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Can they beat the heat? The fate of ectotherms in the Australian arid zone under climate change

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LITERATURE REVIEW

Can they beat the heat? The fate of ectotherms in the Australian arid zone under climate change

L1 Introduction

Mitigating the impacts of anthropogenic climate change on the world’s species is set to be one of the greatest challenges of the 21st century. In order to do this efficiently, accurate predictions of the relative extinction vulnerability of various species must be determined. Species will react differently based on their life history, physiological and demographic traits. Thermoregulation strategy, the way in which an individual regulates their body temperature, is one such trait that is likely to affect vulnerability. Ectotherms are organisms that rely on external energy sources to regulate their body temperature, whilst endotherms are capable of maintaining their bodies at a constant temperature, independent of the environment. Ectotherms may be intrinsically more vulnerable to climate change than endotherms due to their reliance on environmental temperatures, and sensitivity to temperature changes (Amarasekare & Savage 2012; Wilms et al. 2011). Ectotherms make up a significant portion of global biodiversity, and those found in different climates are likely to be affected differently. Much research has been done on the fate of tropical versus temperate ectotherms under climate change (Huey et al. 2012; Huey et al. 2009; Sinervo et al. 2010; Deutsch et al. 2008). It is generally thought that tropical species will be greatly affected by increases in maximum temperatures, due to living in areas of low temperature variability (Sinervo et al. 2010; Deutsch et al. 2008). However, what of arid zone species? These organisms already live in extreme environments, and under climate change are likely to experience higher than average temperature increases, changes in rainfall pattern and extreme weather events (IPCC 2007). Until recently, little attention has been paid in the scientific literature to their fate. For the most part arid zone species have been lumped in with temperate species or assumed to follow generalised, global patterns of latitude (e.g. Deutsch et al. 2008). Recent studies however, are investigating ectotherms’ mechanistic responses to temperature increases and their relationship with the arid environment (Amarasekare & Savage 2012; Clusella-Trullas et al. 2011; Kearney et al. 2009). The results of these suggest that due to the extremes of their current environments, arid zone ectotherms may be more vulnerable to extinction under increasing temperatures that previously considered.

The key to understanding the extinction risk of a species is knowledge of its vulnerability and what drives that vulnerability (Huey et al. 2012; Williams et al. 2008). Vulnerability is made up
of a species’ sensitivity and exposure to environmental factors. Sensitivity of a species depends on intrinsic traits such as thermal tolerance and life history cycle, further influenced by its resilience and adaptive capacity. Resilience is the species’ ability to respond to perturbation by recovering from change and damage, whilst its adaptive capacity is its potential to change, plastically or genetically, in the face of a shifting external environment (Williams et al. 2008). Exposure is affected by regional habitat and climate change and mitigated through microhabitat buffering. This buffering is an interaction between thermoregulation on the part of the ectotherm and ecological structures, making it complex and difficult to evaluate. Microhabitat buffering is a key feature in determining the vulnerability of arid zone species.

Focusing on the Australian arid zone and temperature increase, this review aims to discuss and evaluate the emerging and competing theories on the vulnerability of arid zone ectotherms, relative to their tropical, and temperate, counterparts. I argue that arid zone ectotherms are just as, if not more, vulnerable than tropical species to extinction due to climate change. I will discuss a number of correlative and mechanistic studies and examine findings on the general biology of ectotherms that, when applied to arid zone species demonstrate and explain their vulnerability. There will be a focus on lizards, as the majority of the literature is concerned with them. I identify some key areas of research that are required to better understand threats to arid zone ectotherms and to consider their relative vulnerability to climate change when compared with their tropical or temperate counterparts.
L2 The ecology of arid zones affects ectotherm vulnerability

Arid zones cover more of the Earth’s surface than any other terrestrial climate type, making up 30% of land area (Peel et al. 2007). Despite this, they are one of the least well-represented biomes in scientific literature, particularly in respect to the effects of climate change, community dynamics and history (Byrne et al. 2008; IPCC 2007). Arid areas are characterised principally by low precipitation (generally <250mm/year) relative to temperature. This balance between rainfall and temperature leads to sparse, sclerophyllous vegetation, if any (Byrne et al. 2008).

All of these factors are true of the Australian arid zone. It covers the majority (77%) of the Australian continent, and is even less well studied than its Northern hemisphere counterparts (Morton et al. 2011; Byrne et al. 2008; Hughes 2003). The Australian arid zone has some features that make it unique even amongst arid climates; precipitation is highly unpredictable, with some areas receiving little to no rainfall for years at a time and there is widespread nutrient deficiency (Morton et al. 2011). These features, like the features of many arid zones worldwide, have developed more recently in geological time than the tropical or temperate zones around them. The conditions now faced by Australian arid zone species may be substantially different to those that occurred in their evolutionary history, potentially inhibiting their abilities to respond to climate warming (Byrne et al. 2008).

The arid zone contains few of Australia’s mammals or birds, but 43% of the continent’s non-marine reptiles and a similar proportion of its termites and ants. Worldwide, Australia is a centre of diversity for terrestrial vertebrate ectotherms (Kearney et al. 2009). Its arid zone, particularly spinifex grasslands, supports an unusually high diversity of lizards by global standards (Morton et al. 2011; Read 1995). A better understanding of these ecosystems could provide valuable knowledge on the mechanistic processes behind the vulnerability of ectotherms worldwide, as well as helping to preserve this large proportion of Australia’s unique fauna.

Assessment of climate change impacts on ectotherms is complicated by a lack of clarity about the ecological processes at play in the arid zone. The excess carbon available in the environment, relative to the scarcity of other nutrients, creates a system driven by plant exudates, controlled by environmental conditions (Morton et al. 2011). However, this view of arid systems fails to capture some processes. As arid systems have an abundance of predators and many organisms display camouflage colouration, it is likely that predators have a role in shaping these communities (Ayal 2007). The majority of vertebrates are reptilian ectotherms.
which feed on the abundant detritivores. Predation by larger, ranging predators keeps reptile numbers in check, rather than food supply, which is relatively stable. The ability of ectotherms to avoid predation though will depend, at least in part, on vegetation cover, which is climatically dependent. For example, in the Arizona desert, lizard abundance was strongly correlated to percentage grass cover despite constant prey abundance, and increased predation is likely in more exposed areas (Castellano & Valone 2006). These processes form ecosystems with complex interactions, both between biota and with the environment.

Under various climate change scenarios, it is predicted that mid-latitude arid zones are likely to get drier, and drying has indeed already been observed in some areas (IPCC 2007). Arid zones will be especially likely to be affected as rainfall patterns change and temperature increases reduce soil water availability and alter evapotranspiration rates. This will have flow on effects for primary producers and consumers. Increased fire frequency and intensity is also expected in this region (Hughes 2003). Climate change impact predictions are, however, highly uncertain for many arid zones, particularly Australian deserts (IPCC 2007). This is mostly due to a gap in the scientific literature and raw climate data, but also reflects the uncertainty in many of the driving processes behind the arid zone climate. Few assertions have been made about how these changes will affect the ecosystems and species within them.
L3 The impacts of climate change on arid zone ectotherms

There are a number of recent studies that consider tropical ectotherms under threat from climate warming (Huey et al. 2012; Dillon et al. 2010; Sinervo et al. 2010; Sunday et al. 2010; Huey et al. 2009; Kingsolver 2009; Deutsch et al. 2008; Parmesan et al. 2006;). Many of these studies consider tropical species in comparison to all other ectotherms, as if the remainder were one homogeneous group. Arid species are undistinguished and often dismissed without appropriate evidence. For example, Deutsch et al. (2008) state that tropical ectotherms will be most vulnerable due to low tolerance for temperature change. However, in their supporting material, a map shows that many arid zones have low seasonal differences (one of their main measures of temperature change) similar to tropical regions (fig. L1a). They state that there is a strong correlation between seasonality and tolerance to warming (fig. L1b). However, these findings are not reflected in their discussion, and no mention of the potential vulnerability of arid zone ectotherms is made.

![Figure L1.](image)

**Figure L1.** (a) Map of seasonality worldwide, where seasonality is defined as the standard deviation of monthly mean surface air temperatures. Note that many arid zones (such as the majority Australia, the Sahara and Middle East) have a similarly low seasonal variation to tropical regions (such as the Amazon and Central African rainforests). (b) Relationships between warming tolerance (critical maximum temperature - temperature of habitat) for various taxa of ectotherm. Low seasonality correlates with poor warming tolerance. From Deutsch et al. (2008) Supplementary material.

There is a real likelihood that arid zone ectotherms are just as vulnerable as tropical ones. The nature of finite resource and management allocations is such that priority must be given to species, or areas, based on intrinsic or economic value, vulnerability, probability of success, and cost (Bottrill et al. 2008). A lack of recognition of the vulnerability of arid zone species will, perhaps erroneously, mean they are not prioritised, potentially leading to a loss of global, and Australian endemic, ectotherm diversity. In some cases the information is available, but arid ectotherms are not explicitly discussed. Findings from studies that focus on general physiological principles, rather than specific climates or latitudes, indicate that arid zone species face many of the same problems as tropical ones, and indeed may be under greater threat than...
previously recognised (Amarasekare & Savage 2012; Clusella-Trullas et al. 2011; Wilms et al. 2011; and see Kearney et al. 2009 for specific focus on arid zone species).

L3.1 Tolerance Ranges
The main argument supporting the particular vulnerability of tropical ectotherms is that tropical lizards are intolerant to even slight warming due to narrow temperature ranges (e.g. Deutsch et al. 2008). This is most likely an artefact of living in environments with low temperature variability, a theory first proposed in the 1950’s (Dobzhansky 1950). The narrower a species’ temperature tolerance range, the more likely that even small increases in temperature could push it past its critical threshold. Amarasekare & Savage (2012) examined the mechanisms of the temperature dependence of specific fitness components; namely development, fecundity, and mortality. They propose that the shape of each species-specific tolerance range is due to the temperature responses of these components. A species will be more vulnerable if it has a narrow temperature response of reproduction (i.e. if reproduction occurs successfully over a small temperature range) and a high temperature sensitivity of development. This is indeed the case for many tropical species, providing *prima facie* evidence to support concerns about their ability to persist under climate change (fig. L2). Whilst many studies reach similar conclusions, Amarasekare & Savage (2012) are the first to explicitly state this causal relationship between vulnerability and temperature. It is important to note then, that they caution against simplistic latitude-based assertions of vulnerability (e.g. Sunday et al. 2010), as the reality will be a more complex interaction with other impacts on fitness. Little research has been done on the tolerance ranges of arid zone species in comparison to tropical ectotherms. However, the large diurnal temperature ranges of their environments may suggest wider temperature tolerances than tropical ectotherms.

![Figure L2. Temperature tolerance range in relation to fitness for a theoretical tropical and temperate ectotherm. The narrower range of the tropical species suggests a higher vulnerability to extinction due to climate change. Adapted from Bonebrake & Mastrandrea (2010).](image-url)
An alternative theory posed by Clusella-Trullas et al. (2011) is that diurnal temperature and precipitation range, rather than mean temperature increase, drives species’ thermal tolerance ranges. As a result, it will be changes in these climatic variables that most affect a species’ vulnerability through selection pressure, as they struggle to adapt their tolerance range to the changing temperature and precipitation ranges of their environment. Although arid zones have the largest diurnal temperature ranges (IPCC 1997), they are decreasing the fastest, due to increasing minimum temperatures (Zhou et al. 2009a,b). This may lead to a restriction of their thermal tolerance range, increasing their vulnerability. As Australian arid zone ectotherms already have the lowest thermal safety margins (proximity of optimal temperature to critical maximum) by latitude (Clusella-Trullas et al. 2011), the impacts of these shifting tolerances on their vulnerability could be considerable.

L3.2 Thermal Safety Margins and Microhabitat Availability

Width of temperature range is not the only factor that affects vulnerability, but also the proximity of an ectotherm’s operative temperature to its critical maximum - its thermal safety margin (fig. L3). Lizards thermoregulate to achieve their optimal temperature, but have a steep drop in performance once they surpass it (fig. L3), as their maximum temperature tolerance lies close to this optimum (Amarasekare & Savage 2012; Kearney et al. 2009; Huey et al. 2009; Deutsch et al. 2008; Huey & Berrigan 2001).

![Figure L3. Thermal tolerance curve for a theoretical ectotherm. The optimal temperature (T<sub>opt</sub>) lies close to the critical maximum temperature (T<sub>max</sub>) that the species can withstand (small thermal margin). Adapted from Amarasekare & Savage (2012).](image)

The habit of operating at temperatures close to the maximum threshold, whilst not unique to arid zone lizards, is especially important when one considers their environment. Living in such hot climates, which are predicted to warm faster than the tropics (IPCC 2007), thermoregulation is essential for allowing an individual to maintain an optimum temperature but avoid surpassing the critical maximum. Kearney et al. (2009) found that tropical and arid zone ectotherms both need to thermoregulate, by microhabitat selection, to stay in an optimum temperature range, as
opposed to temperate ectotherms, which can generally remain in full sun. Staying cool already is, and will increasingly become, more challenging than becoming hot, for both tropical and arid ectotherms. As temperature increases with climate change, the importance of selecting shady microhabitats will only heighten. However, the vegetation structure of ecosystems is likely to change under climate warming, as plant life may struggle to adapt to altering conditions (Hughes 2003). This would leave lizards open to more heat stress than they currently endure, where thermoregulation is not possible due to the homogeneity of the landscape and lack of shaded microhabitats. In this regard arid zone species are especially vulnerable, as their habitats provide fewer opportunities for shade, especially in Australian deserts, and this is likely to get worse as the climate warms (Kearney et al. 2009).

L3.3 Metabolism and Hours of Restriction
Hours of activity restriction may also increase greatly for tropical and arid species under climate change. During the middle of the day in hotter months, many ectotherms will have to be inactive either in deep shade or underground (Wilms et al. 2011; Kearney et al. 2009). These restricted activity times may not align with a species’ seasonal activity (mating, social interactions etc.) or metabolic requirements, leaving it energy deficit. Tropical species have been found to have the largest absolute metabolic rate increases due to the baseline warmth of their environment (Dillon et al. 2010). Arid zone species may also experience large metabolic rate increases with increasing temperature, though this has not yet be explicitly studied. Increasing metabolic rates lead to an increased need for energy intake, which may be impossible if activity times are simultaneously restricted. If this is the case, prey capture rate will have to increase substantially in order to maintain energy budgets, which may not be feasible. Increased restriction during summer or spring months may limit breeding or laying opportunities, and if a species is not flexible in the seasonality of such activities then this may lead to demographic collapse (Sinervo et al. 2010; Kearney et al. 2009). Increased temperatures will restrict daily activity, which is likely to place reproductive energetic stress on both tropical and arid zone ectotherms, though it remains unclear which, if either, will be more adversely affected.

L3.4 Synergistic threats
The synergistic effects of other global environmental threats, such as over-grazing and land use change, are likely to compound vulnerability due to climate change (Kingsford et al. 2009; IPCC 2007). Regardless of region, few studies consider the indirect impacts of climate change on ectotherms through changes to habitat structure and community composition (but see Kearney et al. 2009; Williams et al. 2008), because they are hard to predict. Ecosystem structure may play an important role in the relative vulnerability of arid zone ectotherms
For example, the main food sources of most Australian lizards are either termites and other small arthropods, and other vertebrate reptiles (Megías et al. 2011; Whitford 2002). All of these sources are ectothermic, and may suffer the same population declines as their predators (Ayal 2007). Less productive environments, with less primary production, support higher predation of third-order ectotherms by endothermic, ranging, top-predators (Ayal 2007). This means that lizards too will be more vulnerable to predation as vegetation structure changes. This may occur through changes to plant community composition due to climate change, and/or through grazing by feral animals or livestock (Castellano & Valone 2006). When assessing the vulnerability of arid ectotherms to climate change, consideration of these concurrent threats will reduce uncertainty, increasing the chance of successful management (Wintle et al. 2011).
Avenues for future research

One of the main reasons that arid zone ectotherms are not thought of as particularly vulnerable to extinction is possibly because they are not thought of at all. There is a lack of literature on all aspects of arid zones in relation to climate change – raw climate data, behaviour, physiology, and genetic architecture of species, ecosystem functions, and community composition to name a few. Data on the width of thermal tolerance of arid ectotherms is also lacking. This is the first step in validating the basic theory surrounding vulnerability due to temperature increases. If arid zone ectotherms are found to have narrower thermal niches than expected, their vulnerability would be greatly increased, as they would experience the combined impacts of increased proximity to critical maximum, along with decreasing microhabitat availability, as discussed.

