermal tolerance and estimated lethal limits of this species throughout the year and relative humidity remained high (monthly means ranging from 62% to 97%) deep within the burrow system. Similarly, the temperatures we observed at these depths did not exceed the lethal limits known for any other lizard of the Australian arid zone and generally remained within known voluntary thermal tolerances across scincid and agamid lizards (Warburg 1965; Greer 1980; Pianka 1986; Heatwole and Taylor 1987).

With the predicted increases in air temperatures under future warming scenarios, the burrow system will continue to provide a buffer for this species, with burrow system temperatures remaining below the observed maximum T_b at mid and deep depths. Thus *L. kintorei*, and the wide range of other taxa that use their burrow systems or that construct their own, even if only at depths of 30 cm, are likely to be buffered from the direct effects of climate warming on body temperature. For these reasons we conclude that threatening processes other than the direct effect of climate warming must be sought to explain the observed loss of *L. kintorei* at some localities (Cadenhead *et al.* 2015; Moore *et al.* 2015; Moore *et al.* 2017).

Although previous studies have inferred the location (e.g. surface vs. retreat site) of individual reptiles based on body temperature and operative environmental temperatures (e.g. Christian and Weavers 1996; Kerr *et al.* 2004; Davis *et al.* 2008), there have been no studies of the thermal biology of a lizard species during periods of inactivity (not

hibernating) within a subterranean refuge site. We have demonstrated how two widely used thermal ecological methods (the measurement of operative and field body temperatures), can be combined to make inferences on activity budget of a burrowing species, which are inherently difficult to observe. Although we were not able to validate the activity budgets through direct observation of periods of aboveground activity, the contrast in thermal environments above and below ground was so extreme in magnitude, amplitude and phase (Fig. 4-5) that we could be confident in our inferences. Moreover, our inference of patterns of surface activity were consistent with the presence of tracks around the burrow system made during routine and concurrent surveys of the burrow systems (Moore *et al.* 2015), and the activity budgets overall were consistent with field observations (McAlpin unpublished data; Pearson 2001). This research method has enabled us to assess in detail how the burrow system is used by *L. kintorei* throughout the active season, revealing that it spends the vast majority of its time deep in the burrow where temperatures are generally lowest and humidity highest. In addition, we were able to infer that lizards were inactive (or at least not changing depth) for most of the time spent in the burrow. Thus, it appears that *L. kintorei* behaves in a manner that prioritises the conservation of energy and water. The method we developed can be transferred to other reptile, mammal and avian species that construct and maintain a burrow or use existing burrows within the landscape, across a variety of habitats where species specific thermal biology questions are pertinent.

Lizards have been identified as one of the most threatened taxa by climate warming (Huey *et al.* 2009; Sinervo *et al.* 2010; Huey *et al.* 2012). Because our findings reflect the general buffering capacity of underground microclimates, our conclusions for *L. kintorei* are

more generally applicable to burrowing ectotherms within desert environments and highlight the need to consider the buffering properties of retreat sites and species-specific activity phase when forecasting climate change impacts. Our study shows how critical it is to ground-truth predictive models of climate warming impacts carefully against the microclimates available to a given species. Moreover, predictive models must be able to realistically capture this microclimatic variation in addition to the behavioral thermoregulatory capacity for organisms to exploit it (Sears et al. 2011; Buckley 2013; Kearney 2013; Kearney *et al.* 2014; Briscoe *et al.* 2016; Kearney and Porter 2016; Levy *et al.* 2016a; Sears *et al.* 2016). It is equally important to test whether activity time is indeed a significant limiting factor from a thermal perspective, and to put activity budgets into the context of the life cycle, phenology and life history (Kearney 2013; Levy *et al.* 2016b; Maino *et al.* 2016). The modelling tools for such analyses are becoming increasingly available, and such analyses will be of particular importance when considering the management of endangered species to ensure the optimum allocation of resources to the most relevant threatening processes.

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Author's Contributions

All authors conceived the ideas and designed the general methodology. DM collected all field data and led the writing of the manuscript. MK and DM analysed the data. All authors contributed to the drafts and gave their final approval for publication.

References

- Andersen, A. N. (2005). 'Termites of Northern Australia.' (Alice Springs, NT: Barker Souvenirs.)
- Autumn, K., Jindrich, D., DeNardo, D., and Mueller, R. (1999). Locomotor performance at low temperature and the evolution of nocturnality in geckos. *Evolution* **53**(2), 580-599.
- Bakken, G. S., and Angilletta, M. J. (2014). How to avoid errors when quantifying thermal environments. *Functional Ecology* **28**(1), 96–107. doi:10.1111/1365-2435.12149.
- Bakken, G. S. (1992). Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist* **32**, 194-216.
- Bakken, G. S., and Gates, D. M. (1975). Heat-transfer analysis of animals: some implications for field Ecology, Physiology, and Evolution. In: Gates D. M., Schmerl R. B. (eds) Perspectives of Biophysical Ecology. *Ecological Studies (Analysis and Synthesis)*, vol 12. pp. 255-290. (Springer: Berlin, Heidelberg.)

- Bartholomew, G. A., and Tucker, V. A. (1963). Control of changes in body temperature, metabolism, and circulation by the agamid lizard, *Amphibolurus barbatus*. *Physiological Zoology* **36**(3), 199-218.
- Bogert, C. M. (1949). Thermoregulation and ectic body temperatures in Mexican lizards of the genus *Sceloporus*. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México* **20**, 415-426.
- Briscoe, N. J., Kearney, M. R., Taylor, C. A., and Wintle, B. A. (2016). Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. *Global Change Biology* **22**(7), 2425-39.
- Buckley, L. B. (2013). Get real: putting models of climate change and species interactions in practice. *Annals of the New York Academy of Sciences* **1297**, 126-138.
- Bureau of Meteorology (2016). *Climate Data Online*. Available from:
<http://www.bom.gov.au/jsp/ncc/cdio/weatherData>. [accessed July 2016].
- Bustard, H. R. (1967). Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. *Copeia* **4**, 753-758.
- Bogert, C. M. (1949). Thermoregulation in reptiles: A factor in evolution. *Evolution* **3**(3), 195-211.
- Cadenhead, N. C. R., Kearney, M. R., Moore, D., McAlpin, S., and Wintle, B. A. (2015). Climate and fire scenario uncertainty dominate the evaluation of options for conserving the Great Desert Skink. *Conservation Letters* **9**(3), 181-190.
- Chapple, D. G. (2003). Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs* **17**, 145-180.

- Chilton, N. B., and Bull, C. M. (1992). The on-host temperature environment for two Australian reptile ticks. *Australian Journal of Zoology* **40**(6), 583–592.
- Christian, K. A., and Weavers, B. W. (1996). Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological Monographs* **66**(2), 139-157.
- Cogger, H. (2014). 'Reptiles and amphibians of Australia (7th ed.).' (CSIRO Publishing: Collingwood, Australia.)
- Cowles, R. B., and Bogert, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* **83**, 261-296.
- Davis. J. R., Taylor, E. N., and DeNardo, D. F. (2008). An automated temperature-based option for estimating surface activity and refuge use patterns in free-ranging animals. *Journal of Arid Environments*, **72**(8), 1414-1422.
- Dawson, W. R. (1975). On the physiological significance of the preferred body temperatures of reptiles. *Perspectives of Biophysical Ecology* **12**, 443-473.
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Science* **105**(18), 6668-6672.
- Dennison, S. (2015). Social organisation and population genetics of the threatened great desert skink, *Liopholis kintorei*. Ph. D. Thesis. (Macquarie University: Sydney.)
- Dial, B. E. (1978). Aspects of the behavioral ecology of two Chihuahuan desert geckos (Reptilia, Lacertilia, Gekkonidae). *Journal of Herpetology* **12**(2), 209-216.
- Greer, A. E. (1980). Critical thermal maximum temperatures in Australian scincid lizards: their ecological and evolutionary significance. *Australian Journal of Zoology* **28**(1) ,91-102.

- Grant, B. W., and Dunham, A. E. (1988). Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* **69**(1), 167-176.
- Grimm-Seyfarth, A., Mihoub, J. B., and Henle, K. (2017). Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia. *Ecology and Evolution* **7**(17), 6803-6813.
- Heatwole, H. (1970). Thermal ecology of the desert dragon *Amphibolurus inermis*. *Ecological Monographs* **40**(4), 425-457.
- Heatwole, H. F., and Taylor, J. (1987). 'Ecology of reptiles.' (Chipping Norton, Australia: Surrey Beatty and Sons Pty Limited.)
- Henzell, R. P. (1972). Adaptation to aridity in lizards of the *Egernia whitei* species-group. Ph. D. Thesis. (Adelaide University.)
- Hertz, P. E. (1988). Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? *American Zoology* **28**(3), 927-938.
- Hertz, P. E. (1992). Evaluating thermal resource partitioning. *Oecologia* **90**(1), 127-136.
- Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In 'Biology of Retilia' pp. 25-74. (Academic Press: Cambridge, UK.)
- Huey, R. B., and Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology* **62**(4), 991-999.
- Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Pérez, H. J. Á., and Garland, T. (2009). Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London B: Biological Sciences* **276**(1664), 1939-1948.
- Huey, R. B., Losos, J. B., and Moritz, C. (2010). Are lizards toast? *Science* **328**(5980), 832-833.

- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., and Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behavior, physiology and adaptation. *Phil. Trans. R. Soc. B* **367**(1596), 1665-1679.
- Huey, R. B., Peterson, C. R., Arnold, S. J., and Porter, W. P. (1989). Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* **70**(4), 931-944.
- Huey, R. B., and Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology* **51**(3), 363-384.
- Humphreys, W. (1978). The thermal biology of *Geolycosa godeffroyi* and other burrow inhabiting Lycosidae (Araneae) in Australia. *Oecologia* **31**(3), 319-347.
- IUCN (2016). *The IUCN Red List of Threatened Species*. Version 2016-2.
<http://www.iucnredlist.org>. Downloaded on 04 September 2016
- Kearney, M., and Predavec, M. (2000). Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology* **81**(11), 2984-2996.
- Kearney, M., Shine, R., and Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences* **106**(10), 3835-3840.
- Kearney, M. R. (2013). Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters* **16**(12), 1470–1479.
- Kearney, M. R., Isaac, A. P., and Porter, W. P. (2014). microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. *Scientific Data* **1**, 140006. doi:10.1038/sdata.2014.6.

- Kearney, M. R., and Porter, W. P. (2016). NicheMapR - an R package for biophysical modelling: the microclimate model. *Ecography* **40**(5), 664-674.
- Kerr, G. D., Bull, C. M., and Cottrell, G. R. (2004). Use of an 'on board' datalogger to determine lizard activity patterns, body temperature and microhabitat use for extended periods in the field. *Wildlife Research* **31**, 171-176.
- Latz, P., Paltridge, R., and Holmes, J. (2003). Vegetation survey of Newhaven Reserve. A report prepared for *Birds Australia*. (Desert Wildlife Services: Alice Springs.)
- Levy, O., Buckley, L. B., Keitt, T. H., and Angilletta, M. J. (2016a). A dynamically downscaled projection of past and future microclimates. *Ecology* **79**(7), 1888-1888.
- Levy, O., Buckley, L. B., Keitt, T. H., and Angilletta, M. J. (2016b). Ontogeny constrains phenology: opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate. *Ecology Letters* **19**(6), 620-628.
- Lynch, M., and Gabriel, W. (1987). Environmental tolerance. *American Naturalist* **129**(2), 283-303.
- Maino, J. L., Kong, J. D., Hoffmann, A. A., Barton, M. G., and Kearney, M. R. (2016). Mechanistic models for predicting insect responses to climate change. *Current Opinion in Insect Science*.
- McAlpin, S. (2001). 'A Recovery Plan for the Great Desert Skink' (*Egernia kintorei*). (Arid Lands Environment Centre: Alice Springs, NT.)
- McAlpin, S. (2011). Social structure and mating systems of the great desert skink, *Liopholis kintorei*. M.Sc. Thesis. (Macquarie University: Sydney.)
- McAlpin, S., Duckett, P., and Stow, A. (2011). Lizards cooperatively tunnel to construct a long-term home for family members. *PLoS One* **6** e19041.

Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. (2015). Is fire a threatening process for *Liopholis kintorei*, a nationally listed threatened skink? *Wildlife Research* **42**, 207-216.

Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. (2017). Feeling the pressure at home: predator activity at the burrow entrance of an endangered arid-zone skink. *Austral Ecology* online. doi: 10.1111/aec.12547.

Moore, D., Stow, A., and Kearney, M. R. (2018). Under the weather? The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *Journal of Animal Ecology* accepted 10th Jan 2018. doi: 10.5281/zenodo.1157165.

Morton, S. R., and James, C. D. (1988). The diversity and abundance of lizards in arid Australia: a new hypothesis. *American Naturalist* **132**(2), 37-256.

Pearson, D., Davies, P., Carnegie, N., and Ward, J. (2001). The great desert skink (*Egernia kintorei*) in Western Australia: distribution, reproduction and ethno-zoological observations. *Herpetofauna Sydney* **31**, 64-68.

Pianka, E. R. (1967). On lizard species diversity: North American flatland deserts. *Ecology* **48**(3), 334-351.

Pianka, E. R. (1986). 'Ecology and natural history of desert lizards: analyses of the ecological niche and community structure.' (Princeton, NJ: Princeton University Press.)

Pianka, E. R., and Giles, W.E. (1982). Notes on the biology of two species of nocturnal skinks, *Egernia inornata* and *Egernia striatata* in the Great Victoria desert. *West. Aust. Nat* **15**, 44-49.