Precipitation is one of the main areas of uncertainty in climate change predictions, as features such as cloud cover and the role of aerosols are still poorly understood (IPCC 2007). Rain plays a large part in shaping the vegetative community of arid zones and may also affect the optimum temperature preference of a species (Clusella-Trullas et al. 2011; Hughes 2003). In the absence of a better understanding of the mechanisms behind precipitation patterns, uncertainty analyses can determine “worst-case” vulnerability for differing levels of precipitation change uncertainty. This can inform management decisions as to the best investment strategy for minimising ectotherm vulnerability (Wintle et al. 2011). The same should be done for fire regime changes as uncertainty regarding intensity and frequency is high, although both are expected to increase (IPCC 2007).

Although frequently neglected in modelling climate change scenarios, evolutionary dynamics are likely to be important in shaping ectotherm responses to climate change (IPCC 2007). Little is known about how to predict this aspect of adaptive capacity, but heritable variation of temperature-dependant traits will likely be important (Williams et al. 2008). A species’ phylogeny, evolutionary climate interaction and trait co-variation will shape its ability to adapt to changing conditions, whilst short-term plasticity of individuals will also play a role (Gienapp et al. 2008). As genetic techniques improve, research focused on the genetic architecture of thermal sensitivity will be a valuable asset in determining vulnerability.

Many studies, some mentioned in this review, use correlations between species distribution and abundance, and temperature changes to confirm impacts of climate change (Sinervo et al. 2010; Parmesan 2006; Root et al. 2003). However, our understanding of the underlying mechanisms driving these impacts remains poor, making predictions about future impacts uncertain. Mechanistic models explicitly use known processes providing causal relationships between a
species’ biology, behaviour or environment and its distribution and vulnerability. Increased understanding of the reasons behind changes will allow higher confidence when extrapolating to new circumstances and novel environments such as climate change, and will strengthen predictions of extinction risk. What is lacking in this field is a means to fully integrate connections between climate change, habitat change, individual responses (behavioural and energetic) and population responses. Such an approach could provide key information for assessing vulnerability and can lead to better management decisions that can reduce vulnerability.
L5 Conclusion

Little evidence suggests that arid zones species are any less threatened by climate change than tropical species, despite the preponderance of studies extolling tropical species’ vulnerability. There is insufficient research effort to properly quantify that vulnerability in the way that has been done for tropical species. While research in the arid zones has been limited compared to tropical regions, this trend is beginning to change. A number of recent studies, mentioned throughout this review, focus on the importance of environmental features and interactions in determining vulnerability in arid regions. The heterogeneity of the landscape, to allow thermoregulation through microhabitat selection, is of particular importance in arid landscapes where current temperatures require ectotherms to shelter from the heat.

Arid zone species are likely to have wider temperature threshold ranges than their tropical counterparts. This would imply less vulnerability, if considered in isolation, as has been the case with many tropical-focused studies to date. When considering the extinction risk of a species, however, it is necessary to look beyond that singular factor to consider ecological interactions that may compound or buffer arid ectotherm vulnerability. For Australian arid zone ectotherms, a number of ecosystem features may make it more vulnerable to climate change than previously thought. As frameworks for assessing species vulnerability to climate change become more common, and prioritisation of resources more dire, it will be integral to understand the physiological, behavioural and ecological relationship an ectotherm has to temperature, and how this ultimately drives its vulnerability and distribution.
RESEARCH PROJECT

INTRODUCTION

The management of threatened species is subject to large uncertainties. The outcomes of management can be affected by a number of factors that are difficult to predict, such as predation pressure, extreme weather events, and introduction of invasive species or pathogens. Knowledge about the way in which a species interacts with its environment should form the basis for choosing between candidate management actions. However, uncertainties surrounding population-level species’ responses to a changing environment exacerbate uncertainty about the effectiveness of management actions (Hulme 2005). For these reasons it is crucial that managers are provided with the most reliable predictions about the likely implications of climate change for species’ persistence given available knowledge, and a realistic appreciation of the uncertainty inherent in such predictions.

Climate Change

The average global temperature is rising and is highly likely to continue on such a trajectory (Fischlin et al. 2007). Beyond that, there are few gross generalisations that can be made on a global scale in relation to the effects of climate change. Easier to categorise are the changes occurring across different biomes, as ecosystems at similar latitudes are predicted to respond similarly to increasing greenhouse gases (Fischlin et al. 2007). Arid zones, occupying 27.7Mkm$^2$ of the Earth’s surface, are expected to increase in temperature and decrease in rainfall predictability (Fischlin et al. 2007).

Due to the broad nature of the global climate models used to make the IPCC predictions of climate change worldwide, on a more regional scale, large uncertainties are often incorporated (Fischlin et al. 2007). Fine scale predictions made by the CSIRO allow us to take a closer look at what is likely to happen in Australia. Since the 1950s, Australia’s arid zones have warmed more than the global average. For each degree of warming at a global scale, the temperature in central Australia has risen by a minimum of 1.5°C (Suppiah et al. 2007). During this time, precipitation patterns have responded divergently, with summer rainfall increasing but winter rainfall decreasing per global degree of warming (Suppiah et al. 2007). There is high agreement amongst models on the direction and strength of changes in temperature, atmospheric pressure and wind levels throughout central Australia, with rainfall changes less certain in the North West (Suppiah et al. 2007). When modelled at a regional scale, the general pattern of changes remains the same, but more detailed observations are possible, increasing the congruity of precipitation predictions. In the Northern Territory, the very arid centre of the state is predicted
to dry out, with a decrease in rainfall of up to 40%, while the less arid regions and the tropical North range from a 20% increase to a 40% decrease in precipitation (Hennessy et al. 2004). During the winter months, precipitation in the arid centre may decrease by as much as 60%, with delays in the onset on the wet-season expected (Hennessy et al. 2004). Temperatures in the arid regions of the Northern Territory are expected to increase by between 1.0-7.2°C by 2070, with greater warming in the summer months (Hennessy et al. 2004). Moisture balance, the amount of available moisture in the air, is expected to decline 90-400mm, which could decrease available soil moisture and river flow, although this has yet to be formally investigated (Hennessy et al. 2004). These changes to climatic conditions will interact to alter other aspects of the environment, such as community structure and species interactions (Hennessy et al. 2007).

Changes in climate are already affecting species across all taxa (Parmesan 2006; Sinervo et al. 2010). It is difficult to distinguish between population declines due solely to climate change and those due to interactions with habitat loss and fragmentation, loss of symbiotic relationships, invasive species, or novel diseases. As broad ecosystem types are expected to change in similar fashions, it can be useful to investigate the way species endemic to a particular ecosystem will respond to climate change as a group (see Literature Review above for a comparison of arid, temperate and tropical species in response to increasing temperature).

Living in already extreme conditions, arid zone species will be vulnerable to increases in temperature and decreases in rainfall (Fischlin et al. 2007; Simmons et al. 2004; Kearney et al. 2009). Increases in carbon dioxide levels may increase growth rates of some desert plants (Thuiller et al. 2006), which, along with increased rainfall predicted in certain arid systems, could lead to an increase in wildfires, some in systems where fire is currently uncommon and species are maladapted (Bachelet et al. 2003). In arid regions of Australia, in response to a warming, and likely, drying, climate, species are expected to undergo population declines as primary growth decreases, limiting both food and shelter resources (Hughes 2003; Roshier et al. 2001).

**Fire**

Fire is an integral ecosystem process to many systems worldwide. In Australia, fire seasons are ongoing all year round with between 300 000 km² to 700 000 km² of land affected annually (Maier & Russell-Smith 2013). For much of this area, fire provides a valuable service in ‘resetting’ successional habitat dynamics, allowing certain species of plants and animals to establish, or re-establish, in post-fire environmental conditions. Although individual fires are
stochastic events, there are patterns in the timing, size and intensity of fires that differ on a regional scale such as the distribution of the lengths of time between fires in a particular location and the variance of that distribution. For example, in the wetter, cooler temperate forests of Tasmania, fires occur roughly every 400 years (Gilbert 1959), whereas in the centre of continental Australia most places burn at least once every decade (Nano et al. 2012).

The arrival of Aboriginal peoples to mainland Australia approximately 45,000 years ago is thought to have coincided with a drying of the climate (Latz 1995). Subsequent changes in fire regimes across Australia were likely the result of interactions between these two events (Mooney et al. 2012; Sakaguchi et al. 2013). Aboriginal people learnt to control fire in the Australian landscape and developed a ‘fire-stick farming’ method involving the lighting of small spot fires for a number of purposes, mostly associated with food-gathering (Bird 2005; Jones 1969). As a result of this and the decrease in rainfall, fire frequencies are thought to have increased across the continent, tipping the balance towards fire-dependent communities and leading to specialisation of many biota to various stages of the fire cycle (Latz 1995; Sakaguchi et al. 2013).

There is evidence that fire regimes have shifted from small-scale patch burning to larger, more homogeneous fires since the decline of Aboriginal people's fire management practices in the deserts of Australia (Burrows et al. 2006; Mooney et al. 2012). Along with changes to fire regimes, livestock and feral rabbit grazing reduced fuel loads, reducing survival and reproduction of native plants, altering the vegetation composition and ecology of most arid areas. Additionally, direct prevention of fire-lighting by Europeans, concerned for their livestock, and the fragmentation of the land by conversion to agriculture preventing fire spread, also reduced the patchwork quality of fire mosaics, ultimately reducing the fire frequency but increasing fire size and intensity when fires did occur (Allen & Southgate 2002; Burrow et al. 2006a). Loss of traditional knowledge through increased mortality in, and displacement of, the Aboriginal population led to the cessation of traditional burning practices in most arid areas (Bird et al. 2005; Holmes & Jampijinpa 2013). Given the relatively short time since European settlement, most endemic fauna and flora are adapted to the pyric conditions that existed prior to European colonisation. As such, Australia’s biota are likely maladapted to the current, post-colonisation fire regimes.

A number of endemic Australian species have evolved to depend on fire for some phase of their life cycle (Bowman 1998). Common examples of this include obligate seeding Banksias and Callitris species. It is more difficult to identify which animal species depend on fire directly, though there are a number of species that thrive in post-fire environments of the arid zone,
including the knob-tailed gecko, *Nephrurus stellatus* (Smith *et al.* 2012), the Greater bilby, *Macrotis lagotis*, (Southgate *et al.* 2007) and the goanna, *Varanus gouldii* (Bird *et al.* 2013). For these ‘fire-specialist’ species, fires can create food sources through plant-successional dynamics, or prey-population booms. Trees killed in fires can also decay and form trunk hollows, providing valuable habitat (Adkins 2006). Suppression of fires has been shown to decrease populations of knob-tailed geckoes (Smith *et al.* 2012) and there is support for the theory that changes in fire-regimes are a major contributor to the decline of small-to medium-sized mammals in mainland Australia, partly due to a shift toward larger, hotter fires that leave mammals exposed to predation by feral predators (Fischer *et al.* 2013; Woinarski *et al.* 2010; Latz 1995; but see Paltridge 2005 for alternative explanation). In contrast, many plants and animals remained sensitive to fires and do not benefit from fire events. These fire-sensitive fauna can be affected by fire regimes in one of three ways: direct mortality during a fire, through top-down or bottom-up selection pressure. Top-down pressure acts through the reduction in ground cover following a fire, which removes critical shelter, exposing animals to predation and potentially harsh climatic conditions. Bottom-up pressure results from a loss of vegetation as a food source, either directly for herbivores, or indirectly for second- and third-order predators whose prey suffer population declines. These selection pressures can affect fire-specialist species if the fire regime changes unfavourably, reducing the aspects of post-fire habitats that make them suitable.

On a continental scale, fire intervals are expected to shorten across Australia as the climate warms. There will be a larger number of ‘fire days’ where conditions for ignition and spread are extremely favourable (Hennessy *et al.* 2007). Conservative estimates suggest the number of days over 40°C will double by 2070 in central Australia, while others put the figure closer to 7-fold (~111 days of the year over 40°C). With 3-5 day spells over 40°C expected a minimum of 6 times a year by 2070, the number of ‘fire days’ will have increased substantially (Hennessy *et al.* 2004). However, in central Australia, despite this increase in favourable climatic conditions, the opposite outcome is likely and fire intervals may actually increase. This is due to the decrease in rainfall predicted in this area (see figure S1 in Hennessy *et al.* 2004; Whetton *et al.* 2005). The dominant arid plant communities, spinifex and mulga, are adapted to rapid growth following rainfall, and grow slowly in the absence of large precipitation events (Cary 2002; Orians & Milewski 2007; Rice & Westoby 1999). Reduction in the amount and frequency of rainfall events is therefore likely to result in slower growing vegetation and lower fuel loads. So, although the climatic conditions for fires may become more favourable, available fuel loads will be a limiting factor, lengthening fire intervals and possibly increasing the intensity of less frequent fires in the arid centre of the continent. Fire intensity is likely to increase with an increase in extreme fire weather days (Pitman *et al.* 2007). The palaeoenvironmental records
suggest that the response of fire regimes to climate change is rapid, showing no lag during glacial and interglacial changes throughout pre-history (Mooney et al. 2012).

The fire-adapted vegetation of central Australia supports a number of threatened, fire-adapted animals. For example, both rufous hare-wallabies, *Lagorchestes hirsutus*, and bilbies, *Macrotis lagotis*, rely on post-fire resources (Bolton & Latz 1978), although the type of fire may be an important factor. It remains unclear as to whether the difference between pre-European, current and future fire patterns will be critical in determining the viability of the arid zone fauna. Smaller, cooler burns associated with 'fire-stick farming' tend to generate a more complex mosaic of burned and unburned patches that provide food and shelter for fauna and a local source of seed for recruitment of shrubby vegetation.

The great desert skink (GDS), *Liopholis kintorei*, is one such animal thought to be affected by fire frequency, size and intensity. The GDS is a large, nocturnal, burrowing skink distributed in restricted pockets across central Australia in arid and semiarid habitats (McAlpin 2001). The pre-European extent of great desert skinks included much of Western and South Australia as well as the Northern Territory. Now considered threatened with extinction, the true extent of the GDS’ decline and the causes for it are uncertain (IUCN 2001). Loss of small-scale fire mosaics and predation by feral cats and foxes are thought to be the main threats (McAlpin 2001), which may imply an interaction between fire type and feral predator pressure. There are three documented populations of over 1000 individuals left; at Uluru-Kata Tjuta National Park, in the southern reach of the Gibson Desert and in the Tanami Desert (McAlpin 2001). The majority of the Tanami desert population is found on a wildlife sanctuary in the south of the region. Surveys conducted at this sanctuary have noted that recently burnt areas appear to be unsuitable for the GDS, as burrows found in these areas are often abandoned (pers. obs. 2013; D. Moore pers. comm. 2013).

Managers can use fire and fire suppression as a tool for achieving conservation outcomes. This can be a complex undertaking as the relationship between fire, species and ecosystems is often uncertain and different species have differing requirements. What constitutes suitable habitat, how that habitat is maintained by the fire regime, and how fire regimes may change with climate needs to be thought through when designing conservation strategies for species in fire adapted landscapes. Moreover, fire managers must trade between maintaining fire-dependent communities and conserving highly threatened species with highly restricted ranges that may be severely impacted by fires at the wrong time or in the wrong place. The loss of one population through fire, once insignificant in comparison to the benefits of a fire-rejuvenated ecosystem, can potentially sound the death-knell for a species that is on the brink. For example, the loss of
the last rufous hare-wallabies in the Tanami desert was due to one population being eaten by a fox and the other destroyed in a fire (Bolton & Latz 1978). Nonetheless, amongst a suite of difficult-to-control factors, such as climate change, habitat fragmentation and invasive species, fire is one variable that managers can often readily manipulate. This makes it a potentially powerful tool. Important factors in deciding when and where to burn for conserving a threatened species include where the species is found, how connected its populations are, how the species responds to fire, whether they suffer direct or indirect mortality after fire, and how long it takes for the species and its habitat to recover from local disturbance. How local disturbances interact with other threats such as predation pressure, and how accumulation of local disturbances across a species’ range contributes to its regional or global persistence, also determine when and where is best to burn. Additionally, when investigating these factors, the stochastic processes that operate in fire-dominated landscapes make static representation of species distribution of limited value (Chisholm & Wintle 2007). They may be useful for guiding surveys aimed at discovering new populations, but they cannot provide insights into the medium to long-term prospects for the species under changing environmental conditions and management interventions as they offer but a single snapshot of the present, rather than a multi-time-step view of the stochastic landscape processes affecting a species (Fordham et al. 2013). Instead, these factors can be investigated by analysing environmental drivers of a species’ distribution, abundance, and population dynamics within a dynamic landscape using a combination of expert opinion, empirical analyses and simulation modelling (e.g. Açkakaya 2004; Wintle et al. 2005; Bekessy et al. 2009).

While some studies have looked at the specifics of the relationship between a fire-specialist species and current fire regimes (e.g. Smith et al. 2012, Bird et al. 2013), and other studies have outlined an analytical strategy for integrating landscape and climate change into spatially explicit analyses of species long-term persistence (e.g. Gordon et al. 2012; Wintle et al. 2005), we could find no studies that specifically predict the influence of changing fire regimes and management of fire in the long-term persistence of a species. Given that fire regimes are likely to be altered by climate change in the foreseeable future, and that managers can use fire as a tool for achieving conservation objectives, this is a potentially fruitful avenue of investigation that may be particularly instructive in guiding conservation of the great desert skink.

Aims
This study aims to build on the narrative established in previous studies of the relationship between fire-dependent species and patterns of fire (Smith et al. 2012, Bird et al. 2013), to explore the long-term prospects of the great desert skink under changing pyric conditions. I will
investigate the variables that drive distribution and abundance of the GDS in a part of its post-European range. I aim to explore the consequences of various fire regime scenarios and provide specific recommendations about fire regimes that are most commensurate with the objective of securing great desert skink populations in the long-term. More specifically I will;

- characterise the environmental drivers of great desert skink distribution across Newhaven sanctuary in arid central Australia,
- investigate whether fire history can help explain the distribution of skinks at Newhaven using survey data and expert opinion,
- explore how best to characterise the influence of recent fire on GDS distribution, accounting for uncertainty in model selection with a set of competing models,
- investigate how changes in fire regime are likely to influence the trajectory and extinction risk of the population by simulating long-term metapopulation dynamics in the sanctuary,
- evaluate how sensitive the ranking of fire scenarios is to uncertainty in distribution models,
- discuss the implications of my findings in terms of strategies for ensuring the long-term persistence of GDS at Newhaven through the management of fire.
METHODS

Background Information

Great desert skinks
Great desert skinks are large lizards, approximately 160-210mm from snout to vent at adulthood and weighing an average of 350g (McAlpin 2000). They are unusual for reptiles in that they live in family groups and build extensive burrow systems that they inhabit for multiple breeding seasons (McAlpin et al. 2011). Up to 10 individuals, across multiple generations, may reside in a burrow at one time. GDS predominantly eat termites, although their diet can consist of plant materials, insects and even small vertebrates (McAlpin 2000).

Burrow systems can stretch 10 meters across, and be up to 1m below ground level, with several entrances. All members of the family use a communal latrine, located outside the burrow, within a few meters of the entrances (McAlpin 2000). The latrine is a patch of ground sheltered within spinifex hummocks, *Triodia* spp., where all individuals in a burrow deposit their faeces. As many burrowing animals inhabit the same habitat as the GDS, making similarly sized holes, the latrines are the easiest GDS attribute to identify in the field where the white urea of the faeces stand out against the reds and yellows of the desert (pers. obs. 2013). Other species of lizard and the brush-tailed mulgara shelter in both occupied and abandoned GDS burrows, making the GDS a potentially important ecosystem engineer.

Observations of abandoned burrows in recently burnt habitat, has led managers at the sanctuary to speculate that GDS find large recently burned patches unsuitable but appear at highest densities in vegetation that is close to recently burned patches (D. Moore pers. comm. 2012). As their burrows most likely allow the GDS to avoid direct mortality from fires, hiding deep enough underground to escape the flames and heat, the mechanisms behind this apparent decline in occurrence must act on the skinks post-fire. Fires burn away the majority of the ground cover, leaving burrow entrances and foraging skinks exposed to predation, as well as reducing microhabitat availability for behavioural thermoregulation. The primary food source of the GDS is termites, and little is known about termite responses to fire. Termites feed on spinifex, *Triodia* spp., which is highly flammable, and once burnt away, may result in the termites dying off, moving their nests to more suitable areas, or remaining in impenetrable mounds, until conditions are more favourable. All of these eventualities could cause a reduction in skink survival in large burned patches.
Newhaven

This study was conducted at a wildlife sanctuary in the centre of arid Australia. Newhaven Wildlife Sanctuary is located in the Tanami desert, 300km to the Northwest of Alice Springs (fig. 1). It covers 262,000ha and lies in the Lake Bennett and Mackay sub-regions of the Great Sandy Desert bioregion (IBRA7). Characteristic of these bioregions are the sand plains and dunes that cover Newhaven, and the hardy, fire- and arid-adapted vegetation.

![Map of Australia with inset showing location of Newhaven Wildlife Sanctuary](image)

**Figure 1.** Newhaven wildlife sanctuary, with inset showing location within Australia. Vegetation classes shown are as in Appendix 1.

Spinifex, *Triodia* spp., dominates the landscape, while trees and teatree, *Melaleuca* spp., shrubs inhabit the richer soils near palaeodrainage lines (Paltridge 2005). The lakes remain vast salt plains for most of the year, occasionally filling with water during infrequent, heavy rains. The climate of the Tanami Desert is semi-arid, with very hot summers where temperatures frequently exceed 40°C and mild winters. Mean annual rainfall in the southern edge of the desert, near Newhaven, is 322mm, with most rain falling during the summer (Paltridge 2005).
Fire is a common and integral feature in the landscape. Fires burn all year round, although the most widespread and intense fires occur during the extremes of summer. Ignition sources are both natural and man-made, with members of the nearby indigenous communities occasionally lighting spot fires near and on the property, and lightning igniting the rest.

Newhaven is currently managed by the Australian Wildlife Conservancy (AWC). After spending the second half of the 20th century as a cattle station, it has been managed as a wildlife sanctuary since 2000. Currently, managers at the sanctuary have a number of objectives, mostly focused on the maintenance of habitat for threatened species present on the property. Feral animals (mostly camels, foxes and cats) and weeds are either controlled or being monitored for future control programs. Biodiversity surveys also take place each year to monitor populations of all known fauna in the sanctuary. Fire is actively managed, via prescribed burns and wildfire control, with a view to creating a finer mosaic of time-since-fire patches than currently exists. Fires are lit in winter to prevent large-scale intense summer fires from burning large areas of the sanctuary.

Species Distribution Models (SDMs)

Species data
GDS occurrence data was provided by the Australian Wildlife Conservancy (AWC). Individuals with prior experience in GDS surveys collected this data using varying techniques. The records spanned from 2003 to 2012. The first four years of data were collected by Desert Wildlife Services, during which surveys were conducted across the sanctuary, but concentrated along roadsides. Surveyors drove until they sighted patches of soft spinifex, *Triodia pungens*, (what they considered to be ‘suitable GDS habitat’), and then searched the area for burrows (D. Moore pers. comm. 2012). The data from 2008 to 2010 came from 100 2ha plots that form part of an annual biodiversity survey and are surveyed for all animal spoors as part of a larger monitoring program across Newhaven. The 2011 data were collected in a concentrated survey within areas known to contain GDS burrows. Sanctuary managers and volunteers conducted the 2008-2011 surveys. The 2012 occurrence points were obtained in a GDS-targeted trapping survey (S. Dennis, unpublished data).

Due to the way in which the data were collected, not all years contain what could be considered reliable absence data. For example, the data collected by the Desert Wildlife Services does not include coordinates of areas searched for GDS but in which none were detected. Overall, the numbers of presence and absence points were roughly equal, with 245 GDS occurrences and 222 absences (fig. 2).
Figure 2. Map of Newhaven Wildlife Sanctuary showing soft spinifex sand plains alongside presence and absence data. Presence points are almost exclusively restricted to soft spinifex sand plains, indicating that this vegetation type is a strong driver of GDS distribution.

Environmental data

For use in SDMs, environmental data are usually represented by spatially explicit geographic information system (GIS) layers, and represent properties of the landscape that may affect the distribution of a species. Information on the vegetation at Newhaven was obtained from the AWC which had previously commissioned an aerial survey to classify areas into major vegetation classes by an expert (A. James pers. comm. 2012). Although this data had not been extensively ground-truthed, it was known that within some of the areas classified as open saltbush flats, there were patches of soft spinifex present at a finer scale than that captured by the survey. As such, areas classified as open saltbush flat were treated as soft spinifex sand plains during this study. Data on the geology and fire history of Newhaven was also obtained from the AWC (table 1). Fire records for each year were provided, from 1970 to 2012 and were used to create variables of time-since-last-fire and the number of fires in a 44- and 10-year period, at a spatial resolution of 100m. These were prepared in the statistical software package RStudio (RStudio 2012), a GUI version of the program R (R Development Core Team 2013).

Radiometric data represents information on the proportions of certain radioactive elements in the soil, as measured via a gamma-ray spectrometric method (Minty et al. 2009). The varying levels can be interpreted as certain geological formations and soil types, and can be a valuable source of information in explaining distributions. Obtained freely through the GeoScience Australia website, a number of layers are available as geographic information system layers,
mapped at a spatial grain resolution of 250m. Uranium, potassium, ferrous iron, ferrous oxide, thorium, quartz and ‘ternary’ content were all considered. The ternary layer represents the relative proportions of potassium, uranium and thorium at the Earth’s surface.

Climatic variables (ANUCLIM) initially considered for use in modelling were compiled by Kristen Williams (CSIRO; described in Williams et al. 2012).
Table 1. Variables used to determine habitat suitability and identify patch structure for the GDS at Newhaven Wildlife Sanctuary.

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Description</th>
<th>Range (mean)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>elevation</td>
<td>Elevation above sea level (m)</td>
<td>524-791 (552)</td>
<td>ANUCLIM</td>
</tr>
<tr>
<td>feocontent</td>
<td>Ferrous oxide content of Earth’s surface</td>
<td>0-255 (203)</td>
<td>GeoScience Australia (Radiometrics)</td>
</tr>
<tr>
<td>nf</td>
<td>Number of fires in the past 44 years</td>
<td>0-7 (2)</td>
<td>Created in R from AWC fire history maps</td>
</tr>
<tr>
<td>ternary</td>
<td>Relative potassium, thorium and uranium content</td>
<td>51-235 (161)</td>
<td>GeoScience Australia (Radiometrics)</td>
</tr>
<tr>
<td>tsf</td>
<td>Time since last fire (yrs)</td>
<td>1-44 (20)</td>
<td>Created in R using AWC fire history maps</td>
</tr>
<tr>
<td>vegnew</td>
<td>Vegetation class (as defined in Appendix 1)</td>
<td>1-22 (-)</td>
<td>AWC</td>
</tr>
<tr>
<td>nf10</td>
<td>Number of fires in the past 10 years</td>
<td>0-5 (1)</td>
<td>Created in R from AWC fire history maps</td>
</tr>
<tr>
<td>ferrousiron</td>
<td>Ferrous iron content</td>
<td>0-255 (238)</td>
<td>ANUCLIM</td>
</tr>
<tr>
<td>geology</td>
<td>Geological class (as defined in Appendix 1)</td>
<td>1-11 (-)</td>
<td>AWC</td>
</tr>
<tr>
<td>ruggedness</td>
<td>Topographic heterogeneity index</td>
<td>0-81 (2)</td>
<td>ANUCLIM</td>
</tr>
<tr>
<td>twmaxNH</td>
<td>Topographic wetness index (rainfall runoff measure)</td>
<td>6239-21960 (13880)</td>
<td>ANUCLIM</td>
</tr>
</tbody>
</table>
The environmental variables, as GIS layers, were sampled at the geographic coordinates of each of the 467 AWC survey data points to create a data frame for use in modelling GDS occurrence. Each row of the dataset contained an observation (with 0 representing absence and 1 representing a presence point), and a value for each environmental variable (as in Table 1) at that location. When sampling the fire history variables in generating the modelling data frame, the time since fire and number of fires variable values were adjusted to account for the date at which each observation of presence or absence was recorded.

**Model Fitting**
Great desert skink probability of occurrence was modelled using logistic regression methods. Specifically, generalized linear models (GLMs: McCullagh & Nelder 1989), generalized additive models (GAMs: Hastie & Tibshirani 1990), and the machine-learning method boosted regression trees (BRTs: Elith et al. 2008) were all used to fit competing models describing the variation in observation of presence or absence as a function of the environmental variables. Multiple model approaches were used because it was thought that they would potentially provide different insights into the drivers of GDS distribution. GLMS are comprised of (i) a random component that describes the assumed distribution of the observation data, in this case a binomial distribution appropriate for modelling binary response data, (ii) a linear predictor, which combines all of the independent model variables in an linear equation, and (iii) a ‘link’ function describing the mathematical relationship between the response and explanatory variables, in the case of logistic regression, this is a ‘logit’ function; which re-scales the linear predictor into a probability with bounds [0,1] (eq. 1):

\[ f(x) = \frac{1}{1 + e^{-x}}. \]  

where \( x \) represents the value of the predictor variable.

A GAM is a non-parametric version of a GLM, which allows a more flexible description of the relationship between the response and explanatory variables, allowing the data to be fitted more closely (Hastie et al. 2001). BRTs are a combination of statistical and machine learning methods, building a series of simple classification trees and using a boosting algorithm to combine similar models. Regression or classification trees divide predictor space into a series of areas across which the response to the predictor is homogeneous. It then fits a constant response to each region based on either probability or the assumption of a normal distribution of means (Elith et al. 2008). Binary splits are performed on each arm of the tree until some stopping condition is reached. Boosting then improves the accuracy of the models based on the averaging of a number of rules (Schapire 2003), through a stepwise series of model iterations. In general,
BRTs are quite useful in capturing interactions between the independent variables and highly non-linear relationships such as thresholds.

**Initial variable reduction**

All model fitting and evaluation was done in R, using the base functions and libraries ‘gam’ and ‘gbm’ (Hastie 2011; Ridgeway et al. 2013, with additional code described in Elith & Leathwick 2008). Once candidate independent variables were identified (table 1), a further preliminary variable reduction was done by fitting univariate GAMs to each candidate variable with a 5 degrees of freedom in order to (i) identify independent variables that explain a large amount of the variation in species occurrence, (ii) choose the most explanatory and ecologically sensible response shapes for each independent variable, and therefore (iii) choose the maximum degrees of freedom that each independent variable will be allowed to utilize in the stepwise variable selection routine used to identify the most competitive model set (sensu Wintle et al. 2005).