- Pianka, E. R., and Pianka, H. D. (1976). Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* **1**, 125-142.
- Porter, W. P., Mitchell, J. W., Beckman, W. A., and DeWitt, C. B. (1973). Behavioral implications of mechanistic ecology. *Oecologia* **13**(1), 1-54.
- Quinn, G. P., and Keough, J. M. (2002). 'Experimental Design and Data Analysis for Biologists.' (Cambridge University Press: Cambridge, UK.)
- R Core Team (2015). *R: A language and environment for statistical computing*. R foundation for Statistical Computing, Vienna, Austria.
- Reisinger, A., Kitching, R., Chiew, F., Hughes, L., Newton, P., Schuster, S., Tait, A., Whetton, P., Barnett, J., Beeken, S., and Blackett, P. (2014). Australasia. In 'Climate Change 2014: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change'. (Eds B. Fitzharris and D. Karoly.) pp. 1371–1438.
- Roger, M. (2008). Retreat site characteristics and body temperatures of *Saurodactylus brosseti* Bons and Pasteur, 1957 (Sauria: Sphaerodactylidae) in Morocco. *Bull. Soc. Herp. Fr* **128**, 41-48.
- Sears, M.W., Raskin, E., and Angilletta Jr, M. J. (2011). The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr Comp Biol* **51**, 666-675.
- Sears, M. W., Angilletta, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., and Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences* **113**, 10595-10600.

- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., and Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology* **20**, 495-503.
- Shine, R., and Kearney, M. R. (2001). Field studies of reptile thermoregulation: how well do physical models predict operative temperatures? *Functional Ecology* **15**, 282-288.
- Sinervo, B., Mendez-De-La-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M.,...Gadsden, H. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894-899.
- Stafford-Smith, M., and Morton, S. (1990). A framework for the ecology of arid Australia. *Journal of Arid Environments* **18**, 255-278.
- Stirling, E. C., and Zeitz, A. (1893). Vertebrata. *Transactions of the Royal Society of South Australia* **16**, 154-176.
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, K. R., Dulvy, K. N., Longino, J. T., and Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences* **111**, 5610-5615.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C.,...Erasmus, B. F. N. (2004). Extinction risk from climate change. *Nature* **427**(6970), 145-148.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., and Erasmus, B. F. N. (2004). Extinction risk from climate change. *Nature* **427**(6970), 145-148. doi:10.1038/nature02121.

Warburg, M. R. (1964). Studies on the environmental physiology of some Australian lizards from arid and semi-arid habitats. *Australian Journal of Zoology* **13**, 563-575.

Webb, J. K., and Shine, R. (1998). Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biological Conservation* **86**(2), 233-242.

Supplementary material

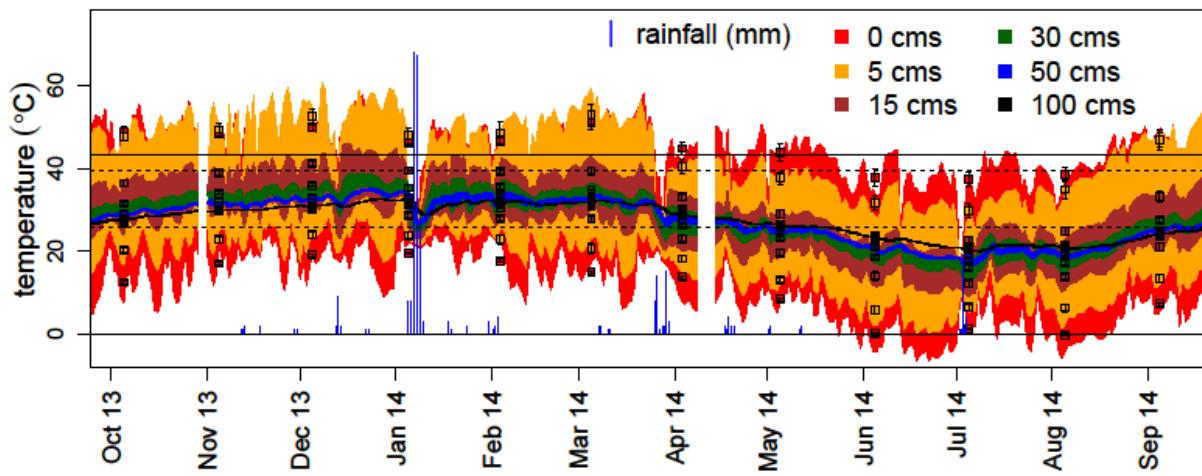


Fig. S5.1 The annual temperature range (daily mean minimum and maximum) of the soil profile. Voluntary maximum field body temperatures of *Liopholis kintorei* is denoted by the dashed black lines with the critical thermal maximum body temperature indicated by the solid black line

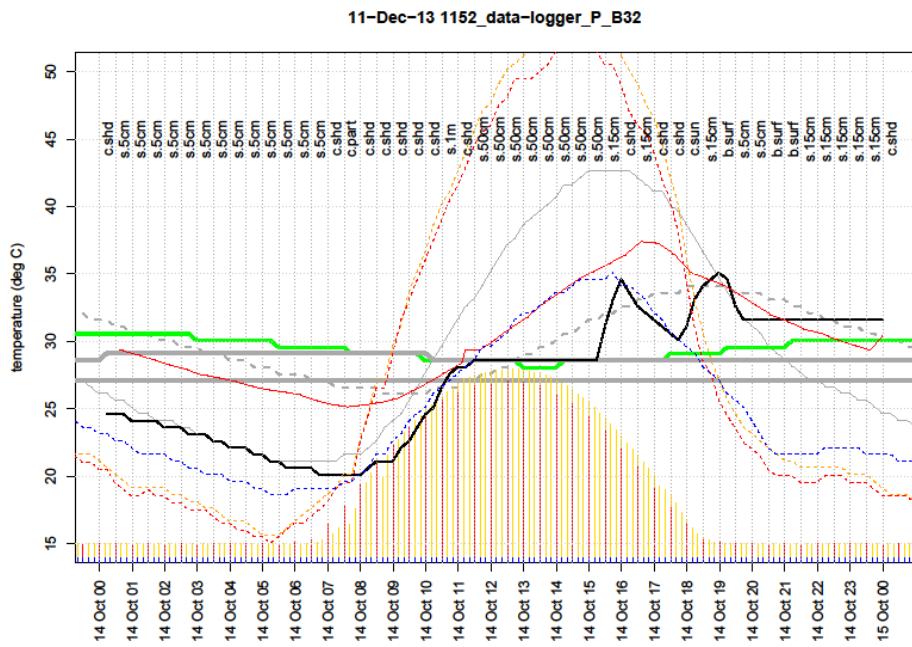
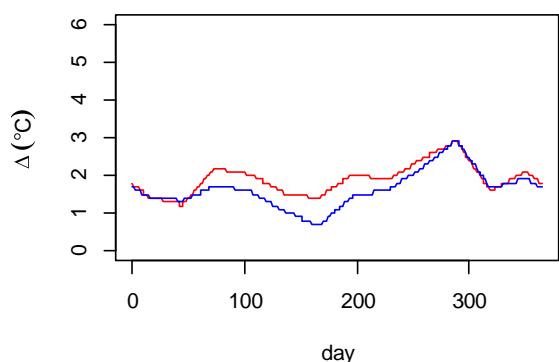
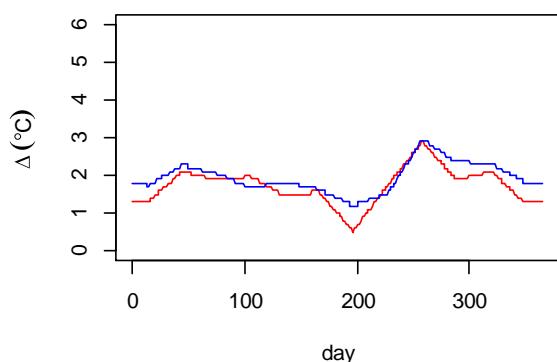


Fig. S5.2 An example of the activity plot output for every half hour over a 24-hour period. The field body temperature of an individual skink is plotted in black, the dashed lines denote operative temperature for an adult skink within the three major surface microclimates: full sun (dashed red); part shade (dashed orange), and; full shade (dashed blue). Sub-surface soil temperatures used as a proxy for burrow system temperatures are denoted as follows: 1 m (solid thick grey); 50 cm (solid thin grey); 30 cm (solid green), 15 cm (dashed grey), and; 5 cm (very thin solid grey). The solid red line denotes the average burrow entrance temperature. Weather conditions are plotted at the base: rainfall (blue horizontal lines); actual solar radiation (red vertical lines); and, predicted solar radiation (red vertical lines). The automatically-generated inferred location of the skink is printed at the top of the plot and was manually observed and corrected where necessary. They have been abbreviated in the following way: 's' for sub-surface soil temperature at the depth indicated, e.g. s.15cm is the temperature of the soil at a depth of 15 cm; 'c' refers to the operative temperatures inferred from the copper models either from deep (c.shd) and partly (c.part) shaded conditions or full sun (c.sun), and; 'b.surf' refers to the temperature at the entrance of the burrow system.

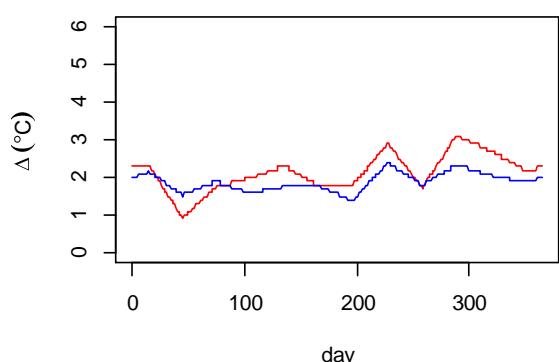
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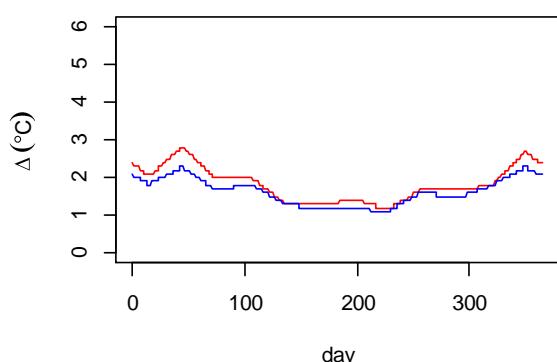
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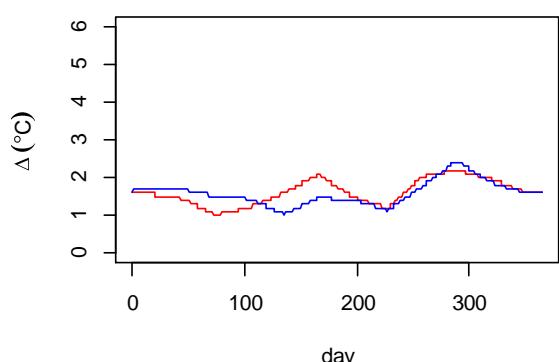
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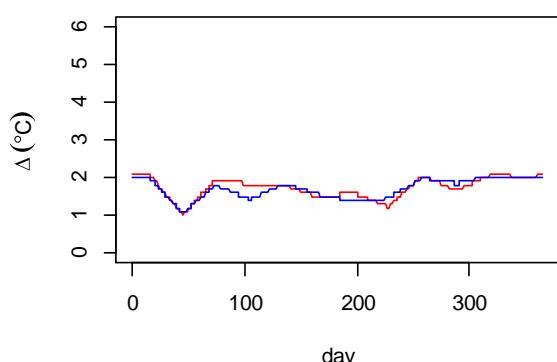
GFDL-CM3 2050



HadGEM2-CC 2050



HadGEM2-ES 2050



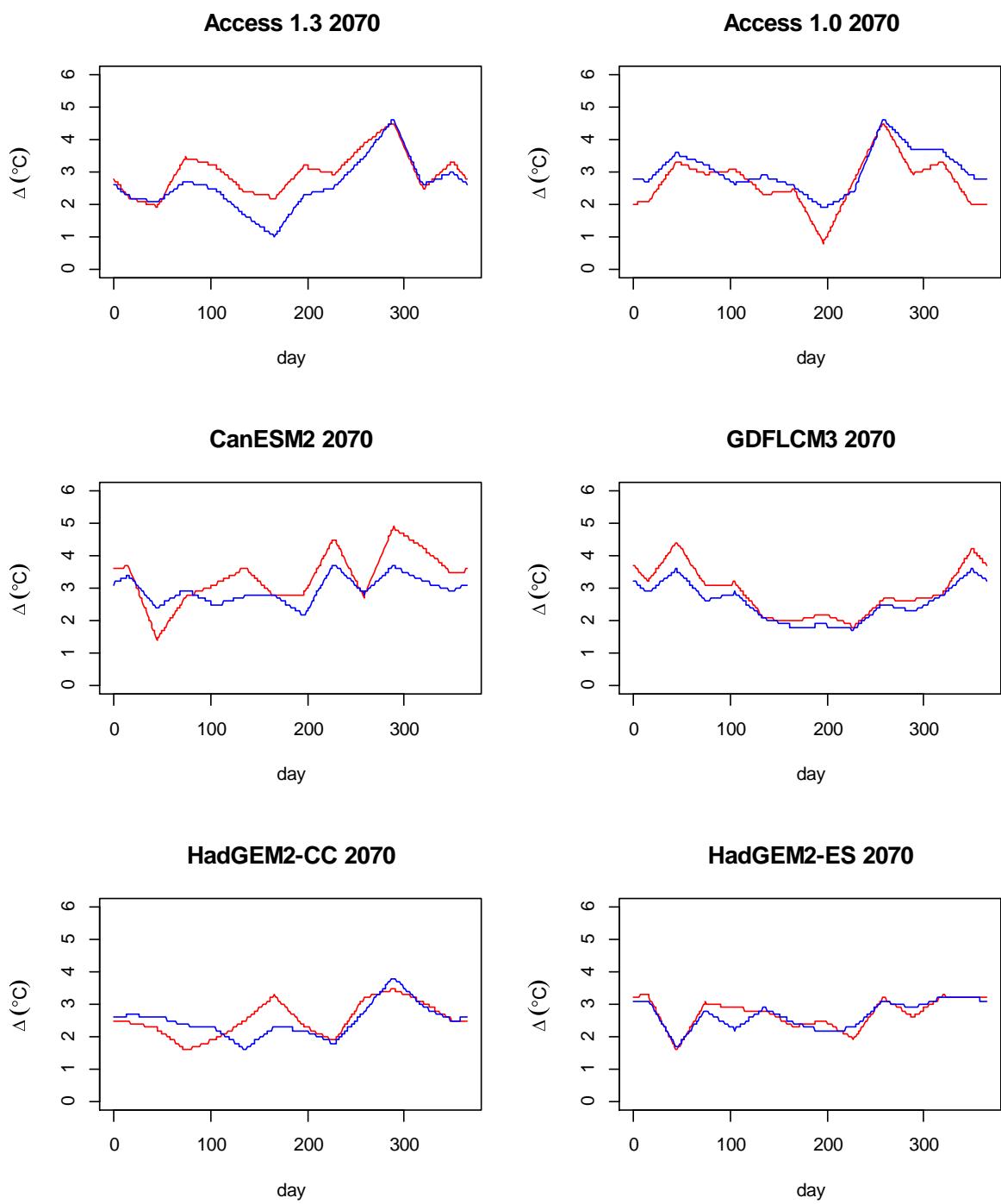


Fig. S5.3 The increases in daily minimum (blue solid line) and maximum (red solid line) temperatures predicted by various models for 2050 and 2070 (see Briscoe *et al.* 2016 for details on the climate models used).

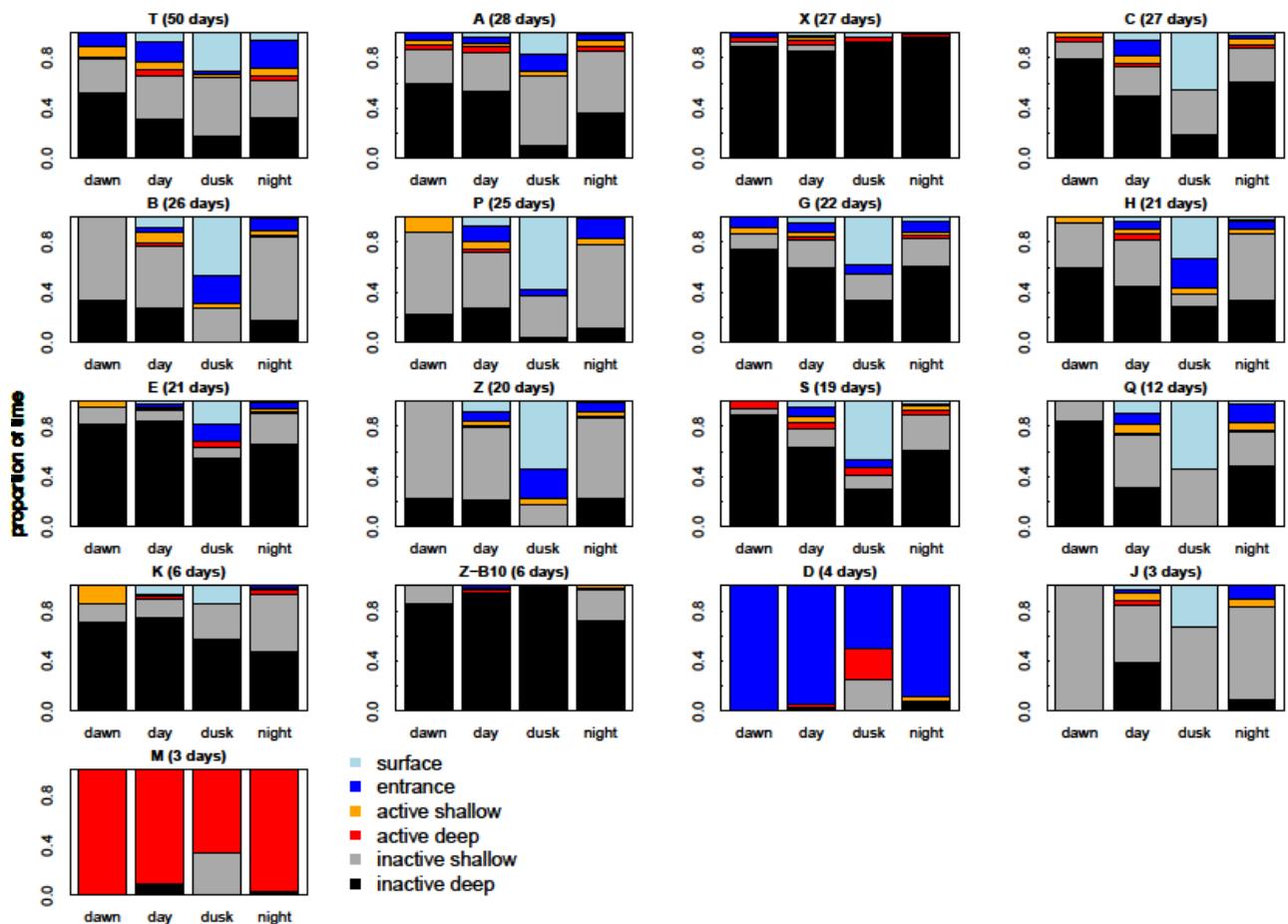


Fig. S5.4 Individual *Liopholis kintorei* activity budgets. Individual lizard identification and the number of days data was collected is indicated above each plot.

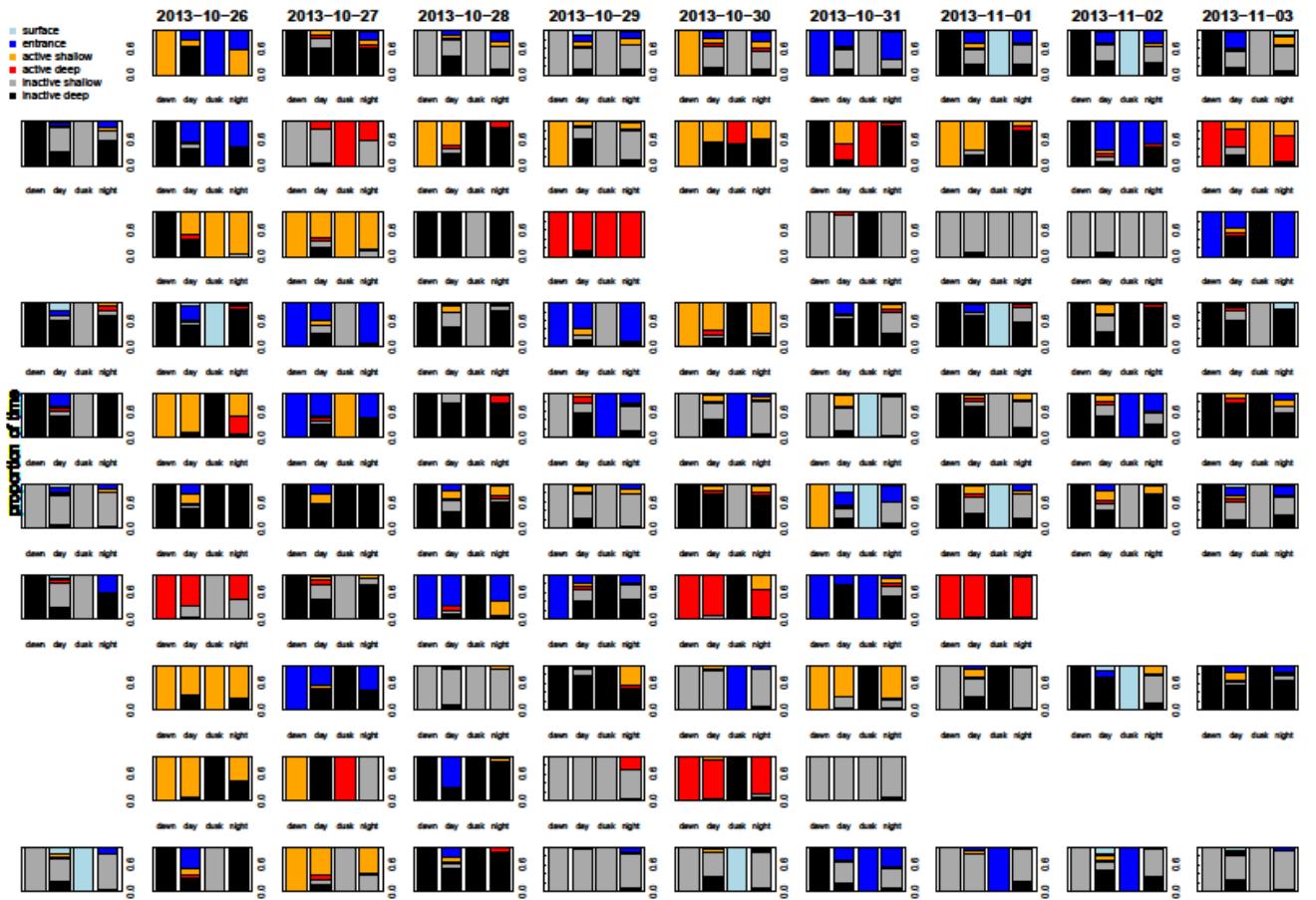


Fig. S5.5 Daily *Liopholis kintorei* activity budgets for 10 individual lizards.

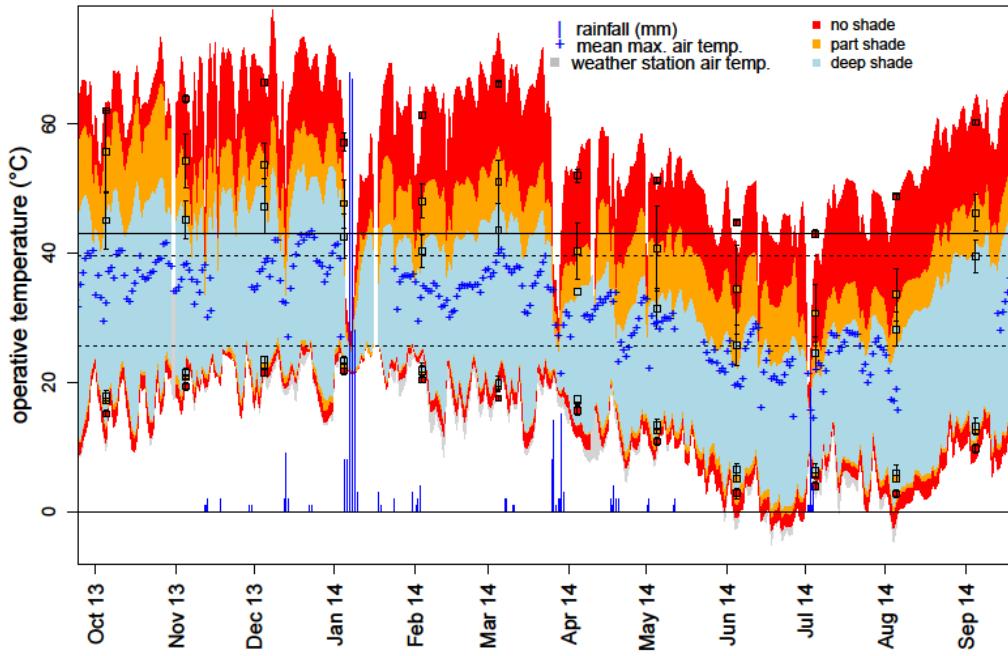


Fig. S5.6 The daily mean minimum and maximum surface operative temperatures for juvenile *L. kintorei* measured at three micro-climates. Monthly minimum and maximum mean temperature and standard deviation per depth are denoted by the open squares and lines. Voluntary minimum and maximum adult field body temperatures of *L. kintorei* are denoted by the dashed black lines with the critical thermal maximum body temperature indicated by the solid black line.