Partial dependency plots were scrutinized to determine whether highly explanatory response shapes made ecological sense. In some cases, highly explanatory fits that could not be justified in a theoretical way were abandoned and the either the variable was excluded from further consideration, or the number of degrees of freedom offered was reduced such that a theoretically defensible relationship was represented. By reducing the variables in this way before stepwise model selection, it lowers the chances of important variables being dropped while irrelevant ones are kept, an unfortunate by-product of the stepwise procedure. Hastie et al. (1996) recommend that less than \( m/10 \) predictor degrees of freedom (PDF) should be offered to a stepwise selection routine, where \( m \) is the number of observations of the least populous class in the dataset (in our case, 222 absences). For the full dataset including AWC data and addition data points compiled during field surveys, application of this rule resulted in a maximum of 22 PDF potentially being offered to the automated variable reduction routine. Vegetation classes were grouped together into *broadly* similar types to reduce the PDF allocated to the vegetation variable.

Collinearity of variables was examined and when pairs of variables had an absolute Pearson correlation coefficient above 0.75, the predictor that explained the least significant portion of the variation was excluded from further models (sensu Wintle et al. 2005).

Ultimately, it was decided that the range of most of the ANUCLIM variables were too small across the sanctuary to make any meaningful difference to the GDS, and they were discarded. For example, the mean annual temperature layer varied by only 1.8°C across Newhaven, and
given that the values are coarse extrapolations from weather stations approximately 100kms away, their applicability to the scale at which the GDS functions was scant.

The ‘step.gam’ function, available in the ‘gam’ package was used to find the set of models with the lowest Akaike’s Information Criterion (AIC: Akaike 1973) via backwards-stepwise selection. This function works by selectively dropping the least statistically significant variable and comparing the new model’s AIC to the previous one until a local minimum is reached. Although stepwise selection has been criticized (Quinn & Keough 2003), it provides a coherent means of determining a candidate model set when there are no theoretical grounds on which to define an a priori set of competing hypotheses that can be represented by discrete combinations of independent variables. A set of ‘AIC-best performing’ (AICbest) models was identified for further use in the study. AICbest performing models were all models within 2 AIC points of the single AICbest model.

Models were evaluated using three statistics: (a) the AIC; (b) the deviation explained; and (c) the area under the receiver operating characteristic (ROC) curve (Hanley & McNeil 1982). The percentage of deviation in the data that is explained by the model gives some indication of how much the combination of variables is describing patterns in the data, and how much is not explained by the relationships fitted in the model. To assess the predictive performance of the AICbest set, 10-fold cross-validation (Hastie et al. 2001) was performed using the area under the ROC curve (Pearce & Ferrier 2000). The ROC value describes ability of the model to accurately predict a randomly-selected presence or absence in the dataset. ROC measures the ability of the model to discriminate between (or correctly rank) presence and absence locations based on predicted probability of occupancy. Hence, ROC is considered a good measure of 'model discrimination'. K-fold cross validation involves randomly splitting the dataset into two subsets and using one set to re-build the model and the other to test against. This data-splitting and testing occurs k times in k-fold cross-validation, with the results indicating the variables which consistently allowed the model to most accurately predict the distribution of presences and absences in the test dataset.

As well as the cross-validation, we decided to collect independent field data to externally validate the performance of the models based on ROC.

**Field validation of the GDS distribution model**
Fieldwork took place during 25th-30th March 2013 with the aim of testing the predictive performance of the GDS distribution model fitted to the AWC-only data and to gain insights
into the distribution and ecology of the GDS in the Newhaven Sanctuary. At the time of field work adult *L. kintorei* were beginning hibernation while juveniles remained active (D. Moore pers. comm. 2013). However, it was always intended that identification of occupied sites would involve searching for active burrows identified by the distinctive latrines where a family of great desert skinks will all deposit their scats (McAlpin 2001). Forty-five sites were surveyed, all within one kilometre of a road, as the climatic conditions were unsuitable for long distance walking and off-road driving is harmful to the soil crust (and inadvisable when driving in areas that you think contain a ground-dwelling threatened animal). Approximately nine sites were covered each day by the two teams.

Sites were chosen at semi-random, within a loose set of requirements. Based on the predictions of the best-fit GLM, GAM and BRT models, areas predicted to be of mid-range (0.4-0.7) probability of occurrence were targeted. These areas represented uncertainty within the models about the occupancy, where further presence or absence data would have the greatest impact in helping the model identify (and parameterise) the drivers of distribution and therefore better discriminate between occupied and unoccupied sites. Within these mid-range areas, sites had to be chosen within 500m of a road, for access and safety reasons. We captured previously unsampled environments by placing sites in areas where we had no occurrence data for a particular environmental variable (e.g. previously unsampled vegetation types).

Sites were rectangular plots of 200m x 100m, containing only one vegetation type and, where possible to distinguish, only one time-since-fire class. For consistency the plots were generally set up so that the longer sides ran north south. Observers spent 30 minutes searching for great desert skink burrows and latrines. Latrine locations were marked with GPS receivers and at the end of the survey time, all team members would attend each potential burrow to authenticate it and make sure no burrows were recorded twice. Due to the preponderance of burrow-like diggings across the sanctuary, the presence of a latrine was necessary to positively identify a great desert skink burrow. The only other species in the area known to use latrines is the closely related night skink, *L. striata*, Sternfeld, 1919, whose scats are noticeably smaller and easily distinguished from those of the great desert skink (pers. obs. 2013). As none of the researchers had prior experience identifying great desert skink burrows, a half-day training period was spent with the managers of Newhaven, learning how to identify the burrows and scats correctly. At each site, vegetation type was noted down to validate the vegetation map, and each observer conducted a count of termite burrows in the plot during the survey.

One of the unexpected advantages of the fieldtrip was the opportunity to talk one on one with the managers of Newhaven, and other staff associated with the GDS recovery plan and annual
surveys. This enabled a greater understanding of the fire management and history of the sanctuary and insight into some expert opinion on the potential drivers of GDS distribution and habitat use. These interviews and observations in the field led to a renewed focus on modelling predominantly in the soft spinifex sand plains as well as a diversification of the fire variables considered in the subsequent analyses following fieldwork.

Field data were used to provide an independent estimate of ROC scores for each of the best performing distribution models constructed using AWC-only survey data fitted with GLM, GAM and BRT models.

**Detection modelling**

Field surveys for GDS active burrows involved multiple observers (between 2 and 6) independently surveying searching sites for active burrows. Steps were taken to ensure that searchers were not influenced by the other searchers when looking for burrows. These included starting surveys at opposite ends (or cardinal points) at survey locations, observers not dwelling over suspected active burrows and not communicating or conferring about observations until the end of the survey. The multiple observer survey strategy enabled us to utilize imperfect detection modelling approaches to estimate the probability that an individual observer would detect at least one active mound if active burrows were present at survey locations (*sensu* Tyer *et al.* 2003). This analysis was conducted for a qualitative assessment of detectability, and was not directly incorporated into any of the models.

A zero-inflated binomial (ZIB) model was fitted in the freeware OpenBUGS (Lunn *et al.* 2009) to simultaneously estimate the single visit (or single-observer) burrow detection probability, and the probability of site occupancy (for sites at which the species was not observed). The probability of site occupancy was allowed to vary with site covariates selected in the AIC-best logistic regression model (‘GLM’ in table 5). Models were fitted on 200000 Markov chain Monte Carlo samples after a burn-in of 10000 samples. Three chains were run to allow visual checks for model convergence. OpenBUGS code for ZIB model is provided in Appendix 2.

**Post-fieldwork species distribution models**

Closer inspection of the contribution of variables to explaining probability of occurrence, as well as expert opinion and personal observations in the field, led us to the conclusion that models should be fitted only within the soft-spinifex vegetation type. During fieldwork, we noted that some areas classified as open saltbush flats contained small patches of soft spinifex sand plain. These patches were interspersed throughout the open saltbush flats in patches too
small to have been included at the scale of the original AWC vegetation mapping. All of the GDS presences collected during fieldwork in these locations were actually in soft spinifex patches. Because the small patches of soft-spinifex could not be discerned from saltbush flats, for the purposes of generating distribution model predictions (and therefore for use in the population models), we decided to treat the two vegetation classes as one, and built GLMs, GAMs and BRTs within this combined vegetation type.

Following testing of the predictive performance of the AWC data-only models using my field data, we then combined both datasets and repeated all of the variable selection, model fitting and cross-validation model evaluation steps described previously on the combined data set, but restricted to within the soft spinifex sandplain vegetation class. These combined models are the ones which underpinned the population modelling.

**Population Viability Analyses**

We used the RAMAS Landscape software package (Akçakaya *et al.* 2003) to construct, from scratch a PVA model for the great desert skink. This package links the landscape-level vegetation dynamic model LANDIS 3.7 (Mladenoff & He 1999) and the metapopulation modelling package RAMAS GIS 4 (Akçakaya & Root 2002). The modelling process starts with the LANDIS software generating a series of maps representing landscape change over time through successional processes and incorporating stochastic (e.g. fire) disturbances. The RAMAS GIS module then performs a patch recognition process on the LANDIS outputs and other GIS inputs provided by the user (e.g. static maps of other habitat variables) to define the metapopulation structure in each time-step in the simulation (in our case, each year). The RAMAS Metapop module runs metapopulation simulations utilizing the dynamic metapopulation structure established by RAMAS GIS. For a schematic representation of this process, see Appendix 3.

Although LANDIS was originally designed for modelling forest landscapes, it is sufficiently flexible in its modelling of vegetation succession and landscape dynamics (primarily based on fire) such that it is suitable for modelling stochastic vegetation dynamics in many different types of ecosystem, including our study area. Moreover, it is the only generic, spatially explicit software available for modelling vegetation dynamics, leaving little choice but to adapt the program for our purposes.
**LANDIS Parameterisation**

The dynamic landscape modelling module of RAMAS Landscape uses a GUI version of the program LANDIS 3.7 (Mladenoff & He 1999). Vegetation types were broadly grouped into classes dominated by 10 species (table 2). These were combined with geological and disturbance characteristics of the landscape to form 24 unique land types with varying pyric characteristics. To accommodate fine scale fire history differences in land types at the start of the landscape dynamics simulations, we split the soft spinifex sand plain habitat into three different classes based on the time since last fire at the start of the simulation (28, 11, and 2 years). These land-type differences were only relevant at the start of the landscape simulations, after which the simulated fires dictated the simulated 'fire history' maps used to determine habitat suitability and carrying capacity of patches in metapopulation model simulations.

Mean fire return interval and time since last disturbance, were identified via fire history maps provided by the AWC. LANDIS allows for increasing fire intensity as a function of the time since last fire. While data on this were not available, we modelled a linear increase to maximum fire intensity at 10 years since the last fire for grasses and shrubs and 40 years for trees. The fire intensity variable determines the proportion of vegetation age cohorts killed by fires in the grid cell being burnt. Probability of (re-)establishment was set to one for the dominant species of that vegetation class, ensuring that no spatial variation in species dominance was modelled in our simulations (i.e. vegetation types were spatially static through time). This is an assumption that could be relaxed if particular hypotheses come to light about likely long-term changes in vegetation composition.
<table>
<thead>
<tr>
<th>Species group</th>
<th>Longevity (y)</th>
<th>Age at maturity (y)</th>
<th>Shade tolerance</th>
<th>Fire tolerance</th>
<th>Sprouting probability</th>
<th>Reclassification coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soft spinifex (<em>Triodia pungens</em>)</td>
<td>20</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>0.6</td>
<td>1</td>
</tr>
<tr>
<td>Acacia shrubs (<em>Acacia spp.</em>)</td>
<td>20</td>
<td>9</td>
<td>2</td>
<td>3</td>
<td>0.4</td>
<td>0.9</td>
</tr>
<tr>
<td>Mulga (<em>Acacia aneura</em>)</td>
<td>300</td>
<td>20</td>
<td>2</td>
<td>3</td>
<td>0.4</td>
<td>0.7</td>
</tr>
<tr>
<td>Grasses (<em>Poa spp.</em>)</td>
<td>10</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>0.7</td>
<td>0.8</td>
</tr>
<tr>
<td>Blue mallee (<em>Eucalyptus polybractea</em>)</td>
<td>200</td>
<td>18</td>
<td>2</td>
<td>4</td>
<td>0.7</td>
<td>0.8</td>
</tr>
<tr>
<td>Desert oak (<em>Allocasuarina decaisneana</em>)</td>
<td>150</td>
<td>20</td>
<td>2</td>
<td>3</td>
<td>0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>Tea tree (<em>Melaleuca spp.</em>)</td>
<td>25</td>
<td>7</td>
<td>2</td>
<td>3</td>
<td>0.7</td>
<td>0.4</td>
</tr>
<tr>
<td>Feathertop spinifex (<em>Triodia schinzii</em>)</td>
<td>20</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0.7</td>
</tr>
<tr>
<td>Desert bloodwood (<em>Corymbia terminalis</em>)</td>
<td>200</td>
<td>18</td>
<td>2</td>
<td>2</td>
<td>0.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Witchetty bush (<em>Acacia kempeana</em>)</td>
<td>20</td>
<td>5</td>
<td>2</td>
<td>4</td>
<td>0.6</td>
<td>0.8</td>
</tr>
</tbody>
</table>
Fire size characteristics were determined from AWC fire records. A fire size coefficient was chosen to allow simulated fire patterns to best match observed patterns. Minimum fire size was set to 0.07km$^2$, maximum fire size to 100km$^2$. Both of these values were restricted by the workings of LANDIS; 0.07km$^2$ is the size of one cell in the simulation, and 100km$^2$ was the largest value able to be input. The minimum fire size observed at Newhaven over the 44 year fire history was smaller than 0.07km$^2$, and the maximum was an order of magnitude larger than the largest possible input that LANDIS allows. Mean fire size, determined from all recorded fires since 1970, was 10.66km$^2$ and so was used as the mean fire size input. The fire size distribution was examined to determine how close to observed conditions LANDIS was able to simulate given the above inputs. Alternative future fire scenarios were characterised by changes to these parameters in the landscape simulations (see 'Sensitivity and scenario analysis' later in Methods).

**Modelling metapopulation dynamics**

The patch structure of the metapopulation is identified in a dedicated patch delineation algorithm in RAMAS GIS that utilizes a habitat suitability map, a threshold below which habitat is considered unsuitable, and an estimate of the maximum daily range movement distance of the species. The three 'AIC$_{best}$' GLM models were used to generate the habitat suitability map for use in the patch recognition algorithm. The GLMs were used in preference to the GAMs and BRTs as the latter two have no simple equation form, and it is not possible to extract information on the coefficients of the terms.

Three competing logistic regression models representing a range of plausible (with respect to available occupancy data) competing hypotheses about the drivers of GDS distribution were used to parameterize the patch delineation algorithm and the patch (population) carrying capacity estimates:

\[
Pr(\text{occupancy}_{\text{model } a}) = \frac{1}{1 + e^{-0.12 - 71.83[\text{elevation}] + 0.29[\text{elevation}^2] - 0.09[\text{shrub}] + 0.99[\text{soil}] + 0.02[\text{soil}^2] + 70.04[\text{soil}] - 18.02}}
\]

\[
Pr(\text{occupancy}_{\text{model } b}) = \frac{1}{1 + e^{-0.09 - 72.22[\text{elevation}] - 0.00[\text{depth}^2] - 0.09[\text{soil}] + 0.02[\text{soil}^2] + 6.18[\text{soil}] + 4.3[\text{soil}^2] + 0.53[\text{soil}]}}
\]

\[
Pr(\text{occupancy}_{\text{model } c}) = \frac{1}{1 + e^{-0.58 - 13.34[\text{elevation}] + 70.34[\text{soil}] + 0.01[\text{depth}] + 0.02[\text{soil}] + 0.01[\text{soil}^2] + 0.53[\text{soil}]}}
\]

where each equation is equal to the probability of GDS occurrence. All terms in square brackets [ ] are as described above in table 1. Numbers in superscript indicate where orthogonalised values of the variable were used.
The suitability threshold signifies the habitat suitability value below which the species cannot live, but is able to disperse through. As each of the models produced a different initial habitat suitability map, each simulation had a different threshold, based on the value above which 90% of presences were found. Neighbourhood distance was set to 1.5 cells, implying that suitable cells up to 1.5 cells apart (~400m) form the same patch. This distance was set based on GDS foraging patterns of “a few hundred meters” (McAlpin 2000).