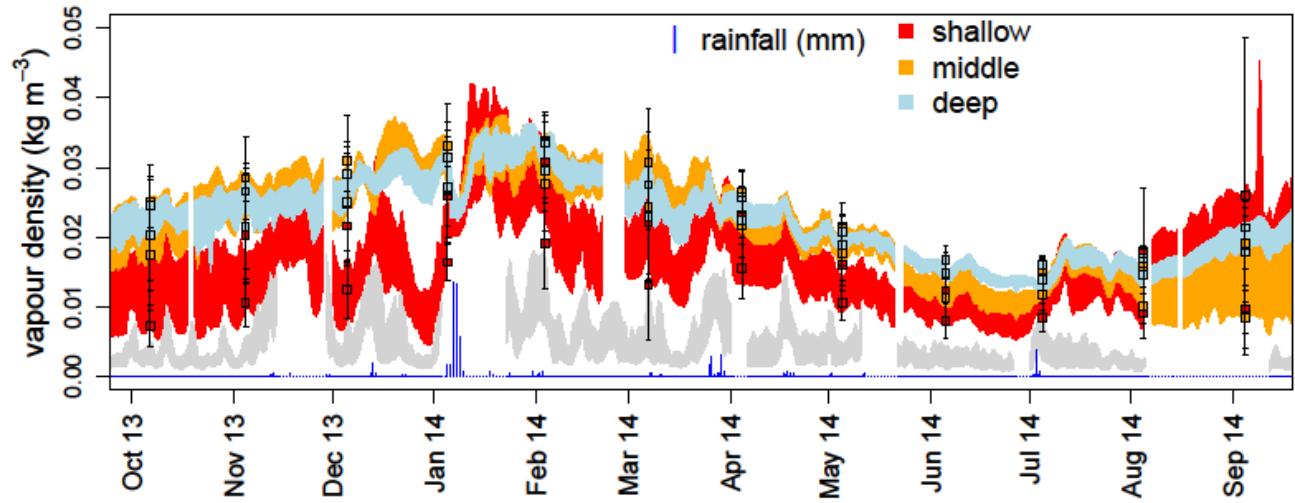
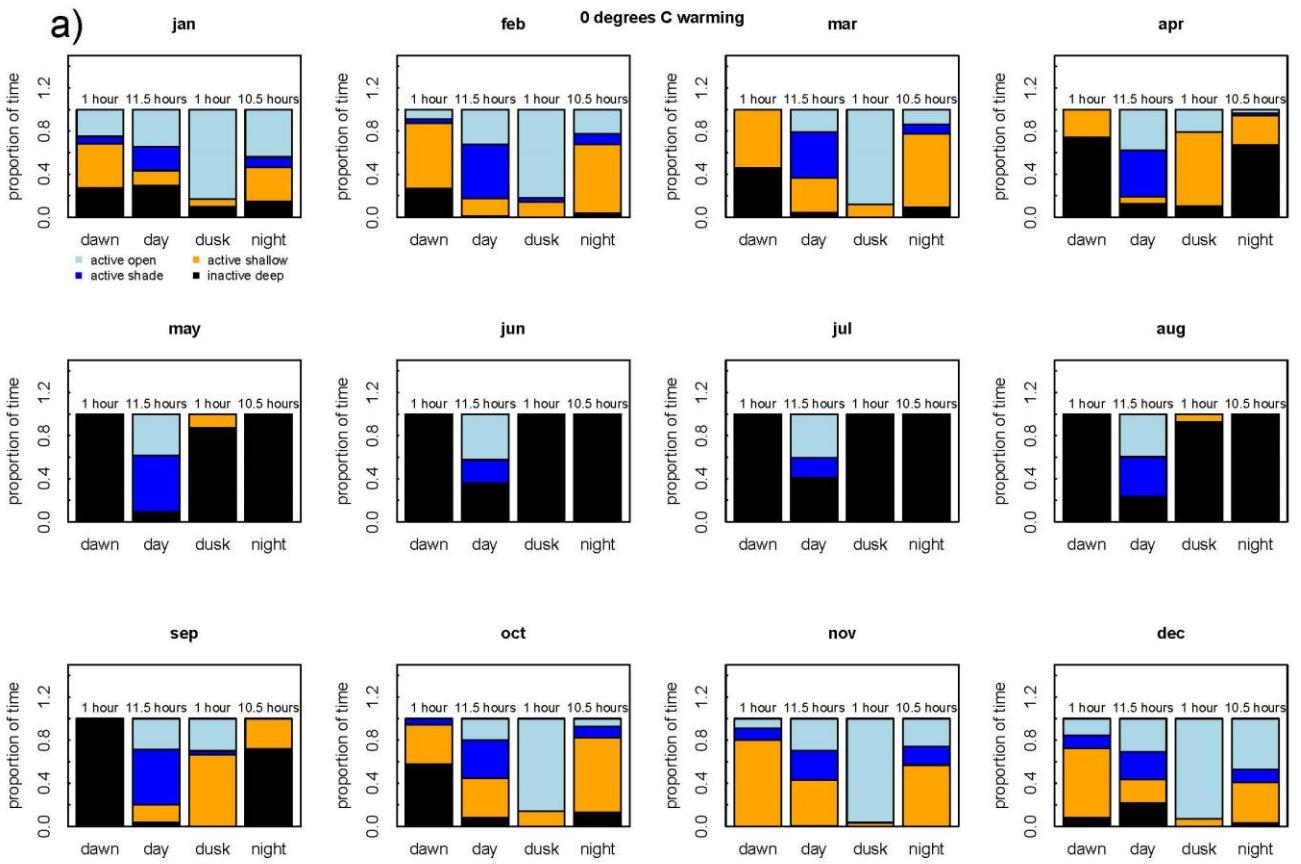


Fig. S5.7 The daily mean minimum and maximum vapour density (kg m^{-3}) within the burrow system. Monthly mean minimum and maximum vapour and standard deviation per depth are denoted by the open squares and lines. Daily mean minimum and maximum vapour density is displayed (light grey).



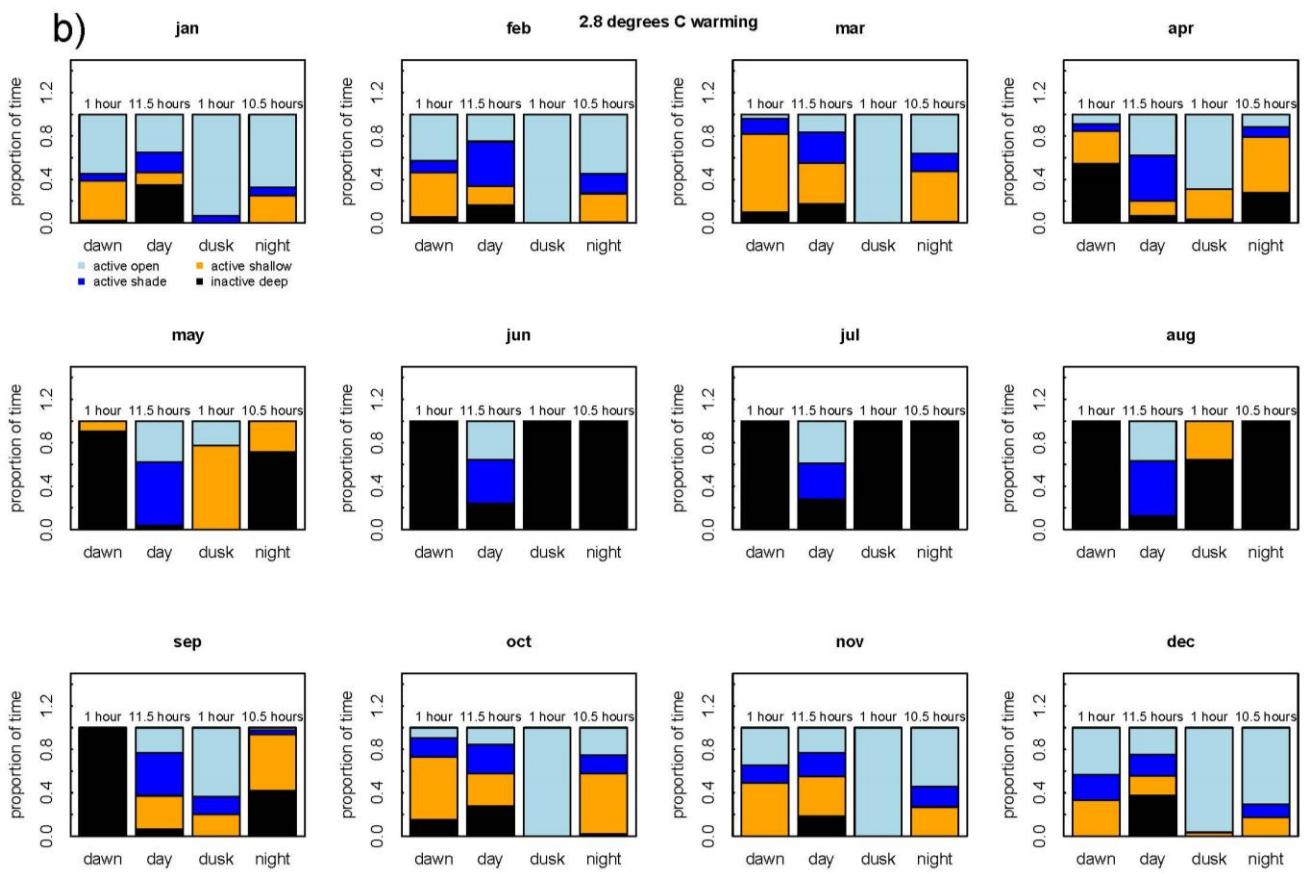


Fig. S5.8 The predicted potential activity per month under present climatic conditions (a)

and with a warming effect of 2.8 °C by 2070 (b).

Table S5.1 The monthly mean maximum and minimum operative temperature of adult and juvenile *Liopholis kintorei* within three micro-climates: exposed, partly shaded and deeply shaded.

	Adult lizards monthly mean T_e						Juvenile lizards monthly mean T_e					
	deeply shaded		partly shaded		exposed		deeply shaded		partly shaded		exposed	
	min	max	min	max	min	max	min	max	min	max	min	max
January	17	52	16	59	12.71	70	17	54	16	61	14	72
February	13	45	13	55	10.61	69	14	45	14	56	12	70
March	12	48	12	57	9	72	12	48	12	57	10	74
April	12	46	11	54	9	71	12	47	11	54	9	72
May	9	39	7	45	7	58	9	36	8	47	8	58
June	-1	33	-2	38	-3	51	0	30	-1	40	-3	51
July	0	32	-1	36	-3	51	0	30	-1	41	-3	51
August	0	36	0	41	-3	58	1	34	0	43	-3	59
September	7	47	6	58	4	66	7	47	7	57	5	65
October	11	51	10	67	8	69	11	51	11	64	10	70
November	14	55	13	68	11	73	14	54	14	67	13	73
December	17	54	16	61	15	76	17	54	16	62	14	78

Table S5.2 The monthly mean minimum and maximum temperature of the burrow system at three depths: deep (depths ranged from 50 cm to 1 m), mid (depths ranged from 30 cm to 50 cm) and entrance (depths ranged from 5 cm to 15 cm).

	Monthly mean maximum burrow system temperature (°C)			Monthly mean minimum burrow system temperature (°C)		
	Deep	Mid	Entrance	Deep	Mid	Entrance
January	34	37	49	24	25	22
February	33	35	43	29	28	22
March	34	36	42	23	19	20
April	31	33	41	24	23	19
May	26	27	30	23	22	16
June	23	23	27	18	15	10
July	22	22	25	14	13	9
August	21	22	28	17	15	9
September	28	31	46	20	19	14
October	32	34	49	26	25	19
November	34	35	47	26	26	24
December	34	37	48	29	29	24

Table S5.3 The monthly mean maximum and minimum relative humidity (%) levels within the burrow system at three depths: deep (depths ranged from 50 cm to 1 m), mid (depths ranged from 30 cm to 50 cm) and entrance (depths ranged from 5 cm to 15 cm).

	Monthly mean maximum RH (%)			Monthly mean minimum RH (%)		
	deep	mid	entrance	deep	mid	entrance
January	100	100	100	39	40	11
February	100	100	100	65	57	35
March	99	94	81	54	18	26
April	100	100	100	72	58	31
May	98	98	93	82	54	36
June	95	91	80	79	56	39
July	100	100	100	82	56	34
August	100	100	94	80	63	43
September	95	87	66	70	22	9
October	97	88	69	44	37	6
November	93	86	77	27	26	6
December	90	85	90	52	43	16

Table S5.4 The monthly mean minimum and maximum vapour density (kg m^{-3}) levels within the burrow system at three depths: deep (depths ranged from 50 cm to 1 m), mid (depths ranged from 30 cm to 50 cm) and entrance (depths ranged from 5 cm to 15 cm).

	Mean monthly maximum VD (kg m^{-3})			Mean monthly minimum VD (kg m^{-3})		
	deep	mid	entrance	deep	mid	entrance
	0.037	0.040	0.044	0.013	0.015	0.004
January	0.037	0.038	0.041	0.025	0.023	0.011
February	0.032	0.038	0.030	0.017	0.011	0.008
March	0.030	0.034	0.033	0.019	0.018	0.010
April	0.023	0.024	0.021	0.017	0.016	0.007
May	0.019	0.020	0.015	0.013	0.008	0.005
June	0.020	0.020	0.022	0.011	0.007	0.005
July	0.018	0.019	0.023	0.012	0.009	0.007
August	0.024	0.023	0.048	0.014	0.006	0.006
September	0.030	0.031	0.042	0.012	0.011	0.004
October	0.030	0.033	0.039	0.007	0.012	0.003
November	0.033	0.037	0.034	0.017	0.014	0.007
December						

CHAPTER 6

MALE-BIASED DISPERSAL AND HIGH NATAL PHILOPATRY IN A GROUP-LIVING LIZARD, *LIOPHOLIS KINTOREI*



A juvenile *Liopholis kintorei* (J. Schofield).

Abstract

Effective conservation management requires knowledge of the movement and dispersal patterns of the focal species. Understanding the dispersal behaviour of spatially structured populations allows us to predict how species may respond to environmental change. The great desert skink, *Liopholis kintorei* is an internationally listed vulnerable species. Here we aim to characterise small-scale movement and with-in patch dispersal patterns for this species. We combine molecular analyses with capture-mark-recapture data to characterise age- and sex-based differences in dispersal. Data from capture-mark-recapture showed that maximum movements between burrow systems was <130 m with significantly greater distances observed for adult males. Spatial autocorrelation analyses revealed significantly elevated genotypic similarity between adult female and between juvenile individuals captured together at the same burrow system, but not for adult males. Furthermore, parentage assignments showed that the locations of mother and full sibling offspring most often coincided in the same burrow system. We therefore conclude that *L. kintorei* exhibits male-biased dispersal whilst adult females and juveniles exhibit high natal philopatry. These data contribute to our limited knowledge of movement and dispersal patterns of this threatened species.

Introduction

Dispersal is one of the most important processes in evolution, population biology and spatial ecology (Greenwood 1980; Coulon *et al.* 2004; Dobson 2013;

Driscoll 2014). Broadly defined as the permanent movement away from an origin, this process plays a key role in the distribution of species, the colonisation of new areas, and the mediation of gene flow within- and between-populations (Greenwood 1980). Dispersal can be driven by inbreeding avoidance (whereby opposite-sex siblings are separated before sexual maturity), kin competition, kin cooperation (as a reason not to disperse), resource competition and environmental stochasticity (Greenwood 1980; Dobson 1985; Dobson 2013 and refs. therein). Patterns of dispersal have consequences for individual fitness, demographic and genetic characteristics, and species' distributions (Bowler 2005; Cote *et al.* 2017). Within a species, the propensity to disperse may vary across individuals, as well as among sex and age classes (Altwegg *et al.* 2000; Beirinckx *et al.* 2006; Bowler and Benton 2009). For example, female-biased dispersal is common in birds, whereas in mammals it is the male who usually disperses (Greenwood 1980). Delayed juvenile dispersal is a common trait within complex social structures (Gardner *et al.* 2001; Stow and Sunnucks 2004; Chapple and Keogh 2005). These differences in dispersal patterns for different categories of individuals may lead to a particular class of individual being more vulnerable to mortality because of the costs associated with dispersal (Waser *et al.* 1994; Bowler and Benton 2005). Moreover, dispersal patterns can be adversely influenced by anthropogenic processes such as habitat modification and fragmentation, resulting in changes to dispersal patterns which in-turn influence other social, genetic and demographic factors (Stow *et al.* 2001; Ahlroth *et al.* 2010; Banks *et al.* 2007 and ref. therein). Knowledge of dispersal patterns and rates of emigration, within-patch movement and immigration, is a critical first step when considering effective species

conservation. Such knowledge allows us to better understand the behaviour of spatially structured populations, and predicting how species are likely to respond to environmental change (Bowler and Benton 2005).

The great desert skink, *Liopholis kintorei* is an internationally listed vulnerable species (Stirling and Zietz 1893; IUCN 2016) endemic to the arid western desert regions of Australia, often inhabiting highly flammable spinifex sandplain habitats (McAlpin 2001; Chapple 2003). Like other species from the subfamily Egerniinae, *L. kintorei* is a group-living species. They uniquely excavate and maintain an extensive burrow system which house close-kin, with some burrows being continuously occupied for up to seven years and containing offspring from multiple cohorts (McAlpin *et al.* 2011). Individuals are known to reside and mate with the same partner across multiple years (Dennison 2015), though genetic polygyny has also been described (McAlpin *et al.* 2011).

Liopholis kintorei has a patchy distribution and has been recorded at approximately 70 localities. At these localities, the density of burrow systems varies greatly, with patches of higher burrow density separated by unoccupied areas, often of seemingly similar habitat (McAlpin 2001). Movement and dispersal patterns within these patches have not previously been described for this species.

Here we combine molecular analyses with capture-mark-recapture (CMR) data to characterise age- and sex-based differences in dispersal by: (i) assessing the difference in relatedness at different spatial scales among individual adult males, adult females and juveniles to infer dispersal patterns; (ii) evaluating sex based differences in directly observed movement among burrow systems for adult male and adult

female lizards, and; (iii) characterising differences in adult and juvenile philopatry to their natal burrow system via the use of parentage analysis. These data will contribute to our limited knowledge of movement and dispersal patterns of this threatened species and will help to guide effective conservation.

Materials and methods

Study site

The study was conducted at Newhaven Wildlife Sanctuary (herein referred to as Newhaven) in central Australia, Northern Territory (22.72°S, 131.17°E; Fig. 6.1). This property is managed for conservation by the Australian Wildlife Conservancy. Newhaven has one of the largest known populations of *L. kintorei* and here their preferred habitat is semi-saline spinifex sandplain (Fig. 6.1; Latz *et al.* 2003). This community is typically dominated by needlewood (*Hakea leucoptera*), Inland tea-tree (*Melaleuca glomerata*) and the sub-shrub *Pluchea ferdinandi-mulleri* over hummock grass (*Triodia pungens*) (the stoloniferous growth form; Latz *et al.* 2003).

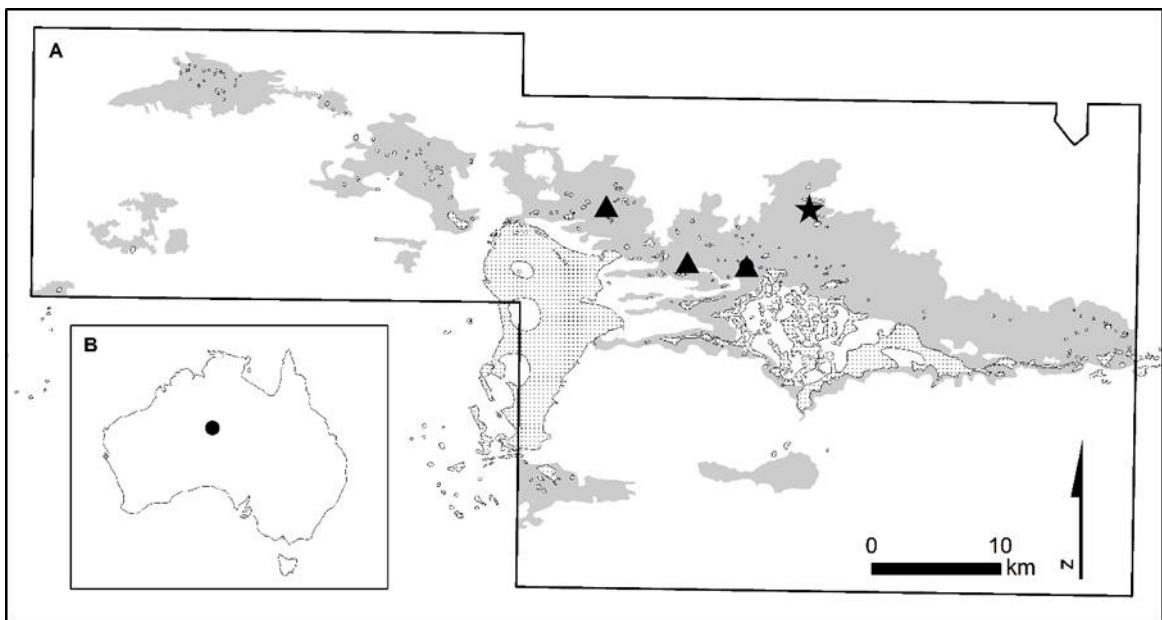


Fig. 6.1 Newhaven Wildlife Sanctuary (A), showing the location of the focal study site (closed star) and the additional sampling sites (closed triangles). The shaded grey indicates potential *Liopholis kintorei* habitat and the hatching indicates ephemeral lakes. The inset map (B) shows the location of Newhaven Wildlife Sanctuary within Australia.

Study species

Liopholis kintorei is a medium sized (< 200 mm snout-vent length [SVL]) viviparous skink (McAlpin 2001; Chapple 2003) found in arid habitats throughout the western deserts of Australia. It is an obligate burrower, constructing a complex burrow system with multiple entrances that can be up to 80 cm in depth. Burrow systems are occupied by close relatives, often consisting of the two parents and two age cohorts of their offspring (McAlpin *et al.* 2011; Dennison 2015). Mating takes place once a year during the spring (September–October) with births occurring in late January and early

February (McAlpin 2001; Chapple 2003). This species is crepuscular, spending the majority of its surface activity time at the burrow entrance (Moore *et al.* 2018

Field sampling

A 20 ha focal study site consisting of 32 active burrow systems was intensively sampled during the breeding season over three consecutive years (2011-2013; Fig. 6.1; Fig. 6.2). This site was determined after significant effort had been made searching for active *L. kintorei* burrow systems, therefore all known burrow systems within the immediate patch were sampled. All lizards were captured from active burrow system using baited Elliott traps (Elliott Scientific Equipment) set at the entrance of a tunnel. Traps were open before dusk each day and were checked and closed the following morning. Approximately 3,010 trap nights were conducted each year. An additional three sites were sampled once in 2012—this datum have been excluded from the fine-scale spatial analysis as no recapture data was obtained (Fig. 6.1).

For all captures we recorded the burrow system coordinates, measured SVL and assigned each individual into an age category, either adult (SVL > 160 mm; Storr 1968) which is attained in the third year of growth, or juveniles (SVL < 160 mm; Dennison unpublished data). Sex was determined by hemipene eversion for all mature adults. A tissue sample (tail-tip approx. 1 cm) was taken and preserved in 90% ethanol. Finally, each lizard was tagged with a subcutaneous passive integrated transponder (PIT-tag; VetPlant 100VB, 1.25; Trovan Ltd). Remote PIT-tag readers (Trovan Ltd) were deployed

in 2012 and 2013 at active burrow systems within the focal study site. Each burrow system was monitored at four active burrow entrances for 3-4 consecutive nights.

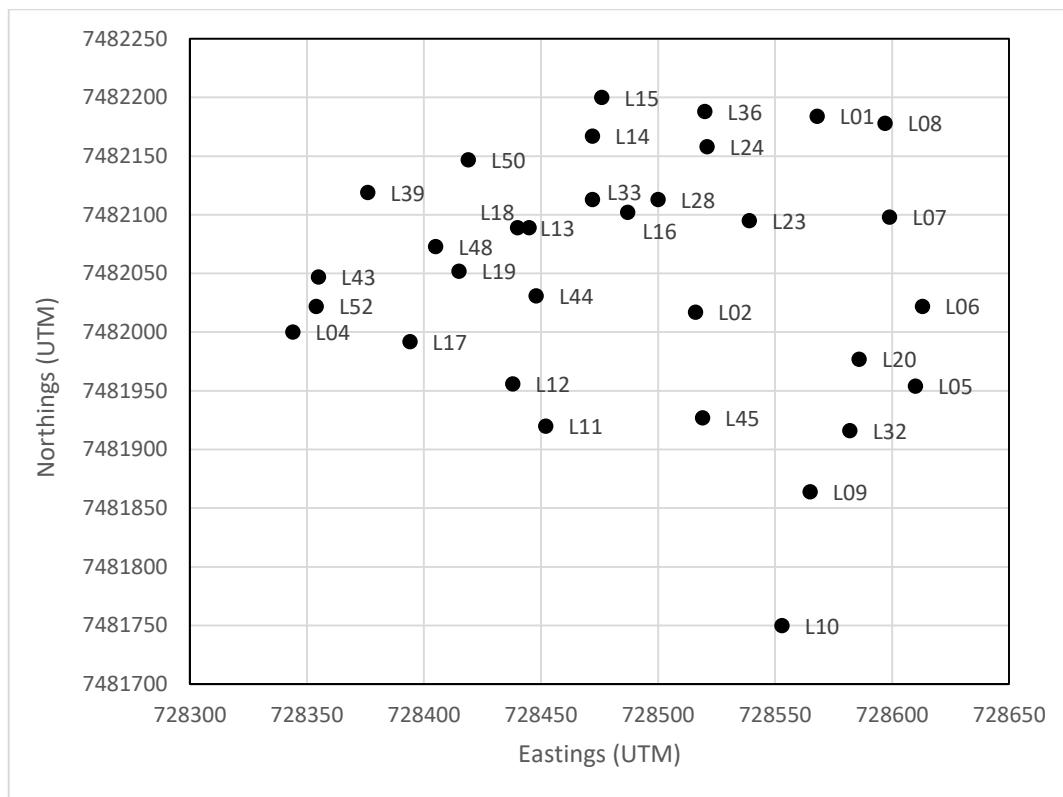


Fig. 6.2 The focal study site with the location of each distinct *Liopholis kintorei* burrow system.

SNP data

We sent 94 individual *L. kintorei* samples of 0.5 µg high quality DNA that had previously been extracted and purified from tissue samples (see Dennison *et al.* 2015 for laboratory procedure details) to Diversity Arrays Technology Pty. Ltd. (Canberra, Australia), where SNPs were discovered and genotyped using the standard DartSeq™ protocol (Petroli *et al.* 2012). This method is based on a combination of Diversity Array (DArT) markers (Jaccoud *et al.* 2001) and next-generation Illumina sequencing (Sansaloni *et al.* 2011). SNPs were then identified and called, following the standard

procedure in DArT pipeline DArTSoft14™ (Diversity Arrays Technology). This pipeline is very similar to the STACKS pipeline (Catchen *et al.* 2013), yet differing in that DArTSoft14™ first calls the sequence clusters for the pooled sample, prior to each individual. As part of the DArT pipeline, all monomorphic clusters were removed and only SNPs that were present in both homozygous and heterozygous forms were called. Loci with very high read depths were removed, leaving SNPs with reproducibility of >95%, read depths ≥5, and an average ratio read depth of 0.72 (range: 0.30-2.98) between alleles. DArT genotyped SNPs for each of the 94 individual *L. kintorei*. We filtered this dataset by excluding SNPs with unknown scores for genotyping, read depth <10, call rate <70%, and repeatability <90%. Additionally, we excluded monomorphic loci and reads with more than one SNP to reduce statistical bias from linkage disequilibrium. Our final dataset contained 5892 SNPs for each individual *L. kintorei*.

Analysis of relatedness, dispersal patterns and philopatry

Genotypic similarity (relatedness) among individuals was estimated from allele frequency data obtained from all 94 samples and dispersal was inferred by examining the geographical structure of relatedness using spatial autocorrelation analysis in GenAIEx 6.5 (Peakall and Smouse 2006). Relatedness was estimated at several distance classes. The first distance bin was chosen to estimate relatedness within a burrow system (distance = 0), averaged for all pairs of juveniles and separately for pairs of adult females (no pair-wise comparisons were available between adult males within a burrow system). Among individuals sampled in different burrow systems,

relatedness was estimated at the following distance categories; 50 m, 200 m and 500 m for all juveniles and adults (approximate extent of focal study site) and an additional two distance classes 5 km and up to 20 km were included for all adults, allowing comparison of adult male and adult females sampled across localities. For each distance class, the significance of any deviation from zero was assessed by 999 permutations and the 95% confidence intervals around relatedness were obtained via bootstrapping 999 times.

In addition, paternity and maternity was tested for all immature individuals (SVL < 160 mm; N = 34) captured at the focal study site using the maximum likelihood method in COLONY (Jones and Wang 2010). All adults captured (SVL > 160 mm; N = 33) were included as potential parents for all immature individuals. The COLONY analysis was run conservatively allowing for both sexes to be polygamous, no sibship prior, and 0.05 probability that candidate parents had been sampled. Parentage was accepted if the parent–offspring match was determined with 95% confidence. For each immature individual we determined the geographic location of the burrow system that was occupied by the mother and/or the father and calculated the geographic distances between them.