The carrying capacity (K) of a patch estimates the number of individuals a patch of suitable habitat can support. For the GDS model it was defined as:

\[ K = e^{6 \times ahs - 3} + 1 \times \left( \frac{noc}{14} \right) \text{ if } noc \geq 3, \]

where \( ahs \) is the average habitat suitability, and \( noc \) is the number of cells in the patch (and 3 is the smallest number of cells able to form a viable patch).

According to eq. 3, a maximum of 21 female skinks can exist in a cell of the highest possible suitability (1). This number was extrapolated from the highest density of burrows observed in the field (pers. obs. 2013) and the number of adult females estimated to occupy an active burrow (McAlpin 2000). This equation is restricted by the suitability threshold in that a patch must consist of groups of three cells or larger each with a habitat suitability value above that of the threshold. The exponential relationship was chosen to reflect the fact that there are likely to be very low numbers of skinks at low habitat suitabilities, after which there is a sharp increase in skinks after some minimum suitable threshold is reached.

Some life history and population parameters were calculated with an R-Fortran implementation of the ‘Niche Mapper’ software package (McCullough & Porter 1971; Beckman et al. 1973; Porter et al. 1973), currently in development for general release (Kearney & Porter, in prep.). The package comprises two programs – a microclimate model and an animal model, which are described in detail in Kearney (2013). The programs solve heat and mass budgets under different microclimatic scenarios for given behavioural strategies. Simulating the temperature, energy use and behaviour of an individual on an hourly basis over the course of its lifespan, the models produce lifetime fecundity, survival and activity estimates for a model GDS. The fecundity estimates were used, alongside data from McAlpin (2000), in the stage matrix. Survivorship for each stage-class was calculated following Adolph & Porter (1993); as a function of hours of activity, a plausible mortality per hour active rate \((5.0 \times 10^{-4})\), and senescence rate (obtained from previous work by Kearney 2013). An intrinsic maximum population growth rate \(R_{max}\) of 1.252 was also calculated from the life table created with the
Niche Mapper outputs. This implies a maximum possible increase in the population of 25% per year under ideal conditions, free of density-mediated resource constraints.

The initial abundance was chosen based on coarse population estimates of over 2000 individuals in the Tanami desert (McAlpin 2001). As only females were being modelled we supposed an initial abundance of 1000 skinks (assuming an even sex ratio: McAlpin 2000). Individuals were distributed evenly between patches, based on the number of cells in the patch. The dispersal-distance function was based on average dispersal distances of 0.5km up to a maximum of 5km, and a maximum of 80% of the population ever dispersing, due to high levels of sub-adult dispersal (eq. 4). It is a negative exponential function, which is similar to the dispersal patterns observed by Wolfenbarger (1946) in 47 species:

\[
m_{ij} = \begin{cases} 
0.8 \times \exp\left(-\frac{x^{1.25}}{0.5}\right) & \text{if } x \leq 5, \\
0 & \text{if } x > 5,
\end{cases}
\]  

(4)

where \(m_{ij}\) is the dispersal between patch \(i\) and \(j\), \(x\) is the distance between the two patches, and 5 is the largest value \(x\) can take, representing the furthest possible dispersal distance (in km) of an individual GDS.

**Metapopulation model parameters**

Metapopulation model simulations were run for 100 years. In general, 1000 replications were implemented for each unique combination of metapopulation parameters being tested. Unlike the LANDIS component, RAMAS Metapop time steps are not fixed at 10 years, so were set to 1 year, the timeframe in which a full reproductive cycle occurs. Because only females were modelled, all further parameters details refer only to females. All populations were modelled under contest-type density dependence, which affected all vital rates (i.e. both fecundity and survival). Contest-type density dependence describes when individuals compete for a limited resource (Nicholson 1954). Having obtained this resource, an individual has enough to survive and reproduce, and the loser of the contest has none. In this instance, we imagined that space to dig a burrow might be a limiting resource, and in a competition, an individual would either obtain the space or not, resulting in contest-type density dependence.

We modelled three life-stages – juvenile, sub-adult, and adult. The juvenile stage typically consists of the first two years of life, during which an individual will live in its natal burrow and forage with its parents. This guarded foraging behaviour reduces mortality and as such, juveniles have a higher survival rate than sub-adults (table 4) (McAlpin 2000). Sub-adults are individuals in their first year of leaving the burrow. They will disperse up to 5km, create their
own burrow and may reproduce, if they are large enough. Their mortality rates are quite high (see table 4) as they are without a burrow for a time and the act of creating burrows leaves them exposed to predators. Adults are lizards over three years of age, with established burrows and in full reproductive swing. Though males appear to suffer higher mortality as a result of generally being the burrow diggers (McAlpin 2000), a lack of data led us to assume equal mortality rates for the sexes, and as such did not affect our female only modelling strategy. Each stage displayed different dispersal behaviours and proportions of the population contributing offspring (table 3). We nominated 95% of adults to breed in a given year, and 50% of subadults, to reflect variation in mating success, from both a behavioural and physiological standpoint.

Table 3. Relative dispersal and breeding contribution of GDS different life-stages.

<table>
<thead>
<tr>
<th>Life-stage</th>
<th>Relative dispersal</th>
<th>Breeding proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sub-adult</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Adult</td>
<td>0.7</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Survival and fecundity of the various stages were calculated, as with the R\textsubscript{max}, from the NicheMapper model (Kearney 2013). Standard deviations were 10% of matrix values for survival probabilities and to ±1 offspring for fecundities.

Table 4. Survival and fecundities of various GDS life-stages, shown in a Lefkovitch matrix, with transitions in the sub-diagonal. * indicates fecundities, all other values represent survival proportions.

<table>
<thead>
<tr>
<th></th>
<th>Juvenile</th>
<th>Sub-adult</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile</td>
<td>0.297</td>
<td>1*</td>
<td>3*</td>
</tr>
<tr>
<td>Sub-adult</td>
<td>0.023</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adult</td>
<td>0</td>
<td>0.25</td>
<td>0.52</td>
</tr>
</tbody>
</table>

Initial abundances were distributed between the stages according to the stable age distribution represented by the stage matrix (table 4).

Modelling landscape stochasticity

Any individual run of the LANDIS model encapsulates only one realization of possible future landscape dynamics. In order to characterise the role of landscape dynamic stochasticity in driving changes in GDS populations, it was necessary to run many landscape simulations coupled to many metapopulation model simulations. For replication of the landscape runs, we
ran the whole RAMAS Landscape program within a ‘wrap around’ program called ‘RAMAS Repeater’ (Chisholm & Wintle 2007; Gordon et al. 2012) which automates replication of the LANDIS of RAMAS components within RAMAS Landscape.

**Fire scenarios**

In order to test the sensitivity of the models to fire, we ran the PVAs under three alternate fire scenarios. These scenarios were chosen to represent current fire conditions, an increase in frequency and severity of fires, and a decrease. The parameters that best estimated ‘current’ fire conditions have been described above. The ‘high’ fire scenario serves as an extreme example of the potential results of climate change, if favourable fire days increased, and fuel was abundant (due to large rainfall events, for example). For this, two aspects of LANDIS were altered. The overall fire size coefficient was increased 10-fold to 120. Minimum and mean fire sizes were doubled, however maximum fire size, already set to the largest value possible, was forced to remain the same. For each of the land types, the mean fire return interval was halved, as was the corresponding fire probability coefficient. The ‘low’ fire scenario represents, albeit in the extreme, the potential for climate changes to impede fires, most likely through a decrease in fuel availability. This low frequency, small fire size scenario had a reduced fire size coefficient of one while the minimum fire size remained the same (the area of one cell). The maximum fire size was set to 14,450 m$^2$ (the area of two cells) and the average to 10,000 m$^2$. The mean fire return interval of each land type was doubled along with the fire probability coefficient.

**Sensitivity analyses**

Sensitivity analyses provide a means of determining how important identified uncertainties are in population modelling and predicting long-term viability. The influence of uncertainty around key model parameters or assumptions such as the relationship between fire history and occupancy, demographic parameters, and the relationship between habitat suitability and carrying capacity were tested using sensitivity analysis (sensu Gordon et al. 2012). One way of comparing the sensitivity of the models to various parameters is through ranking the expected minimum abundance (EMA) of different scenarios. While the absolute values output by PVAs, such as those for the carrying capacities (K) and total abundance (TP), can be highly uncertain, by ranking the outputs of each scenario, we can gain a better understanding of the relative outcomes (McCarthy et al. 2003; Wintle et al. 2005a). The EMA is the most reliable model output for ranking (McCarthy et al. 2003).

Numerous parameters estimated in the development of the distribution and population models are highly uncertain, as is the structure (composition and form) of the models themselves, and
the future environmental conditions under which they will operate. For example, the true shape of the relationship between the GDS and time since fire is unknown because of imprecision in mapping of fire, the location of occupied and unoccupied sites, and the random population and biogeographic processes determining occupancy of any place at any given time. There is substantial uncertainty when selecting models to represent species relationships to environmental predictors. Some of that uncertainty can be characterised with cross-validation, and multi-model inference (sensu Burnham & Anderson 2002), both used here. Characterising the magnitude of uncertainty is the first step toward analysing how important uncertainties are for robustly predicting the long-term viability of a species.

To estimate the uncertainty surrounding the RAMAS Metapop parameters we tested changes in:

i. the carrying capacity function,
ii. initial abundance of the population,
iii. intrinsic rate of population growth ($R_{\text{max}}$),
iv. survival and fecundity matrix values,
v. dispersal distances, and
vi. seed dispersal method.

Where possible, we used plausible alternative values for the parameters, based on expert opinion, to test sensitivities. Carrying capacity is increased or decreased by 25%; this was based on expert opinion of the estimates around highest burrow density per hectare in “ideal” habitat (S. McAlpin 2014 pers. comm. 2013). The initial abundance of the population was reduced to 500 individuals, the lower estimate of skinks at the sanctuary, and 2000, an upper estimate, based on expert opinion (D. Moore pers. comm. 2013). The range tested for this parameter was quite high, to reflect the high uncertainty in the current abundance of GDS at Newhaven. To test the ramifications of a population with very low growth, we reduced $R_{\text{max}}$ to 1.1, or a population increase of only 10% per year. To test a (plausibly) fast-growing population we increased the growth rate to 1.5, or a 50% population increase per year. This would be possible under higher juvenile and sub-adult survival, both of which are relatively low due to predation. Survival matrix values, obtained from a mixture of Niche Mapper and expert opinion, were altered based on variation surrounding the ‘best estimates’ used in the model. As such, survival values were reduced or increased by 20% (cf. Gordon et al. 2012) and fecundity by ±2 offspring. Dispersal distances were changed to their upper and lower estimates, based on expert opinion (S. McAlpin pers. comm. 2013). Lowered dispersal parameters were decreased to a maximum of 60% individuals dispersing with an average distance of 200m and a maximum of 1km. Increased dispersal raised the maximum to 100% of the population dispersing, an average of 600m and a maximum of 4km.
RESULTS

Fieldwork Data
Across 45 sites we recorded 14 presences and searched 31 sites without finding evidence of GDS burrows (fig 3). The presence sites ranged in abundance from 1 burrow at a site to 7, with a total of 38 burrows recorded. The average number of burrows per presence site was just under 3. When detected by one observer, burrows were consistently seen by over half the observers. Burrows in recently burnt habitat were easier to detect than those in long-unburnt, dense spinifex (pers. obs. 2013). There appeared to be a slight trend towards more termites burrows at presence sites, however, this was not statistically investigated due to the subjectivity in the estimation of termite burrow abundance at each site. A total of five sites were deemed, by personal observations, to have been burnt in the last two years. One inactive burrow was noted (but marked as an absence), and no active burrows were recorded at these sites.

Figure 3. Location of great desert skink occurrence data collected during 2013 fieldwork at Newhaven wildlife sanctuary.

Detectability: A zero-inflated binomial model for estimating active burrow detectability in field data
The ZIB model for estimating observer-level detectability of active burrows during field surveys converged after 200K iterations, based on visual checks of the three chains (Appendix 2). The ZIB model estimated a single-visit (observer) detection probability (p) of 0.41 with a 95% credible interval of [0.20, 0.59] (Appendix 2 for code and results). This indicates a reasonable degree of confidence that our field survey effort of between 2 and 6 visits was
satisfactory to detect active burrows at most survey sites that contained them. For example, at sites visited by two observers, the probability of failing to detect active burrows \((1-p)^2\) if the site contained an active burrow is 0.33. For sites visited by 3 or 6 observers the probability of failing to detect active burrow is 0.19 and 0.04 respectively.

**Species Distribution Models**

*Environmental variables*

Using the AWC fire history maps (the spatial extent of fires for each year going back to 1970) we created a number of fire variables for use in distribution and population modelling (Figs 4 and 5). The time since last fire, number of fires in the past 10 years, and number of fires in the past 44 years calculated for each occurrence cell in the landscape.

![Number of fires from 1970-2013](image)

**Figure 4.** The number of fires across Newhaven sanctuary from 1970 to 2013 (a 44 year period). More frequently burnt areas are darker red.
Variable Selection

After examination of response shapes and consideration of their ecological realism, a number of candidate model variables were discarded. Further culling of variables prior to model selection was undertaken on the grounds of poor sampling of the occurrence points across the range of the variable. Most parsimonious univariate relationships (models with only one predictor variable but potentially several predictor degrees of freedom) provided a final candidate set of predictors (and predictor degrees of freedom) to be offered to the stepwise variable selection routine (fig. 6)
Figure 6. Univariate GAM response plots for each variable considered for inclusion in GDS distribution models. Fitted function shows the shape that best fits the data to an ecologically realistic degree, given a choice of three or fewer degrees freedom. Functions shown in red represent variables that were discarded before building the initial model.

The correlation coefficients of the variables were compared and we chose not to include the number of fires in 44 years in the same model as number of fires in 10 years due to their high correlation (0.87). Time since fire showed a weaker negative correlation with the other two fire variables (-0.69 for number of fires in 44 years, and -0.74 for fires in 10 years) such that it could be included in the automated variable selection process with all other variables.

Models were fitted with the remaining variables (all those in black in fig. 6), including *either* number of fires in 44 years, or number of fires in 10 years. Common to all final models was the vegetation type variable, ternary soil content, elevation, time since fire, and ferrous oxide content (table 1). Models differed mostly in the importance assigned to the number of fires in a given period and the shape of the relationship between the fire variables and occupancy probability. Ultimately, models with number of fires in 44 years always out-competed those with fire in 10 years, across all modelling techniques.
Model Selection & Evaluation Statistics

The GLM and GAM AIC_{\text{best}} models included the same terms, in the same equivalent forms for all but one of the variables (time since fire) (table 3.1). The externally validated ROC values of all three modelling techniques indicate that we should be wary of their ability to correctly predict suitable habitat. The BRT performed the best in this regard, as well as in deviance explained.
Table 5. Strongly performing presence-absence models for different modelling techniques as well as their cross-validated estimates of predictive discrimination (ROC) and the predictive discrimination achieved when tested on independent field validation data collected during the 2013 survey. Deviance explained (%) obtained through 10-fold cross validation. “ROC(cv)” indicates the results of the 10-fold cross validation, while “ROC(field)” is the externally tested ROC for the best-performing model of each technique. “s(variable, n)” and “poly(variable, n)” indicate variables included as polynomial (‘poly’) or smoothed (‘s’) terms with ‘n’ degrees of freedom. Italics in the lower half of the table indicate changes to that model compared to the best performing model in the upper half of the table. AIC, Akaike information criterion; ROC, receiver operating characteristic.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Final form</th>
<th>AIC</th>
<th>Deviance explained (%)</th>
<th>ROC(cv)</th>
<th>ROC(field)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLM</td>
<td>PA ~ poly(elevation, 2) + poly(ternary, 2) + tsf + poly(nf, 2) + feocontent + vegnew</td>
<td>323.86</td>
<td>59.24</td>
<td>0.93</td>
<td>0.60</td>
</tr>
<tr>
<td>GAM</td>
<td>PA ~ s(elevation, 2) + s(ternary, 2) + s(tsf, 2) + s(nf, 2) + feocontent + vegnew</td>
<td>339.36</td>
<td>51.20</td>
<td>0.91</td>
<td>0.54</td>
</tr>
<tr>
<td>BRT</td>
<td>--------------------------------------------</td>
<td>n.a.</td>
<td>84.03</td>
<td>0.96</td>
<td>0.65</td>
</tr>
<tr>
<td>GLM₂</td>
<td>PA ~ poly(elevation, 2) + poly(ternary, 2) + poly(tsf, 2) + poly(nf, 2) + feocontent + vegnew</td>
<td>324.14</td>
<td>53.56</td>
<td>0.92</td>
<td>-</td>
</tr>
<tr>
<td>GLM₃</td>
<td>PA ~ poly(elevation, 2) + poly(ternary, 2) + poly(nf, 2) + feocontent + vegnew</td>
<td>325.37</td>
<td>52.75</td>
<td>0.92</td>
<td>-</td>
</tr>
<tr>
<td>GAM₂</td>
<td>PA ~ thorium + s(elevation, 2) + s(ternary, 2) + s(tsf, 2) + s(nf, 2) + vegnew</td>
<td>340.49</td>
<td>51.03</td>
<td>0.90</td>
<td>-</td>
</tr>
<tr>
<td>GAM₃</td>
<td>PA ~ thorium + s(elevation, 2) + s(ternary, 2) + tsf + nf + feocontent + vegnew</td>
<td>340.78</td>
<td>49.48</td>
<td>0.89</td>
<td>-</td>
</tr>
</tbody>
</table>
The GLM and GAMs both dropped three variables (geology, topographic wetness and thorium), while the BRT simplification technique determined that no variables should be dropped from the full model. The BRT model appeared to far outperformed both other modelling techniques in null deviance reduction, accounting for over 84% of the variation in the data, while the other two each described just over half (table 5). The ROC scores were similar for all three, although BRT had the highest value for internal cross-validation. Of the two regression models, the GLM performed better on all fronts, including AIC value. The GLM contained one less predictor degree freedom (PDF) compared with the GAM, as it includes time since fire as a linear variable, where the GAM fitted it as a non-linear term.

For each of the multiple-regression models, the final fitted functions were examined for ecological realism. The shape of the response curve reveals the relationship between the environmental variable and the probability of occurrence, holding all other variables in the model at their mean value. The scale on the y-axis of partial plots gives an indication of the strength of the relationship – the larger the range, the more significant the relationship between that variable and probability of occupancy (seen on a logit scale in the graphs presented in this paper). The shape of the line itself shows how that relationship changes over the value of the environmental variable. For example, in figure 7 below, the ‘nf’ variable ranges from no fires in 44 years, to 5. Probability of GDS occurrence is highest when there have been no fires, steadily decreases towards two or three, and then increases again when there have been four or five fires in the past 44 years (roughly one per decade). What we see here is actually the opposite relationship to that seen when this variable is used alone (see Fig. 6). In that case, probability of occurrence is highest in the mid-range of two to three fires and decreases either side of this. This is because, in the final GLM model, the relationship we see between number of fires and occupancy is the result of the fire variable explaining residual (left-over) variation in occurrence not explained by other variables. In this case, it is likely that, due to the negative correlation between number of fires and time since fire, and the fact that time since fire has a stronger relationship with occupancy.

Other than time since fire, the partial dependency plots for the GLM (fig. 7) and GAM (fig. 8) models are very similar. In fitting a polynomial relationship between times since fire and probability of occupancy, the GAM model suggests that when there has been a fire in the past 0-5 years, the habitat is less suitable than if that time has been closer to 10 or 15 years. The GLM model does not capture this subtlety in habitat suitability change, rather stating that the shorter the time since last fire, the more suitable the habitat for GDS.
The BRT fitted functions tend to be overfitted, but have the ability to capture subtle changes in the relationship between a variable and occupancy. By adding a smoothing function to the plots in figure 9, it becomes clearer that the fitted shapes are roughly similar to those of the GAM (and to a less extent the GLM). The congruence in fitted functions between all three independent modelling techniques gives confidence that the true nature of the relationship is being captured at least to some degree.

**Figure 7.** Partial plots of the relationship between the probability of occupancy and environmental variables included in the final GLM model for the GDS. The X-axes represent the range of values for each environmental variable and probabilities on the Y-axes are plotted on a ‘logit’ scale. Response shapes represent the relationship between each variable and the probability of GDS occurrence in the context of the multivariate model, when all other variables are held at their mean. Dashed lines represent standard errors around the fitted response shape. Internal axis ticks show distribution of sites across the range of the variable. Variable names are as described in Table 1.
Figure 8. Partial plots of the relationship between the probability of occupancy and environmental variables included in the final GAM model for the GDS. The X-axes represent the range of values for each environmental variable and probabilities on the Y-axes are plotted on a ‘logit’ scale. Response shapes represent the relationship between each variable and the probability of GDS occurrence in the context of the multivariate model, when all other variables are held at their mean. Dashed lines represent standard errors around the fitted response shape. Internal axis ticks show distribution of sites. Variable names are as described in Table 1.
Figure 9. Partial plots of the relationship between the probability of occupancy and environmental variables included in the BRT model with grouped vegetation classes. Contribution of each variable to explaining the variation in the model is shown as a percentage in brackets next to the variable name. The X-axes represent the range of values for each environmental variable and probabilities on the Y-axes are plotted on the ‘logit’ scale and are centred to have zero mean over the data distribution. A smoothed version of each relationship is shown in red. Response shapes represent the relationship between each variable and the probability of GDS occurrence in the context of the multivariate model, when all other variables are held at their mean. Internal axis ticks show distribution of sites, in deciles. Variable names are as described in Table 1.
Model testing

K-fold cross-validation results indicate strong expected out-of-sample predictive performance with ROC values ranging from 0.92 to 0.93 for AIC-best GLMs and 0.89 to 0.91 for AIC-best GAMs (table 5). The 'gbm.step' function automatically performs cross-validation of the BRT model and provides statistics describing the relative contribution of each variable (Figure 10).

![Figure 10](image)

**Figure 10.** The optimal number of trees fitted to the BRT model (left) and the relative influence of each variable on the model (right).

The apparently strong out-of-sample predictive performance of all AWC data-only models based on cross-validation is at odds with the 'true' out-of-sample predictive performance achieved by the AWC data-only models when tested against the independent 2013 field data (table 5). Independent testing indicated ROC values ranging from 0.54 – 0.65, though the BRT model remained the best ROC model of the three model types. The difference between the cross-validation and field-validation ROC results is likely to be due to the fact that our field validation took place only in areas of at least moderately suitability, meaning that there were no areas of poor habitat at which it is 'easy' for the model to accurately predict the absence of the species. Chance population dynamics and unmapped stochastic disturbance (e.g. fire or
predation) mean that areas of high predicted probability of occupancy may not actually contain the species, though this principle applies to both cross-validated and field-validated results.

**Soft Spinifex Sand plain (SSP) Models**

After field-validating the predictive performance of the AWC data-only models (table 5), we re-fit the AWC only-data models with a new dataset that included our collected data. On inspection of these we decided to focus further modelling efforts solely in soft spinifex sand plain (SSP) habitat, given that all of the 2013 presences were located in this area (fig. 2 in Methods). By modelling within this area we hoped to capture finer detail on the drivers of GDS distribution at the sanctuary.

The variables chosen for SSP model selection were similar to those included in the full AWC only-data models (see fig. 6, table 5 for AWC-only variables). The main difference was the exclusion of the strongly significant vegetation variable, as we were modelling within one vegetation class. Re-analysis of the correlation between variables again indicated that the two fire frequency variables (‘nf’ and ‘nf10’; see table 2.1) should not be included in the same model. Number of fires in 44 years (‘nf’) was less highly correlated with times since fire (-0.7) and so was preferentially included.
Figure 11. Univariate models of each variable included in full SSP model. Fitted function shows the shape that best fits the data to an ecologically realistic degree, given a choice of three or fewer degrees freedom when fitted with a GAM and undergoing backwards stepwise selection. Functions previously excluded for poor distribution in AWC only-data model are not shown here (including ruggedness and ferrous iron content). See Table 1 for variable names and descriptions.

The variables excluded for poor distribution of occurrence points were ruggedness and ferrous iron content, as with the previous models. Those included for full SSP model selection can be seen in figure 11 with the degrees freedom that corresponded to the lowest AIC values.

Model Selection & Evaluation
For the GLM and GAM models, all variables were initially included with two degrees of freedom, except ‘geology’ which is a categorical variable and therefore had ‘n-1’ degrees freedom where ‘n’ is the number of geological classes (no equivalent available for BRTs). The GLM and GAM ‘best’ models differed in the two additional variables that the GAM included; geology and topographic wetness (table 5). They performed similarly under both AIC and ROC measures, although the GLM fared slightly better. In contrast to the original AWC only-data models, the GLM for the SSP model includes thorium content instead of ternary, and fitted time since fire as a polynomial, rather than linear, function (fig. 12). The BRT model included the
same variables as in the AWC-only models (fig. 14), with the exception of the vegetation type variable (which was excluded from the SSP-dataset as there was only one vegetation type). The BRTs consistently outperformed the multiple linear regression models in explaining deviance and ROC values as they are able to fit interactions between the variables, which was not a feature included in the GLMs and GAMs.

All three SSP models performed worse than the AWC-only data models in explaining the variation in the data. Cross-validation ROC scores were similar, but slightly lower, to the cross-validated ROC scores of the AWC data-only models with the final GLM ROC 0.84, GAMs 0.81 and BRT 0.88. As these models were built on a dataset that included the 2013 field data, they were unable to be independently validated, although I predict that any external validation of the ROC values would be lower than the cross-validated results as with the AWC-only models.

Table 6. Final SSP presence-absence models for different modelling techniques as well as the cross-validated estimate of predictive discrimination (ROC) and AIC estimates. Deviance explained (%) and ROC values obtained through 10-fold cross validation.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Final form</th>
<th>AIC</th>
<th>Deviance explained (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLM</td>
<td>PA ~ poly(elevation, 2) + poly(tsf, 2) + poly(nf, 2) + feocontent + thorium</td>
<td>262.53</td>
<td>34.73</td>
</tr>
<tr>
<td>GAM</td>
<td>PA ~ s(elevation, 2) + thorium + s(tsf, 2) + feocontent + s(twmaxNH, 2) + geology + s(nf, 2)</td>
<td>271.22</td>
<td>34.59</td>
</tr>
<tr>
<td>BRT</td>
<td>-------------------------------------------------</td>
<td>n.a.</td>
<td>69.12</td>
</tr>
</tbody>
</table>

Partial dependency plots were examined as with the AWC data-only models. The fitted functions were similar to those of the AWC-only models in the shape and strength of relationships for all three modelling techniques.
Figure 12. Partial plots of the relationship between the probability of occupancy and environmental variables included in the final GLM model for the GDS. The X-axes represent the range of values for each environmental variable and probabilities on the Y-axes are plotted on a ‘logit’ scale. Response shapes represent the relationship between each variable and the probability of GDS occurrence in the context of the multivariate model, when all other variables are held at their mean. Dashed lines represent standard errors around the fitted response shape. Internal axis ticks show distribution of sites. Variable names are as described in Table 1.
Figure 13. Partial plots of the relationship between the probability of occupancy and environmental variables included in the final GAM model for the GDS. The X-axes represent the range of values for each environmental variable and probabilities on the Y-axes are plotted on a ‘logit’ scale. Response shapes represent the relationship between each variable and the probability of GDS occurrence in the context of the multivariate model, when all other variables are held at their mean. Dashed lines represent standard errors around the fitted response shape. Internal axis ticks show distribution of sites. Variable names are as described in Table 1.
Figure 14. Partial plots of the relationship between the probability of occupancy and environmental variables included in the SSP BRT model with grouped geology classes. The X-axes represent the range of values for each environmental variable and probabilities on the Y-axes are plotted on the ‘logit’ scale and are centred to have zero mean over the data distribution. A smoothed version of each relationship is shown in red. Response shapes represent the relationship between each variable and the probability of GDS occurrence in the context of the multivariate model, when all other variables are held at their mean. Internal axis ticks show distribution of sites, in deciles. Variable names are as described in Table 1.

There were a number of GLMs that were similar in AIC value and were all considered plausible relationships between GDS and their environment. Three models that differed in the fitted functions of the two fire variables were chosen to represent our uncertainty in the true relationship between GDS and fire. These models were subsequently used as the habitat suitability functions in the simulations for the population viability analyses. The models contained the terms in table 7; a quadratic function for elevation, linear relationships for ferrous iron and thorium content, and then time since fire and number of fires as either linear or quadratic terms. Model A treated both fire variables as quadratic functions; model B fitted only time since fire as a quadratic function and number of fires in 44 years as linear; and both fire terms were linear in model C.
Table 7. The estimated coefficient values and the standard errors of the final GLM models chosen for the RAMAS Landscape simulations. Quadratic terms are denoted by $'^{2}$', and all terms were significant at $p<0.01$ or smaller. ‘-----’ denotes where a term was not included in that model. Due to the way the quadratic terms are orthogonalised in the GLM fitting method, the coefficients of variables that are quadratic in one model and not the next are not directly comparable.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>Intercept</th>
<th>elevation</th>
<th>elevation$^{2}$</th>
<th>tsf</th>
<th>tsf$^{2}$</th>
<th>nf</th>
<th>nf$^{2}$</th>
<th>feocontent</th>
<th>thorium</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>262.53</td>
<td>10.32 ±2.15</td>
<td>13.60 ±5.48</td>
<td>-68.29 ±13.02</td>
<td>-16.62 ±5.63</td>
<td>-10.03 ±3.33</td>
<td>-18.04 ±5.65</td>
<td>10.60 ±4.09</td>
<td>0.007 ±0.002</td>
<td>-0.09 ±0.02</td>
</tr>
<tr>
<td>B</td>
<td>267.91</td>
<td>10.03 ±2.19</td>
<td>12.22 ±5.47</td>
<td>-67.57 ±12.91</td>
<td>-6.18 ±3.82</td>
<td>-4.80 ±2.58</td>
<td>-0.55 ±0.26</td>
<td>------</td>
<td>0.007 ±0.002</td>
<td>-0.08 ±0.02</td>
</tr>
<tr>
<td>C</td>
<td>269.42</td>
<td>10.58 ±2.23</td>
<td>13.24 ±5.26</td>
<td>-71.35 ±12.57</td>
<td>-0.03 ±0.02</td>
<td>------</td>
<td>-0.53 ±0.26</td>
<td>------</td>
<td>0.007 ±0.002</td>
<td>-0.08 ±0.02</td>
</tr>
</tbody>
</table>
Species distribution maps

The fitted relationship between the environmental variables and the known GDS locations allow us to predict the probability of occupancy of GDS at any place in the sanctuary (figs. 15, 16 & 17). Because each of the different model fitting techniques and different competing models within a model type interpret the relationship between the environment and GDS occupancy differently, each of the final models produced a different map of predicted GDS probability of occurrence. The more flexible fit of the GAM predictors to the response variable results in the GAM map predicting more mid-range values of occurrence probabilities than the fitted GLM version. The differences in the BRT model map could be due to the additional variables included, geological class, thorium content, and topographic wetness. Only the single AIC$_{\text{best}}$ and BRT models within SSP are provided in figures 15-17.

The prediction maps are restricted to within SSP and open saltbush habitat, as the models were not fitted to areas outside of this range. This can be seen as the roughly diagonal section of suitable habitat running East-South-East to north-west through the sanctuary. It is likely that the fire and geological variables are responsible for the finer scale variation in probability within the SSP areas. The predicted probabilities of occurrence are similar to the AWC only-data models for each of the modelling techniques. The BRT predicts less areas of very high probability of occurrence than the other two models (fig. 17).