Analysis of observed within-patch movement

Observed within-patch movement patterns for adult individual lizards sampled from the focal study site were characterised to better understand movement patterns between burrow systems, their burrow system use, and to determine if any sex-bias difference existed. CMR data from the 20 ha focal study site over three consecutive

years was generated from both trapping of lizards and the PIT-tag readers. Adult male and adult female lizards recaptured ≥ 2 times over the sampling period were included in the within-patch movement analysis (juveniles that matured throughout the three years were excluded). Within-patch movements for adult male and adult female lizards were characterised by calculating the: (i) mean maximum distance between two burrow systems that an individual was recorded at, and; (ii) mean number of distinct burrow systems an individual was recorded at. All statistical analyse were performed in R 3.2.3 (R Core Team 2015).

Results

Relatedness, dispersal patterns and philopatry

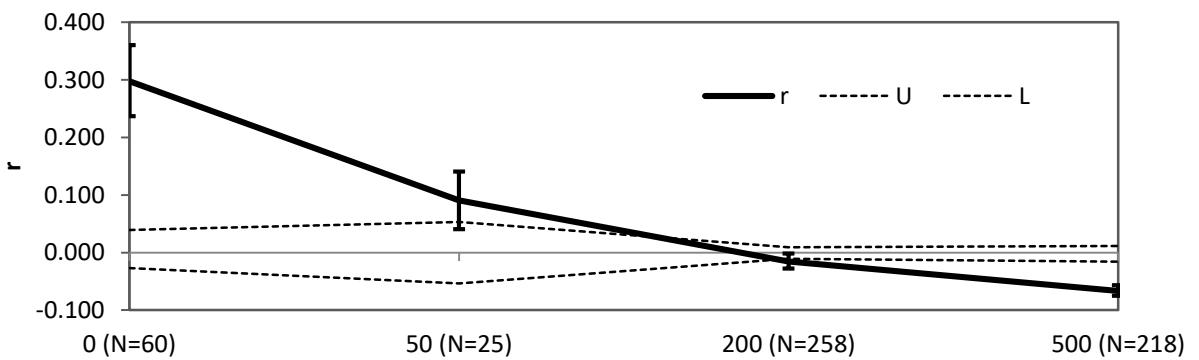
The spatial distribution of relatedness demonstrated high natal philopatry for juvenile lizards (Fig. 6.3a). Levels of relatedness within a burrow system (class distance = 0) were high (mean $r = 0.3$) and significantly greater than the relatedness among juvenile lizards located within different burrow systems, even those located within 50 m (mean $r = 0.092$; Fig. 6.3a). High natal philopatry in juvenile lizards was also shown by groups of full sibling juvenile lizards occupying the same burrow system in 7 of the 8 (87.5%) accounts where at least two juvenile lizards were sampled from the same burrow system. In one case, two full siblings within the same age cohort were sampled from two distinct burrow systems 49 m apart.

Similarly, high levels of relatedness were found among adult female lizards within a burrow system (mean $r = 0.312$; Fig. 6.3b). Relatedness between adult female individuals located in different burrow systems decreased significantly with distance,

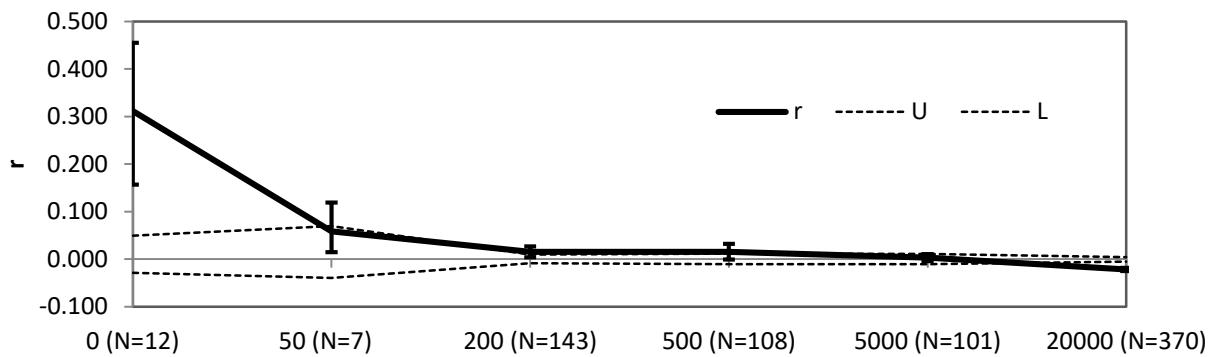
even between individuals sampled from burrow systems as close as 50 m (mean $r = 0.058$; Fig. 6.3b). This spatial distribution of relatedness implies a low level of dispersal for adult females from their natal burrow systems.

In contrast, we sampled only two males together within the same burrow system, therefore could not conduct a pairwise relatedness analysis at the distance class of 0. Average relatedness among adult male lizards sampled from burrow systems located within 50 meters was relatively high (mean $r = 0.2$; Fig 6.3c) though high variability was reflected by large 95% confidence intervals. These data indicated a higher level of dispersal of adult male lizards from their natal burrow system.

(a) juvenile



(b) adult female



(c) adult male

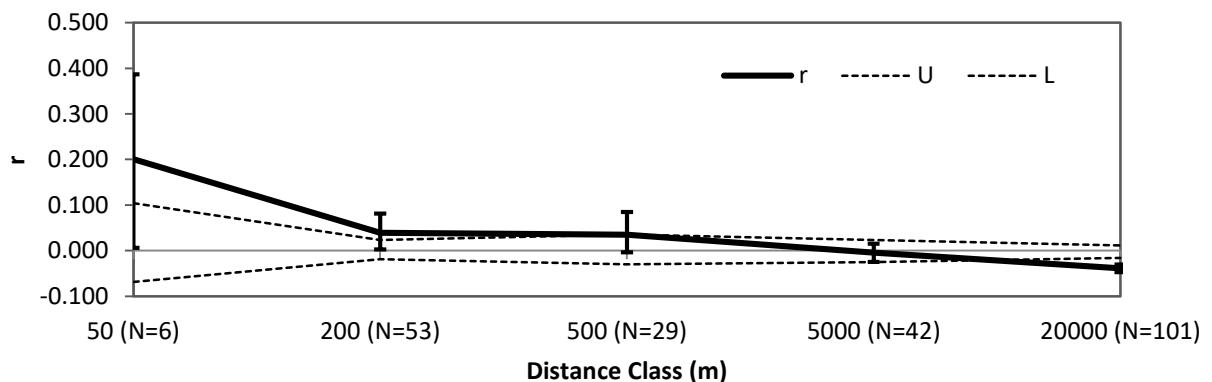


Fig. 6.3 The distribution of genetic similarity (r) at geographic distance (meters) for all juveniles (a), adult females (b) and adult males (c). The solid line tracks relatedness, dashed lines represent upper (U) and lower (L) 95% confidence intervals around

random expectation, while the bars around 'r' show the 95% confidence interval around this estimate determined by bootstrapping. The distance class 0 meters in plot 'a' and 'b' contains the 'r' estimate among individuals sharing the same burrow.

Of the 34 immature individuals captured at the focal study site over the three-year period, we identified mothers for 24 of these and fathers for 19. Of these, 83% of juveniles were sampled from within the same burrow system as their mother. In contrast, only 16% of juveniles were sampled from the same burrow system as their father. When parents were not sampled from the same burrow system as their offspring, no significant difference in mean distance was found between a burrow system occupied by a mother ($N = 4$; mean distance \pm s.d.: 78.8 ± 16.7) or father ($N = 14$; mean distance \pm s.d.: 91.4 ± 9.7) and that of their offspring (Welch Two Sample t-test; $t = 0.69$, $df = 4.06$, $P = 0.52$).

Observed within-patch movement

Over the three-year study period, 447 observations of the location of individual *L. kintorei* were made. Analysis of the movement between distinct burrow systems for 12 individual adult females and 14 individual adult males indicated that movement between burrow systems was minimal with the maximum distance between burrow systems recorded being 127.3 m (Fig. 6.4). The mean maximum distance observed between recaptures for adult males ($53.5 \text{ m} \pm 13.6 \text{ m}$) was significantly greater than that observed for adult females ($17.5 \text{ m} \pm 7.6 \text{ m}$; Welch two Sample t-test; $t = -2.3$, $df = 17.45$, $P = 0.03$; Fig. 6.5; Table 6.1). Adult lizards of both sexes visited multiple

burrow systems over the sampling period and no significant difference in the number of distinct burrow systems visited was observed (Fig. 6.4).

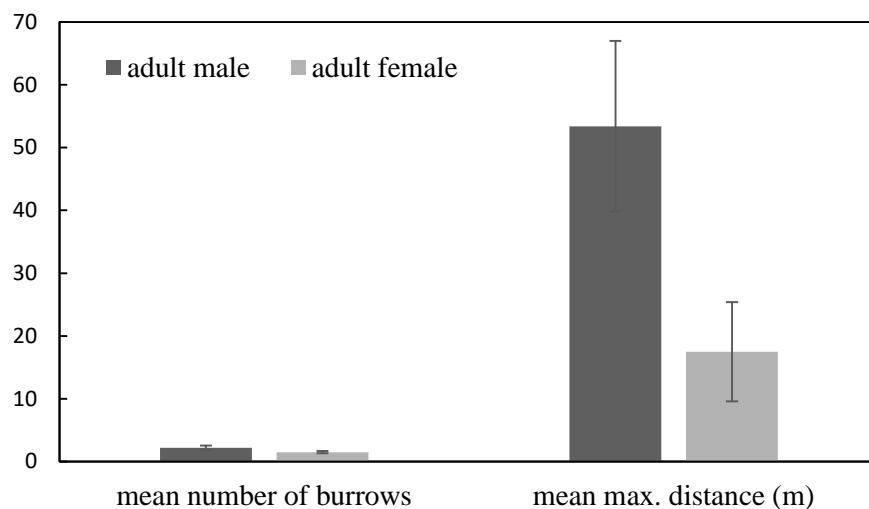


Fig. 6.4 The mean number of distinct burrow systems from which individual adult male and adult female *Liopholis kintorei* were captured and the mean maximum distance between captures over three consecutive years. The bars represent one standard deviation.

Table 6.1 The mean number of distinct burrow systems from which individual adult male and adult female *Liopholis kintorei* were captured over three consecutive years and the mean maximum distance between captures. ‘N’ indicates the number of individual adult lizards that were captured at more than one burrow system.

	No. burrow		Max. distance	
	<i>N</i>	systems (max.)	systems (Mean \pm SE)	Max. distance (m)
			(Mean \pm SE)	
Male	12	5	2.25 \pm 0.4	127.3
Female	14	3	1.5 \pm 0.2	89.9

Discussion

Our data show that *L. kintorei* has low vagility, with observed distances travelled by an individual between burrow systems (sampled over three consecutive years) being < 150 m. Differences in dispersal for different categories of individual were observed. Low rates of dispersal and high natal philopatry in juveniles and adult female lizards was inferred. In contrast, male biased dispersal was indicated by direct observations of movement and significantly fewer instances of fathers being located in the same burrow system as their offspring.

Little conclusive evidence exists of sex-biased dispersal from other members of the subfamily Egerniinae. For example, Chapple and Keogh (2005) found conflicting results when assessing sex-bias dispersal in *Liopholis whitii* and Stow *et al.* (2001) found that sex-bias dispersal in *Egernia cunninghami* was only evident within populations sampled within modified habitat. Male-biased dispersal has been predicted to occur in polygynous species (Greenwood 1980; Dobson 1985) and, although low levels of polygyny have been reported for other members within the subfamily Egerniinae (Gardner *et al.* 2001; Stow *et al.* 2001; Stow and Sunnucks 2004; Chapple and Keogh 2005; While *et al.* 2009), high levels (40%) have been reported for *L. kintorei* at a different location to where this study was conducted (McAlpin *et al.* 2011). It would be of interest to investigate further the mating system of this species, as intraspecific variation may potentially occur across its distribution because of differences in environmental conditions.

Several other lizard species belonging to the closely allied subfamily Egerniinae (e.g. *E. cunninghami*, *E. saxatilis*, *E. stokesii* and *L. whitii*) also live in tightly clustered groups of highly related individuals, reflecting kin-based sociality (Garner *et al.* 2001; Stow *et al.* 2001; O'Connor and Shine 2003; Stow and Sunnucks 2004; Chapple and Keogh 2006; While *et al.* 2009; McAlpin *et al.* 2011; Duckett *et al.* 2012), however, the loss of sociality has also been noted for some species within these groups distributed within arid regions (e.g. *E. depressa*, *L. striata* and *L. inornata*; Chapple 2003; Cogger 2014). Furthermore, high levels of juvenile natal philopatry have been associated with kin-based groups of other members of the *Liopholis* and *Egernia* genera (Gardner *et al.* 2001; Stow *et al.* 2001; Stow and Sunnucks 2004; McAlpin *et al.* 2011) suggesting that these behaviours may provide net benefits. For example, McAlpin *et al.* (2011) reported that this species is unique in that it cooperatively constructs and maintains a burrow system for family members and that this behaviour benefits offspring, or siblings, over several breeding seasons. As birthing of live young occurs in mid-summer when air temperatures are high, delayed dispersal of juveniles from their natal burrow system may well increase the likelihood of offspring survival as the burrow system provides an essential buffer to maximum extremes of temperature (\approx 40 °C reduction from potential surface temperatures), and desiccation (burrows near 100% humidity; Moore *et al.* 2017b). Moreover, delayed dispersal may reduce dispersal costs imposed by conspecific aggression predation risk (O'Connor and Shine 2004; Griesser and Ekman 2005; Bonte *et al.* 2012; Halliwell *et al.* 2017), and the inherent risks associated with the construction of a new burrow system, which involves considerable energy expenditure.

Conservation implications

Across its distribution, *L. kintorei* generally inhabits highly flammable spinifex grasslands (McAlpin 2001; Moore *et al.* 2015). Within these grasslands, fire induced habitat modification and fragmentation occurs, with effects varying in space and time. Its decline within these habitats has been attributed to fire—as demonstrated by a higher proportion of unoccupied burrow systems and fewer successful breeding events post-fire, particularly when all ground cover is lost (Moore *et al.* 2015), and through predation by feral cats (Moore *et al.* 2017a).

It is well recognised that habitat fragmentation affects the distribution and abundance of species (Fahrig 2003; Fisher and Lindenmayer 2007). Habitat fragmentation has been identified as a key threatening process for many terrestrial species (Fahrig 1997; Brooks *et al.* 2002; Henle *et al.* 2004; Fisher and Lindenmayer 2007; Crooks *et al.* 2017). Within fragmented landscapes the persistence of isolated populations in part depends on a species' ability to disperse. It is well understood that declining and isolated populations of threatened species are susceptible to local extinction (Frankham *et al.* 2010), because they are susceptible to inbreeding and reduced genetic diversity, resulting in lower reproductive fitness in the short-term and a compromised ability to evolve longer-term (Wilcox 1985; Couvet 2002; Frankham 2005; Baguette *et al.* 2013; Pavlova *et al.* 2017). These risks are compounded by small isolated populations at greater risk of stochastic events that reduce the population size further, resulting in an 'extinction vortex' (Spielman *et al.* 2004; Frankham 2005). However, less-understood are the effects of habitat fragmentation on within-group processes such as mating opportunities, kin group structures, sociality, philopatry and

dispersal (Banks *et al.* 2007; Cote *et al.* 2016; Fardila *et al.* 2017). However, more recent studies have shown that habitat fragmentation affects home range behaviour, group size, kin interactions, mate location, pair formation and mating systems (e.g. Banks *et al.* 2007 and refs. therein).

If adult males are more mobile among burrow systems and are the dispersing sex, as this study suggests, then they are likely to be more susceptible to predation than are adult females and juveniles. Furthermore, this predation risk for adult males would only be enhanced post-fire where ground cover has been reduced or completely removed (Moore *et al.* 2015). Consequently, depending on the scale and severity of fire and concurrent predator pressure, natural recolonization of suitable habitat may be considerably delayed because of low-dispersal propensity among females and reduced success of adult male dispersal between-patches (Bowne and Bowers 2004, Baguette *et al.* 2013). Furthermore, remaining isolated and declining groups of individuals may be at risk of inbreeding if adult male immigration attempts are unsuccessful. As such, management practices should take this into account and monitor natural recolonization of areas post-fire, assisting if necessary through the relocation of adult males into other areas to actively facilitate gene flow. In addition, prescribed burning programs should aim to maintain high levels of ground cover within key *L. kintorei* populations and focused predator management should be conducted particularly during the breeding season (September/ October) when dispersing adult males are likely to be most mobile and therefore most vulnerable. Future research focused specifically on the effect of fire-induced habitat

fragmentation on connectivity between and genetic diversity within isolated sub-populations would further inform conservation land management practices.

References

- Ahlroth, P., Alatalo, R. V., and Suhonen, J. (2010). Reduced dispersal propensity in the wingless waterstrider *Aquarius najas* in a highly fragmented landscape. *Oecologia* **162**(2), 323-330.
- Altwegg, R., Ringsby, T. H., and Sæther, B. E. (2000). Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology* **69**(5), 762–770.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., and Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews* **88**(2), 310-326.
- Banks, S. C., Piggott, M. P., Stow, A. J., and Taylor, A. C. (2007). Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. *Canadian Journal of Zoology* **85**(10), 1065-1079.
- Beirinckx, K., Van Gossum, H., Lajeunesse, M. J., and Forbes, M. R. (2006). Sex biases in dispersal and philopatry: insights from a meta-analysis based on capture-mark-recapture studies of damselflies. *Oikos* **113**(3), 539–547.
- Bonte, D., Van Dyck, H., Bullock, M. J., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., and Schtickzelle, N. (2012). Costs of dispersal. *Biological Reviews* **87**(2), 290-312.

- Bowne, D. R., and Bowers, M. A. (2004). Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology* **19**(1), 1-20.
- Bowler, D. E., and Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* **80**(2), 205-225.
- Bowler, D. E., and Benton, T.G. (2009). Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. *Journal of Animal Ecology* **78**(6), 1234-1241.
- Cadenhead, N. C. R., Kearney, M. R., Moore, D., McAlpin, S., and Wintle, B. A. (2015). Climate and fire scenario uncertainty dominate the evaluation of options for conserving the Great Desert Skink. *Conservation Letters* **9**(3), 181-190.
- Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., and Cresko, W. A. (2013). Stacks: an analysis tool set for population genomics. *Molecular Ecology* **22**(11), 3124-3140.
- Chapple, D. G. (2003). Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetol Monographs* **17**(1), 145-180.
- Chapple, D. G., and Keogh, J. S. (2005). Complex mating system and dispersal patterns in a social lizard, *Egernia whitii*. *Molecular Ecology* **14**(4), 1215-1227.
- Chapple, D. G., and Scott Keogh, J. (2006). Group structure and stability in social aggregations of White's skink, *Egernia whitii*. *Ethology* **112**(3), 247-257.
- Cogger, H. (2014). 'Reptiles and amphibians of Australia.' (CSIRO Publishing: Collingwood, Australia.)

- Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D., and Baguette, M. (2017). Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography* **40**(1), 56-73.
- Coulon, A., Cosson, J. F., Angibault, J. M., Cargnelutti, B., Galan, M., Morellet, N., Petit, E., Aulagnier, S., and Hewison, A. J. (2004). Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. *Molecular Ecology* **13**(9), 2841-50.
- Couvet, D. (2002). Deleterious effects of restricted gene flow in fragmented populations. *Conservation Biology* **16**(2), 369-376.
- Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R., Di Marco, M., Rondinini, C., and Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proceedings of the National Academy of Sciences* **114**(29), 7635-7640.
- Dennison, S. (2015). *Social organisation and population genetics of the threatened great desert skink, Liopholis kintorei*. Ph. D. Thesis. (Macquarie University: Sydney.)
- Dobson, F. S., and Jones, W. T. (1985). Multiple causes of dispersal. *The American Naturalist* **126**(6), 855-858.
- Dobson, F. S. (2013). The enduring question of sex-biased dispersal: Paul J. Greenwood's (1980) seminal contribution. *Animal Behaviour* **85**(2), 299-304.
- Driscoll, D. A., Banks, S. C., Barton, P. S., Ikin, K., Lentini, P., Lindenmayer, D. B., Smith, A. L., Berry, L. E., Burns, E. L., Edworthy, A., and Evans, M. J. (2014). The

trajectory of dispersal research in conservation biology. Systematic review. *PLoS One* **9**(4), p.e95053.

Duckett, P. E., Morgan, M. H., and Stow, A. J. (2012). Tree-dwelling populations of the skink *Egernia striolata* aggregate in groups of close kin. *Copeia* **2012**(1), 130-134.

Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**, 603–610.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**(1), 487–515.

Fardila, D., Kelly, L. T., Moore, J. L., and McCarthy, M. A. (2017). A systematic review reveals changes in where and how we have studied habitat loss and fragmentation over 20 years. *Biological Conservation* **212**, 130-138.

Fischer, J., and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**(3), 265-280.

Frankham, R. (2005). Genetics and extinction. *Biological Conservation* **126**(2), 131-140.

Frankham, R., Ballou, J. D., and Briscoe, D. A. (2010). 'Introduction to Conservation Genetics' (2nd Edition). (Cambridge University Press: Cambridge, UK.)

Gardner, M. G., Bull, C. M., Cooper, S. J. B., and Duffield, G. (2001). Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii*. *Molecular Ecology* **10**, 175-83.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**(4), 1140-1162.

Griesser, M., and Ekman, J. (2005). Nepotistic mobbing behaviour in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour* **69**(2), 345-352.

Halliwell, B., Uller, T., Chapple, D. G., Gardner, M. G., Wapstra, E., and While, G. M. (2017). Habitat saturation promotes delayed dispersal in a social reptile. *Behavioral Ecology* **28**(2), 515-522.

IUCN (2016). *The IUCN Red List of Threatened Species. Version 2016-2*.

<<http://www.iucnredlist.org>>. [accessed 04 September 2016].

Jaccoud, D., Peng, K., Feinstein, D., and Kilian, A. (2001). Diversity arrays: a solid state technology for sequence information independent genotyping. *Nucleic Acids Res.* **29**(4), e25.

Jones, O. R., and Wang, J. (2010) COLONY: A program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources* **10**(3), 551–555.

Latz, P., Paltridge, R., and Holmes, J. (2003). *Vegetation survey of Newhaven Reserve*. A report prepared for Birds Australia. (Desert Wildlife Services: Alice Springs.)

McAlpin, S. (2001). *A recovery Plan for the Great Desert Skink (Egernia kintorei)*. Arid Lands Environment Centre. (Arid Lands Environment Centre: Alice Springs.)

McAlpin, S., Duckett, P., and Stow, A. (2011). Lizards cooperatively tunnel to construct a long-term home for family members. *PloS one* **6**, e19041.

Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. (2015). Is fire a threatening process for *Liopholis kintorei*, a nationally listed threatened skink? *Wildlife Research* **42**(3), 207-216.

- Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. (2017a). Feeling the pressure at home: Predator activity at the burrow entrance of an endangered arid-zone. *Austral Ecology* **43**(1), 102-109. doi 10.1111/aec.12547.
- Moore, D. R., Stow, A., and Kearney, M. (2017b). Under the weather: The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and the burrow system. *Journal of Animal Ecology*, in press.
- O'Connor, D., and Shine, R. (2003). Lizards in 'Nuclear Families': A novel reptilian social system in *Egernia saxatilis* (Scincidae). *Molecular Ecology* **12**(3), 743–752.
- O'Connor, D., and Shine, R. (2004). Parental care protects against infanticide in the lizard *Egernia saxatilis* (Scincidae). *Animal Behaviour* **68**, 1361-1369.
- Pavlova, A., Beheregaray, L. B., Coleman, R., Gilligan, D., Harrisson, K. A., Ingram, B. A., Kearns, J., Lamb, A. M., Lintermans, M., Lyon, J., and Nguyen, T. T. (2017). Severe consequences of habitat fragmentation on genetic diversity of an endangered Australian freshwater fish: A call for assisted gene flow. *Evolutionary Applications* **10**(6), 531-550.
- Peakall, R. O., and Smouse, P. E. (2006). GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Resources* **6**(1), 288-95.
- Petroli, C. D., Sansaloni, C. P., Carling, J., Steane, D. A., Vaillancourt, R. E., Myburg, A. A., da Silva Jr, O. B., Pappas Jr, G. J., Kilian, A., and Grattapaglia, D. (2012). Genomic characterization of DArT markers based on high-density linkage analysis and physical mapping to the Eucalyptus genome. *PLoS One* **7**(9), e44684.

R Development Core Team (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

Sansaloni, C., Petroli, C., Jaccoud, D., Carling, J., Detering, F., Grattapaglia, D., and Kilian, A. (2011). Diversity Arrays Technology (DArT) and next-generation sequencing combined: genome-wide, high throughput, highly informative genotyping for molecular breeding of Eucalyptus. *BMC Proceedings* **5**(7), 54.

Spielman, D., Brook, B. W., and Frankham, R. (2004). Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences of the United States of America* **101**(42), 15261-15264.

Stirling, E. C., and Zeitz, A. (1893). Vertebrata. *Transactions of the Royal Society of South Australia* **16**(2), 154-176.

Stow, A. J., Sunnucks, P., Briscoe, D. A., and Gardner, M. G. (2001). The impact of habitat fragmentation on dispersal of Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. *Molecular Ecology* **10**(4), 867-878.

Stow, A. J., and Sunnucks, P. (2004). High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology* **13**(2), 419–430. doi: 10.1046/j.1365-294X.2003.02061.x

Waser, M. P., Creel, S. R., and Lucas, J. R. (1994). Death and disappearance-estimating mortality risks associated with philopatry and dispersal. *Behavioural Ecology* **5**(2), 135–141.

While, G. M., Uller, T., and Wapstra, E. (2009). Within-population variation in social strategies characterize the social and mating system of an Australian lizard, *Egernia whitii*. *Austral Ecology* **34**(8), 938-949.

Wilcox, B., and Murphy, D. D. (1985). Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* **125**(6), 879–887.

Supplementary material

Table S6.1 Within-patch movement data obtained from the focal study site over three consecutive years—the number of captures recorded for each individual lizard, the number of distinct burrow systems each lizard was recorded in and the maximum distance between each distinct burrow system.

Individual id.	Sex	No. captures	No. burrows	Max. distance between burrows
204	f	2	3,3	89.8
508	f	7	1	0
601	f	8	1	0
701	f	17	3	29.61
801	f	2	2	29.614
902	f	7	1	0
1305	f	11	1	0
1702	f	13	1	0
1703	f	12	1	0
1801	f	5	2	5
1902	f	4	2	25
2406	f	18	2	65.521
4301	f	5	1	0
4502	f	3	1	0
702	m	4	2	107.35
803	m	13	2	29.61
901	m	2	2	100.62
1304	m	23	4	93.6
1501	m	2	1	0
1601	m	18	5	127.28
1602	m	11	3	66.7
1701	m	12	3	66.6
2301	m	14	1	0
2402	m	5	2	49.82
3601	m	3	1	0
4201	m	2	1	0

CHAPTER 7

GENERAL CONCLUSIONS



A trace in the sandplain—a foot track of a *Liopholis kintorei* (J. Schofield).

Reviewing the list of extinct and endangered species from Australia is a sobering task. When I first began this research in 2013, I was able to write '*no known Australian lizard has become extinct since European settlement*'. However, it was only the following year that the first Australian lizard extinction occurred (since European settlement) with the death of an individual *Emoia nativitatis* (Christmas Island forest skink) named Gump. Reptiles too, along with mammals and avian species, certainly face serious threats with one in five reptile species being threatened with extinction globally and one in four species of Australian reptiles considered to be in decline, including the study species of this thesis, *Liopholis kintorei*, which is an internationally listed vulnerable species (Woinarski *et al.* 2007, Wilson 2012, IUCN 2016; Tingley *et al.* 2016).