Figure 15. Probability of GDS occurrence across soft spinifex sand plain at Newhaven sanctuary, based on predictions made with a GLM shown in table 6.
Figure 16. Probability of GDS occurrence across soft spinifex sand plain at Newhaven sanctuary, based on predictions made with a GAM shown in table 6.

Figure 17. Probability of GDS occurrence across soft spinifex sand plain at Newhaven sanctuary, based on predictions made with a BRT shown in table 6.

Dynamic landscape and metapopulation modelling

Fire simulations

The variation between the final models was in the shape of the fire dynamics variables (table 7). Each LANDIS run produced maps of the fire severities across the landscape per decade. These were used to create maps of the number of years since last fire and number of fires in the past 40 years, for inclusion in the habitat suitability GLMs. Both were considered relevant variables.
The two were negatively correlated (-0.7), however, their contribution to a model was significant only in the presence of the other, and as such, all models presented below contain both fire variables.

For the current fire regime scenario, fire was parameterised so that the fire size distribution each decade matched that of the present as closely as possible (fig. 18). For the high fire scenario, 90% of the sanctuary burns in a 10 years period (1 time step), while in the low fire scenario less than 10% burns. During the current fire regime, it is closer to 60%.
Figure 18. Histograms showing the distribution of the area of the sanctuary at each 'time since fire' stage in each year of the simulation up to year 100.
**Habitat and carrying capacity change**

Changes to carrying capacity (K) can be used to assess the effects of each scenario on habitat suitability and availability. We considered two possible future fire scenarios in combination with competing distribution models representing different hypotheses about how the GDS respond to the environment and fire. We initially ran the models over 250 years, in order to visually interpret whether population equilibrium was reached. By 100 years into each simulation, population trajectory stabilised, and as such, all further analyses were conducted on 100-year simulations.

Carrying capacity change as defined in eq. 3 is dependent on the size of a patch and its average habitat suitability. That habitat suitability in turn is defined by the GLM model used in the simulations. Figure 19 shows the differences that emerge between the 3 models over the course of the 100 year simulation. Under the current fire regime, models B and C are much more sensitive to fire events than model A, which remains relatively constant over the course of the simulation. Model A is the model that best fits the data, but the small difference in AIC values means we are uncertain of the true relationship. In models B and C, the purple and green lines on figure 19 respectively, the step-like behaviour of the carrying capacity is a reflection of the response to a fire. LANDIS and RAMAS GIS are set up to interface in such a way that the effects of any dynamic landscape changes are felt at the mid-point of the decade, meaning that we see the changes to carrying capacity (and subsequently population size) in these mid-range years. Every 10 years there is an abrupt change in carrying capacity, which, given that this is the same timespan as a LANDIS time step, corresponds to a fire event.
Figure 19. Changes in carrying capacity for each model, under the current fire regime, over original 100 year simulation. Model A (both fire terms polynomial) is shown in orange, model B (time since fire polynomial) in purple, and model C (both terms linear) in green. Solid lines represent the mean of 3 model iterations; the dotted lines are ±1 standard deviation around this mean.
Figure 20. Effect of each model and fire regime on the carrying capacity of the environment at Newhaven over a 100 year simulation. Black lines describe current fire conditions, pink, high fire scenarios and blue, low fire. Mean carrying capacity over three model iterations is shown as a solid line. Dashed lines show one standard deviation around the mean which may be indistinguishable due to small deviations.
Under model A, the high intensity fire scenario differs little in terms of its effect on K from the current regime. The low intensity/infrequent fire scenario leads to a slight increase in carrying capacity, after 33 years, of about 60 individuals (fig. 20). Under model B we see much the same relationship, whereby the current and high fire scenarios are similar, and the low fire scenario is appreciably higher. In this model however the differences are more pronounced, with carrying capacity increasing by approximately 1500 individuals in one time step (fig. 20). The high fire scenario also has a consistently lower carrying capacity than the current regime and have a mean difference of 300 individual summed over the length of the simulation. Model C is markedly different in terms of the response to fire compared with the other two models (fig. 20). The low fire scenario has the lowest carrying capacity, which drops to under 400 around time 80. As with model B, the high fire scenario consistently performs worse than the current, with a mean difference of nearly 200 individuals.

**Population dynamics**

While the same general patterns observed in carrying capacity change over time are observed in population size, the population dynamic parameters serve to generally dampen the difference between scenarios in a relative sense. Similar to the carrying capacity, population size is more stable under model A than the other two models which fluctuate across a range of about 1000 individuals. However, the higher carrying capacities of models B and C don’t translate to larger populations. The maximum and minimum population estimates all show strong overlap across all models and scenarios, with the only strongly distinguishing pattern being that model C generally has the highest maximum population estimates after 45 years. Model B has the largest fluctuations in mean population, with the most abrupt population declines leading to likely extinction at around 100 years (fig. 21).
Figure 21. Effect of each model and fire regime on the population trajectory of GDS at Newhaven over a 100 year simulation. Black lines describe current fire conditions, pink, high fire scenarios and blue, low fire. Mean population size over three model iterations is shown as a solid line. Dashed lines show the maximum and minimum values obtained over at least 200 metapopulation simulations and 3 landscape simulations.
The interaction between model uncertainty and fire scenarios

Population trajectories respond in a broadly similar fashion to carrying capacities under different fire scenarios. This indicates that the population parameters themselves, such as annual survival, are having less effect on the trajectories than the environmental dynamics on habitat suitability. This is discussed further in the sensitivity analyses below. Little variation between fire scenarios is born out under species distribution model A, while a strong interaction between fires scenarios and distribution model choice is observed in the context of the low fire scenario. Under a low fire scenario, model A predicts a stable population, model B predicts a twofold population increase and model C predicts certain extinction (figs. 20 and 21). The estimated minimum abundances describe the same patterns as those seen in the population trajectories and carrying capacities. While only one scenario predicts a non-zero probability of extinction under a particular distribution model assumption, expected minimum abundances vary substantially across future fire scenarios and distribution model assumptions (fig. 22).

Figure 22. Expected minimum abundances for each model (A, B, and C) under low, current, and high future fire scenarios.
Sensitivities

Under the model A, current fire scenario, the EMA was not very sensitive to any of the parameters tested (fig. 23). The effect of carrying capacity appears the largest in figure 23, but this represents a doubling or halving of the carrying capacity, where most other parameters were simply increased or decreased by 20%. A doubling in the carrying capacity of the environment led roughly to a doubling in the EMA. This 1:1 ratio indicated that the model is not especially sensitive to this, or any other parameter tested. There was a weak effect of decreasing the initial abundance, but again the model was not highly sensitive to this parameter. I chose to test the AIC_{best} model under the most realistic scenario (model A, current fire regime) as a baseline and it is possible that the other models and fire scenarios would have more exaggerated sensitivities to these parameters. This lack of sensitivity of the model to other parameters indicates that the parameters under investigation in the main analysis - the effects of fire on habitat suitability – are the meaningful ones to be investigated.
Figure 23. Sensitivity of EMA estimations to RAMAS model parameters, as a percentage change from model A, current fire conditions. Model parameters are: ‘cbp’, model A, current fire scenario, used here as a baseline for comparison; ‘sdh’, seed dispersal maximum distance; ‘sdl’, seed dispersal mean distance; ‘kh’, carrying capacity doubled; ‘kl’, carrying capacity halved; ‘dds’, density dependence type scramble competition; ‘rmaxh’, intrinsic population growth increased by 20%; ‘maxl’, intrinsic population growth decreased by 20%; ‘inah’, initial abundance doubled; ‘inal’, initial abundance halved; ‘disph’, dispersal distance increased by 20%; ‘displ’, dispersal distance decreased by 20%; ‘math’, survival and fecundity matrix values increased by 20%; ‘matl’, survival and fecundity matrix values decreased by 20%.
DISCUSSION

GDS distribution is driven, in part, by the fire history of the landscape. All three modelling techniques included both time since fire and number of fires in their AIC$_{best}$ models. The relationship between probability of occupancy and time since fire was consistently stronger than the relationship between occupancy and the number of fires in 44 years. The BRT models found that time since fire contributed to the explanation of between 6.6 to 15.5% of the deviation in the data, depending on the area being modelled (SSP only or the whole sanctuary). Given that expert opinion indicated a positive relationship with time since fire, we expected to find some evidence of a relationship between the GDS and fire. Contrary to expert expectations however, although there was a relationship, it was not a positive correlation. Rather, in the majority of the AIC$_{best}$ models, time since fire was fitted with a more complex interaction, where mid-range values were most suitable, and habitat suitability declined either side of this (e.g. figs. 7-9). This relationship with time since fire has been observed in other arid and semi-arid dwelling lizards, *Ctenophorus fordi* and *Nephrurus stellatus* (Driscoll et al. 2012). Given that fires can alter the habitat structure and composition (Allen & Southgate 2002; Griffin 1990), it is unsurprising that other central Australian arid zone species are sensitive, not only to time since fire, but to a number of different facets of fire history. Sand monitor lizards, *V. gouldii*, are more abundant near the edges of different fire-age patches within a fire history vegetation mosaic (Bird et al. 2013). The greater bilby, *M. lagotis*, uses recently burnt areas to forage for food, and its occurrence is negatively correlated with distance to patches burnt in the past year (Southgate et al. 2007). Knob-tailed geckoes, rufous hare-wallabies, and western hare-wallabies have all been shown to respond to fire history of the landscape, and the population declines of the latter two are partially attributed to a halt in small-scale patch burning (Smith et al. 2012; Burrows et al. 2006; Burbidge & Pearson 1989; Bolton & Latz 1978). Like many animals in the arid interior of Australia, GDS appear to be sensitive to the fire history of their habitat, including the time since last fire and number of fires in a certain timeframe.

As well as fire, GDS distribution within the Newhaven Sanctuary appears to be strongly driven by vegetation type, elevation and soil geology. In each of the AWC-only models, vegetation was amongst the three most important variables in explaining variation in the GDS observation data. The grouped vegetation class that included SSP was the only class that contained presence records in the AWC-only model. This, combined with the experts’ assertion that GDS are found solely within soft spinifex sand plains, which was affirmed during fieldwork, led to the refinement of the scope of distribution model fitting to soft spinifex sand plains only. When a species specialises in one habitat type, the fine-scale variation in this vegetation can become an
important determinant of occupancy (Driscoll et al. 2012). This may be the scale at which fire variables operate in reality and that is approximated within the models presented here. The effects of fire on spinifex distribution and structure probably drive GDS distribution at a fine scale within this landscape. This assertion is supported by the fact that, in comparing the BRT models, both fire variables explained more than twice the variation in the data in the SSP models than the AWC-only models (figs. 9 and 14). The effect that fire is having on GDS occupancy is likely due in a large part to its influence on spinifex structure.

In all modelling techniques and across all modelled datasets, elevation was consistently the most important variable in determining probability of GDS occupancy. Elevation contributed to between 30-40% of the explanatory power of the BRT models. GDS probability of occurrence was highest in areas of around 545m above sea level, and declined either side of this (to values of 525m and 585m respectively at which occurrence probabilities were roughly halved). These areas corresponded to palaeodrainage lines and the adjacent sand plains found across the sanctuary. The ancient drainage lines contain more fertile soil and are more consistently productive, due in part to the amount of rainfall run-off they receive (Foulkes et al. 1995). The sand plains by contrast are far less fertile and are characterised by dense hummocks of spinifex and an abundance of termites, which consume the spinifex leaves (Morton & James 1988; Morton et al. 2011). Despite their less fertile conditions, the sand plains receive slightly more run-off than surrounding dunes due to their low relief. A lack of nutrients leads to the dominance of spinifex which is able to out-compete other vegetation in a low-nutrient environment (Morton et al. 2011). Paltridge and Southgate (2001) found that small reptiles were equally abundant in the sand plains and palaeodrainage lines at a site near Newhaven, despite the higher productivity of the drainage lines. A possible explanation for this, as well as for the presence of GDS on these sand plains, is the abundance of termites, which feed on the spinifex that dominates the habitat, and which is likely less common on the more fertile soils (Stafford-Smith & Morton 1990). Termites make up the majority of the diet of GDS and many other small reptiles (Pianka 1986). The GDS burrows found in the palaeodrainage habitat may be a sign that the skinks use this area as refuge during extreme droughts. It has been postulated that the higher nutritional value of these habitats allows them to act as refugia for a number of desert animals during extreme climatic events (Holmgren et al. 2006; Morton 1990). Reptiles are the most persistent animal class during drought periods in the Tanami (Paltridge & Southgate 2001), suggesting that they may utilise drainage lines during times of hardship.

Lower levels of thorium were always more favourable towards GDS occurrence, while the relationship between occupancy and ternary ratios tended to be negative. Both of these variables are a proxy for the geological and soil properties of the earth. Low thorium content corresponds
to basic igneous and carbonate parent rock beds, which are usually covered by sandy, iron-rich soils, while the ternary ratios indicate the presence of sandy loam soil, similar to that found on a sand plain (Mernagh & Miezitis 2008; Hoatson et al. 2011). These two variables reinforce the hypothesis that GDS is restricted to the spinifex sand plains across the sanctuary, where the properties of the soil favour spinifex growth and may be favourable to burrow digging. Southgate et al. (2007) found rocky, laterite landscape features to be an important determinant of bilby presence, a trend also common to spectacled hare-wallaby Lagorchestes conspicillatus (Masters et al. 1997). This is potentially due to the growth patterns of spinifex hummocks in these areas, which grow in more discrete structures, providing easier foraging and navigation (Southgate unpublished data). The elevation and relief of rocky features may also draw a greater variation in run-off and run-on of rainwater, resulting in higher plant nutrient availability (Southgate et al. 2007). In contrast to these findings, our burrow-digging skink did not favour rocky, laterite areas, but rather the topographic relief of the sand plains and palaeodrainage lines. Differences in diet may explain these preferences, as the bilby will preferentially consume a variety of seeds and bulbs plant (Southgate & Carthew 2006), while the GDS’ reliance on spinifex-consuming termites makes the spinifex dominant, hummock-dense sand plains better suited. Together, these variables lead us to conclude that GDS occurrence is most likely in palaeodrainage lines and adjacent sand plains dominated by soft spinifex burnt between 8 and 25 years ago.

There is considerable uncertainty surrounding the true relationship between fire variables and GDS occurrence. Species distribution model uncertainty arises from the incomplete nature of the occurrence data, as well as false absences due to imperfect detection, and vagaries of model fitting methods (Buckland et al. 1997). All model selection and fitting techniques have their strengths and weaknesses. GLMs are inflexible in the form of the relationship that they allow between the response and predictor variables, enforcing a generalised linear shape (Moisen et al. 2006). GAMs, and GLMs, are limited by the degrees of freedom offered to them, and do not easily explore and accommodate estimation of potential interactions between predictor variables (Quinn & Keough 2002). In contrast, BRTs are prone to over-fitting to a degree that is unlikely to reflect any true ecological principle, but rather, an estimate of sampling bias (Elith & Graham 2009). They also penalise model complexity less severely than AIC methods, resulting in larger models where some variables explain less than 1% of the variation in the data (Elith et al. 2008; see figs. 9 and 14). They do, however, allow investigation of model term interactions. By combining three modelling techniques, we increased our confidence in the outcomes common to all. The inclusion of the elevation, vegetation, geological and fire variables in all final models with some degree of explanatory power, serves as an example of this. Model evaluation techniques are used to assess the predictive performance of the models, as well as their fit to the
data and ability to explain deviation therein. In these respects, the BRT model explained the most deviance once the data was restricted to SSP. The AWC-only models performed better than the SSP models in predictive ability based on cross-validation analysis alone because the cross-validation on the full Newhaven area allowed the model to do well in predicting the species to be absent from many areas that were not included in the soft spinifex sandplain model comparison. This indicates that the cross-validated ROC values for the AWC data-only models were probably inflated. This was reinforced by the field-validation exercise which found predictive discrimination of those models to be ‘fair - poor’ (Swets 1988) in the soft spinifex and saltbush areas surveyed in 2013.