Liopholis kintorei is unique in being the only lizard species known to construct and maintain a long-term home for family members, providing a rare example of lizards behaving cooperatively (McAlpin *et al.* 2011). These deep and complex family burrow systems provide exceptional thermal refuges against extreme temperatures and periods of low humidity, not only for those individuals inhabiting the burrow system, but for numerous other species that coexist within the spinifex sandplain habitats that may retreat to these micro-habitats. *L. kintorei* is therefore an important ecosystem engineer within the western deserts.

Although several potential threatening processes have been identified as the likely cause of reptile population declines and local extinctions (including habitat alteration, increased predation pressure caused by invasive species, in particular cats and foxes, climate warming and over exploitation) few studies have explicitly

investigated the mechanisms and drivers of endangerment associated with individual reptile species' population declines (Woinarski *et al.* 2007, Wilson 2012; Bohm 2013; Ducatez and Shine 2016).

The broad objective of this research was to investigate the key ecological processes identified as possible threats for the endangered skink *L. kintorei* (IUCN 2016) and to identify the underlying mechanisms that relate to the observed population declines. Several potential threatening processes have previously been identified including: habitat alteration caused by changes in recent fire regimes; predation by introduced predators including feral cats and European fox, and; more recently climate warming (McAlpin 2001; Woinarski *et al.* 2007; Sinervo *et al.* 2010). My research is the first to determine if the previously identified threatening processes are indeed processes that directly threaten *L. kintorei*. The results of this research will assist conservation land managers to focus efforts aimed at conserving this species by clearly identifying the underlying mechanisms associated with the declines and recommending informed conservation land management strategies for key populations under active management.

I developed four specific aims to meet this broad objective:

1. to examine the effect of fire on *L. kintorei* burrow-system occupancy and breeding success at different spatial and temporal scales;
2. to identify predators of *L. kintorei* and assess potential predator pressure at their burrow systems;

3. to further understand the potential role of climate warming as a threatening process by examining current and future thermal constraints on *L. kintorei* activity patterns, and;

4. to characterise age- and sex-based patterns of philopatry and dispersal. These data will contribute to our limited knowledge of movement and dispersal patterns of this threatened species and will help to guide effective conservation.

The key outcomes of this research are summarised below. I discuss the main findings with reference to the specific aims, as well as the implications of these results for the conservation of this species and make concise conservation land management recommendations. Lastly, I identify opportunities for further research.

Summary of key findings, conservation implications and management recommendations

Key finding 1

When examining the effect of fire on *L. kintorei* burrow-system occupancy and breeding success at different spatial and temporal scales, the unique employment of two approaches, namely, a manipulative field-experimental approach and an examination of a naturally occurring situation, allowed me to explore the effect of fire type on burrow-system occupancy and breeding success. The manipulative field experiment allowed me to investigate more closely how fire may be influencing the observed patterns of burrow-system occupancy within the broader landscape. This component of the research found no significant effect of fire on burrow-system occupancy one month after experimental burns. However, burrow-system occupancy

was significantly higher at unburnt sites four months after experimental burns and two years post-fire, suggesting that a secondary effect was taking place. The effect of fire was thus not immediate and direct, such as burn injury or voluntary migration from the area, but may instead be related to an increased efficiency and success of hunting attempts by predators at burrow-systems within open burnt habitats. In addition, breeding success was significantly higher at unburnt sites.

I conclude that fire adversely affects *L. kintorei* burrow-system occupancy and breeding success within spinifex grasslands, particularly when all ground cover is lost from the immediate area around the burrow-system.

Conservation implications and management recommendations: 1

This key finding has demonstrated that *L. kintorei* is adversely affected by fire within spinifex grasslands, most likely due to an indirect impact on predation levels. The increased effectiveness of hunting by mammalian predators at occupied burrow systems within open burnt habitat following fire is likely a key threatening process for this species. Therefore, I recommend:

- (i) Prescribed-burning practices aimed at maximising ground cover within *L. kintorei* habitat by reducing the frequency, intensity and size of fires that impact the area. More specifically, in the absence of predator control, I recommend fire exclusion from key sites within distinct localities where *L. kintorei* is known to be locally abundant.
- (ii) Implement a fire risk-management strategy within key sites, such as fire breaks, to ensure that any unwanted ignitions do not result in the loss of all

vegetation cover. This management recommendation aims to reduce the incidence of ground-cover loss caused by fire within key sites, while maintaining suitable habitat over more extensive areas.

- (iii) Fire management within key sites should be conducted in conjunction with targeted feral predator management, specifically for feral cats. The suppression of feral predator numbers whilst ground cover is minimal may reduce the impacts of predation on burrow-system occupancy and breeding success.

Key finding: 2

I aimed to investigate the ecological mechanisms that underpin great desert skinks response to fire by determining: 1) the magnitude of predation on great desert skink by large mammalian predators generally across the sanctuary, 2) the level of potential predator pressure that exists at great desert skink burrow-systems, and 3) if predator pressure was influenced by the presence and type of fire.

This component of the study provided the first direct evidence that feral cats are a significant predator of *L. kintorei*. Feral cat activity at *L. kintorei* burrow-systems was significantly higher than all other potential terrestrial predator (dingo, European fox, brush-tailed mulgara and woma python) activity and the remains of *L. kintorei* were found significantly more frequently in feral cat scats compared to fox and dingo scats.

Conservation implications and management recommendations: 2

Predation by feral cats should be considered a key threat for this nationally listed threatened species within spinifex grasslands. I recommend that conservation

management of *L. kintorei*, particularly at key sites, should incorporate intensive targeted control of feral cat populations.

Key finding: 3

I aimed to further understand the potential role of climate warming as a threatening process by investigating the thermal constraints of *L. kintorei*. Specifically, I assessed if the reported local extinctions for *L. kintorei* could be explained by a restriction of activity period due to an increase in field body temperatures and I further assessed the potential for future activity restrictions under climate warming scenarios. In addition, I evaluated the extent to which the burrow-system constructed and maintained by *L. kintorei* could provide a buffer against current extreme maximum temperatures and those predicted by future climate warming.

This component of the study resulted in the confirmation that climate warming is not a single direct threat for *L. kintorei*. I found that the overall potential for surface activity will likely be increased, not restricted, with climate warming. In addition, I found that the burrow-system provides an exceptional buffer to current and future maximum extremes of temperature ($\approx 40^{\circ}\text{C}$ reduction from potential surface temperatures), and desiccation (burrows near 100% humidity).

Conservation implications and management recommendations: 3

The results of this component of the study will enable conservation land managers to ‘rule out’ the immediate and direct impacts of climate warming as a single factor threatening this species. This information allows for optimum allocation of resources

to the most relevant threatening processes when considering the management of *L. kintorei*. There are no management recommendations associated with this key finding.

Key finding: 4

Finally, I aimed to describe within-patch movement, dispersal and philopatry patterns for this species. I combined molecular analyses with capture-mark-recapture (CMR) data to characterise age- and sex-based differences in philopatry and dispersal. I discussed the results in the context of fire, which is simultaneously a key threatening process and a critical conservation land management tool (Cadenhead *et al.* 2015; Moore *et al.* 2015).

This component of the project showed that maximum movements between burrow systems was <130 m with significantly greater distances observed for adult males. Spatial autocorrelation analyses revealed significant positive local genetic structure at the burrow system for adult female and juvenile individuals, but not for adult males. Furthermore, parentage assignments show the location of mother and full sibling offspring most often coincide in the same burrow system. From these data I conclude that *L. kintorei* exhibits male-biased dispersal whilst adult females and juveniles exhibit high natal philopatry.

Conservation implications and management recommendations: 4

If higher vagility makes adult males more susceptible to predation, therefore reducing successful dispersal (and therefore gene flow), conservation land management practices, principally prescribed burning programs, should aim to maintain high levels of ground cover within key *L. kintorei* populations. In addition, focused predator management should be conducted particularly during the breeding season (September/ October) when dispersing adult males are most mobile and therefore vulnerable.

The potential threats identified and quantified in this study are unlikely to act alone, but rather are more likely to interact synergistically. For example, although the immediate and direct impacts of climate warming as a single factor threatening this species has been ‘ruled out’, climate warming may result in *L. kintorei* spending more time active on the surface, potentially increasing its vulnerability to introduced prey, specifically feral cats. Similarly, climate warming may influence the frequency and intensity of fire within unmanaged fire prone landscapes potentially reducing ground cover vegetation resulting also in an increased predation risk within burn habitat.

The above listed conservation implications and management recommendations refer generally to key sites and key populations. These are populations that:

- (a) are known to have relatively high densities of *L. kintorei* (AWC and CLC unpublished data):

- Newhaven Wildlife Sanctuary (Australian Wildlife Conservancy (AWC);
- Lungarta Jarra, known as the Sangster's Bore population (Central Land Council (CLC).

(b) are currently known to be genetically different (Dennison *et al.* 2015):

- Uluru-Kata Tjuta Land Trust (Parks Australia) and Katiti Land Trust (Ayers Rock Resort Corporation);
- Newhaven (AWC), Lungarta Jarra (CLC);
- Wataru Indigenous Protected Area.

(c) have a high potential to be genetically different:

- Karlamily National Park and Parnngurr (Kanyirinpa Jukurpa, Dept. Parks and Wildlife WA);
- Ngaanyatjarra Indigenous Protected Area (Ngaanyatjarra Council).

(d) are currently managed through active conservation management programs:

- Newhaven Wildlife Sanctuary (AWC);
- Uluru-Kata Tjuta Land Trust (Parks Australia) and Katiti Land Trust (Ayers Rock Resort Corporation);
- Karlamily National Park and Parnngurr (Kanyirinpa Jukurpa, Dept. Parks and Wildlife WA);
- Kiwirrkura Indigenous Protected Area (Central Desert Native Title Services).

The organisation responsible for the delivery of conservation management is provided in parenthesis.

Opportunities for further research

- Contrary to predictions proposed within this study, feral cat activity at the burrow-system was not influenced by the small-scale experimental burns that were conducted. However, this does not preclude: 1. an effect of larger scale fires within *L. kintorei* habitat, and; 2. an effect on hunting success by feral cats at burnt burrow-systems. We recommend further research exploring this, specifically to determine if there is a relationship between feral predator hunting success of *L. kintorei* and the proportion of ground cover at a burrow-system. In addition, further research that demonstrates if introduced predators are contributing to or causing longer term population declines or extinction would be of value to further assess this threatening process.
- The prevailing dry conditions that occurred throughout the study period may have influenced the activity budget results. A study conducted under laboratory conditions where atmospheric humidity could be manually controlled would determine if nocturnal activity in high humidity occurred more frequently than observed during the study presented here.
- Is inbreeding a key threat to isolated and small populations of *L. kintorei*? A landscape-scale assessment of gene flow to evaluate the effect of habitat connectivity is recommended.
- This study did not investigate the impacts of harvesting for food on populations that exist within close proximity to Indigenous communities. In

some cases, this remains a key threat to very small and isolated populations and remains an important issue to explore.

- One study has been conducted investigating the mating system of *L. kintorei* at Uluru-Kata Tjuta National Park, Northern Territory, Australia (McAlpin *et al.* 2011). This study reports female monogamy and high levels of male polygamy (40%). This level of genetic polygyny is relatively high within the *Egernia* and *Liopholis* genera. It would be of interest to further investigate the mating system, philopatry and within-patch movement of *L. kintorei* at numerous locations, as intraspecific variation may occur across its distribution.
- Also valuable would be further investigation into habitat requirements of the species in relation to the capacity to construct deep burrow systems that provide both thermal and hydric buffers. For example, the high humidity observed in burrow systems may be related to water table levels which may explain some of the current distribution patterns that are associated with semi-saline sandplains and bore-fields.
- We also recommend additional longer-term studies exploring seasonal changes to predation pressure on *L. kintorei* by feral cat, fox and dingo.

Conclusion

Liopholis kintorei is a threatened skink restricted to the western deserts of Australia (IUCN 2016). This research identifies the key threatening processes for *L. kintorei* within spinifex grasslands as being broad-scale fire that removes all ground cover and predation by feral cats. It will be necessary for key populations across its wide

distribution to be formally identified and these key threats actively managed to ensure that the distribution of this species does not continue to decline significantly.

References

- Cadenhead, N. C. R., Kearney, M. R., Moore, D., McAlpin, S., and Wintle, B. A. (2015). Climate and fire scenario uncertainty dominate the evaluation of options for conserving the Great Desert Skink. *Conservation Letters* **9**(3), 181-190.
- Ducatez, S., and Shine, R. (2017). Drivers of extinction risk in terrestrial vertebrates. *Conservation Letters* **10**(2), 186-194.
- IUCN (2016). *The IUCN Red List of Threatened Species. Version 2016-2*.
<<http://www.iucnredlist.org>>. [accessed 04 September 2016].
- McAlpin, S. (2001). *A Recovery Plan for the Great Desert Skink (Egernia kintorei)*. (Arid Lands Environment Centre: Alice Springs, NT.)
- McAlpin, S., Duckett, P., and Stow, A. (2011). Lizards cooperatively tunnel to construct a long-term home for family members. *PLoS One* **6**, e19041.
- Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. (2015). Is fire a threatening process for *Liopholis kintorei*, a nationally listed threatened skink? *Wildlife Research* **42**(3), 207-216.
- Sinervo, B., Mendez-De-La-Cruz, F., Miles, D. B. et al. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**(5980), 894-899.
- Tingley, R., Meiri, S., and Chapple, D. G. (2016). Addressing knowledge gaps in reptile conservation. *Biological Conservation* **204**(Part A), 1-5.

Wilson, S. K. (2012). 'Australian lizards: a natural history.' (CSIRO Publishing, Collingwood.)

Woinarski, J. C. Z., Pavey, C., Kerrigan, R., Cowie, I., and Ward, S. (2007). 'Lost from our landscape: threatened species of the Northern Territory.' (Department of Natural Resources, Environment and The Arts: Palmerston.)

Appendix 1 of this thesis has been removed as it may contain sensitive/confidential content