The use of GLMs in the PVAs, although necessary due to the requirement for an explicit equation in the RAMAS Landscape program, was not a disadvantage. GLM predictive performance was comparable to that of the other methods (tables 5 and 6) and the variables chosen and important in describing variation in occurrence were consistent across methods. However, competing GLM models with roughly equivalent AIC values provided quite a divergent picture about which fire histories were most suitable for GDS persistence. During the development of the GDS PVA we focused our attentions on whether uncertainty about the relationships between GDS occupancy and fire variables would affect our ability to predict population persistence under different fire regimes over time. The differences between the PVA model assumptions about the role of fire led to divergent predictions about how carrying capacity is likely to change over time, especially under a low-fire future scenario, which is considered likely under a warming and drying future climate in the region (Hennessey et al. 2004). Despite the apparently small divergence between the distribution models (each differed by only a predictor degree of freedom), the carrying capacity in some cases differed by thousands of individuals over the simulation. Under current conditions, model A (the nominal AIC_{best} model) indicated a long-term population that was about 300 skinks less than if models B and C were the true model (fig. 21). Under high fire scenarios, the differences were equivalent, with only slightly lower overall estimates (fig. 21). Under the low fire scenarios however, the three models diverged greatly, with model A estimating a relatively stable carrying capacity of around 1500 GDS, model B estimating an increase to approximately 3800, and model C predicting a rapid decline leading to carrying capacity of less than 400 after around 80 years. This led to almost certain extinction of the skinks over that period due to population dynamic process of local extinction and failure to recolonise locally extinct areas. These differences in model outcomes demonstrate that model choice is an important factor in estimating the carrying capacity of Newhaven for GDS into the future. The relationship between fire and habitat suitability is one that ultimately affects the ability of the environment to support GDS.
To investigate whether difference in carrying capacity across the future fire scenarios and distribution model assumptions played out in terms of variation in population persistence, we undertook metapopulation simulations which revealed some interesting patterns. Under current fire conditions, population persistence is not greatly affected by model choice. Altering the fire regime however, leads to large differences in population trajectories depending on the assumed distribution (ipso-facto carrying capacity) change model. The differences in carrying capacities between models tended to be somewhat dampened in population persistence. The small difference in carrying capacity doesn’t translate to a difference in population trajectory between the three models under current conditions, or a high fire scenario. The low fire scenario however, retains its large differences between the models, with model C resulting in the extinction of the metapopulation after approximately 100 years. In all cases, the realised mean population sizes never reach the upper limit of the carrying capacity, likely due to the effects of the density dependence, demographic stochasticity, and relatively poor dispersal leading to areas of relatively high carrying capacity not being occupied over long periods. Given that a decrease in fire events is a likely scenario under future climate change (Hennessey et al. 2004; Whetton et al. 2005), the pronounced differences in model choice cannot be ignored. It is important to recognise that the response of GDS to a decrease in fire size and frequency, whether due to climate change or management action, is highly unpredictable and dependent on the true relationship between the skinks and fire events. From a management perspective, this presents some problems regarding what course of action to take to achieve a certain objective. Investigation of the true relationship between GDS occurrence and local fire history and pattern will be essential to underpin robust predictions about the long-term fate of the GDS in Newhaven. Regardless of model choice and other uncertainties, GDS population persistence is likely to hinge to a large extent on the future of fire in the arid zone.

A risk-averse manager of the Newhaven Sanctuary may be particularly interested in the implications of the model C, low fire scenario. If preventing the loss of the GDS at Newhaven, then avoiding the low fire scenario until the true nature of the relationship between fire history and occupancy can be established would be a prudent endeavour. Although the increases in population under models A and B with a low fire scenario would be welcome, and may help support global persistence, the outcome of low fire could be disastrous. Taking the chance that the relationship described in model C is not the true GDS response to fire is a potentially risky strategy given that there appears to be little cost associated with the other strategies under all assumptions tested here. However, we acknowledge that we have definitely not tested all possible plausible assumptions about the response of GDS to fire that may provide a similarly good fit to the existing data. Given the apparent benefits to a range of species of maintaining frequent, low intensity, cool fires, prescribed burning and desisting from fire suppression in...
cooler conditions appears to be good options. Given the potential dangers of decreasing fire sizes and frequencies, it would be necessary to implement monitoring of fire frequency to determine whether it is changing over time, possibly in response to climate change.

In contrast, low fire appears as a good option based on the assumption that model B explains GDS response to fire well. If the current situation were considered dire enough for the GDS because the species’ numbers are so low that it will be committed to extinction if population size doesn’t increase (e.g. Allee effects: Courchamp et al. 1999), then it may be worth risking a catastrophic outcome for the potential windfall of an increasing population under a low fire scenario, punting on model B. However, given that the current analysis doesn't paint too dire a picture for GDS in the sanctuary under current conditions, it would appear reckless to embrace a risky strategy at this point.

Perhaps the most pertinent course of action would be to devise an experiment that will allow managers to either lend more support to, or disprove, model C. If a negative linear relationship between time since fire and GDS occurrence could be disproved, there would be less concern regarding the effects of fire on the persistence of the skinks. As model C under the low fire scenario is the only one of the nine scenarios that led to a non-zero probability of extinction risk, by disproving this relationship the long-term effects of fire could potentially be regarded as a low-priority management concern. There are a number of uncertainties throughout the models however which may affect the outcomes of the scenarios, and caution when making management decisions would be advisable.

**Study limitations and challenges**

There are a number of limitations in this study, including uncertainty in the quality of the data used to build the models and the limited knowledge available for estimating population and landscape change parameters. Uncertainty about the quality of the occurrence data may impact on the relationships fitted by the species distribution models. We are certain only of the conditions under which the 2013 fieldwork data was collected. The preceding years of data were collected under less rigorous circumstances, and by a variety of groups of people, decreasing our confidence in the quality of the data. None of the presence records in the 2013 data represent inactive burrows, as the existence of a latrine was necessary in positively identifying a burrow as belonging to a GDS, and latrines degrade quickly after abandonment (D. Moore pers. comm. 2013). Given the greater expertise of the observers collecting the AWC data, it is plausible that they would not have required a latrine to positively identify a burrow, and therefore may have included inactive burrows as presence locations. Considering the energy
cost and increased predation risks of digging a burrow, it is likely that the skinks only abandoned their burrows if conditions have become unfavourable in some way (McAlpin 2001). For example, if the habitat has become less suitable due to fire or if elevated local predation rates had led to the local extinction at that site. The issue then, is that inactive burrows, recorded as false presences, may in reality represent unsuitable habitat, but have been recorded as presences, effectively telling the model that these areas represent suitable habitat. While this does not hinder the model in more accurately discriminating habitat suitability for static variables, such as elevation, it confounds temporal variables, such as time since fire, where the conditions for occupancy must be precisely recorded at the time of occurrence.

The 2013 field data were not without their sources of error either. There was between a 19 and 33% chance that, for each site that was marked as an absence, the observers failed to detect a GDS latrine or burrow. These false absences impact the ability of the model to correctly determine suitable habitat, as areas with favourable combinations of environmental variables are discounted as being unsuitable due to an absence of GDS. This type of error is likely present in the pre-2013 occurrence records too, although a lack of data on the time spent searching each location makes estimations of the probability of this error difficult to calculate. False absences have been shown to have negative effects on both species distribution models (Tyre et al. 2003) and metapopulation models (Moilanen 2002). Fitting a detectability curve for the GDS (sensu Wintle et al. 2005b) would provide information on how many observers, or how many re-surveys, would be necessary to reduce the likelihood of a false absence to a particular level of confidence.

Across all three models, more frequent and larger fires led to, at most, slight decreases in carrying capacity and population persistence. This may be an underestimation of the damage that fire could have on the GDS population at Newhaven. Within the LANDIS sub-program used to model dynamic landscape changes, the length of a time step was fixed at 10 years. Although this may be an appropriate length of time by which to model generally slow-growing forests, the dynamics of the arid system operate on a shorter timescale (Morton et al. 2011). The inability to simulate fires on a yearly basis results in some loss of detail in the overall picture, as the study site, and indeed most of the Australian arid zone, may experience multiple fire events each year (Nano et al. 2012). Simulation of fires is such that each cell is only able to burn once within a time step, regardless of the flammability properties of the land type, resulting in an enforced minimum time since fire of 10 years. In models A and B where time since fire is polynomial, this masks the subtle negative effects of fire events in the first 10 years on GDS probability of occurrence. Although much of the landscape already burns in a 10-year time step under current conditions, the potential decline in habitat suitability that would take place in
areas burnt between 0 and 10 years ago, is not being captured by the increased area that does burn under the high fire scenario.

As discussed earlier, there is evidence to suggest that the GDS primarily use the sand plains, where spinifex growth is most dense, instead using the palaeodrainage line habitat in times of extreme drought, when the sand plains are unable to support local populations (D. Moore pers. comm. 2013; Paltridge & Southgate 2001). If this is the case, the skinks recorded in the palaeodrainage lines are, to an extent, in an ecological trap, or ‘sink’ population, where they are occupying habitat that is sub-optimal for their survival (Battin 2004; Pulliam 1988). Likely because this habitat was, at one time in the recent past, of a higher quality than the sand plains, but conditions have since changed and these populations have failed to move back into the SSP. Species distribution models assume that individuals are only present in suitable conditions, and use this assumption to discriminate between suitable and unsuitable areas (Wintle et al. 2005a). Inclusion of variables which describe past extreme climatic events is one way of attempting to incorporate violation of the assumption that we are modelling a species in equilibrium (as described by Austin 2002). Another extreme event not included in our models that may have shaped the current GDS distribution is flooding. Roughly decadal flooding events characteristic of the region turn the palaeodrainage lines into temporarily flowing channels (D. Moore pers. comm. 2013; Morton et al. 2011). These events would flood GDS burrows, making the areas uninhabitable for a time, and likely resulting in direct mortality for those populations in the low-relief drainage lines. The interactions between the drought events which may drive skinks to the palaeodrainage lines and the floods which drive them out again, could be an important set of variables to include in a future model.

The other challenge in characterising GDS response to fire and predicting the implications of change in fire regimes is the mismatch between the true fine scale patterning of fire which may determine the suitability of habitat and the resolution at which fire can be mapped in order to build regression models characterising the effect of fire on occupancy. There is a high degree of uncertainty surrounding the AWC fire history maps which were created from aerial photographs, and only the perimeter of the area burnt by a fire is captured. Within this larger area, it is highly likely that patches remained unburnt, as fire can be highly spatially variable on a small scale (Clark et al. 2003). The ‘completeness’ of the burn – the extent to which the vegetation burns within the larger perimeter of a fire event – is dependent on a number of climatic and historical factors. In central Australia, the intensity of a fire, and subsequently the extent to which it homogeneously burns the landscape, is often correlated with the time of year (Allan & Southgate 2003). Winter fires tend to be cooler, patchier and smaller in size, whilst the heat of summer brings severe fires that can burn areas hundreds of square kilometres, leaving
little unscathed (Allen & Southgate 2003). The previous fire history of an area also dictates how it will burn in the future, as reduced fuel loads in recently burnt patches will be unable to re-ignite, and the successional stage of the vegetation may determine the flammability and intensity of a burn (Nano et al. 2012). Rainfall can act as an inhibitor or abettor of fire extent, as recent rains may at first dampen vegetation, but will then lead to an increase in fuel loads as vegetation grows in response to the available water (Nano et al. 2012). All these factors conspire to make coarse-scale fire mapping an inaccurate measure of fine-scale habitat use, which is particularly problematic for species with small foraging ranges, like the GDS, that are likely affected by environmental variation on a fine-scale.

The models did not appear to be highly sensitive to any of the population viability parameters tested, however, there may be other aspects of the PVAs that could be more carefully parameterised based on quantitative data. Additionally, the high and low fire scenarios were chosen to represent potential extremes where the high fire scenario burnt over 90% of the habitat in a 10-year cycle, and the low fire scenario burnt less than 10%. These extremes may not represent realistic future fire scenarios under climate change, and again, parameterisation of the mean fire sizes and intervals based on quantitative predictions could result in more realistic estimations of population persistence.

Due to the coarse scale at which the fire history maps were created, there is little confidence in the exact values of the fire variables. This is compounded by spatial error in observation records which results in occurrences and absence points appearing in the statistical modelling data frame with the wrong fire history covariate values. For each of the occurrence observations, presence or absence, it is difficult to know whether the site was actually burnt in the year that the data states. In reality, fire may have passed over that patch, or may have only lightly burnt the vegetation, without causing enough damage to set in motion successional changes in composition and structure. Given the sensitivity of population model findings to the exact representation of GDS response to fire, spatial mapping error has the potential to impact significantly on results. To combat this source of scale-based uncertainty, ground-truthing of the fire variables at each survey site would need to be conducted by people with expertise in the fire dynamics and responses of the region. This would, however, incorporate uncertainty associated with the subjectivity of the experts, as well as difficulties with correctly aging burnt patches. Assessing the width and height of a spinifex hummock is a common form of aging a patch of vegetation (Rice & Westoby 1999), however, spinifex growth rate is more strongly associated with rainfall events, growing rapidly following heavy rains, making such estimates potentially unreliable (Driscoll et al. 2012). The scale of the fire data introduces uncertainty about the true relationship of the GDS to fire, which we have tried to characterise by using multiple models.
for our inference and predictions. Refining an understanding of the GDS true response to fire history at a landscape scale may improve as spatial mapping of fire footprint improves. Future research could collect more on-ground data to ground-truth this variable. Costs could be offset by integrating finer scale assessment of fire history and occupancy with yearly monitoring efforts.

There may be some relationships between GDS and fire that we have failed to consider. We investigated the effects of time since fire, fires in 44 years and fires in 10 years (as well as briefly considering fires in 5 years) on GDS occurrence. This does not represent all of the possible forms in which fire can affect a species, merely those we had the ability to construct from the given data. An additional variable that was considered but ultimately unable to be constructed from the data was fire intensity. Fire intensity is the amount of heat given off by a fire, and is related to the energy consumed as the fuel is burnt (Byram 1959). It can be an important determinant of the effects of a fire on the vegetation structure and successional patterns, as well as its suppression potential (Catchpole 2003). For GDS, fire intensity may affect the probability of direct mortality, the response of the spinifex, and subsequently the response of termites and chance of predation. The LANDIS program is capable of incorporating fire intensity information, provided you have some way of making sensible decisions on the values in relation to the time since last fire. What is required first, however, is data on fire intensity that can be used to fit the habitat suitability model. Although many of the fire history GIS layers contained information on the season in which the burn occurred, consultation with Newhaven managers led us to decide that this information was not reliably interpretable as intensity. On a coarse-scale, although winter fires tend to be cooler and less intense than summer fires (Allen & Southgate 2007), on a fine-scale, this may not reliably apply. We were therefore unable to utilise this feature of RAMAS Landscape, but more detailed data collection in the future or real-time fire mapping based on remote sensing technologies may make this possible.

Another fire interaction not investigated in this study is the shortest amount of time in between successive fires. The time between fires can exert a strong influence on plant survival (Bradstock et al. 1998; Regan et al. 2003). Although we examined the number of fires in a certain time period, the variable did not capture information on the length of time between those fires. When two or more fires occur in close succession, within a shorter than average interval, vegetative re-growth from the first fire may be destroyed by the second (Bradstock et al. 1998; Rice & Westoby 1999). Early re-growth, whether in the form of seedlings or re-sprouting existing individuals, is often much more sensitive to fire than a mature plant (Whelan et al. 2003). There is likely species-region-specific threshold for fire interval, below which seedlings,
seed banks and re-sprouting plants are destroyed (e.g. Regan et al. 2003). There would probably be a strong interplay between fire interval and fire size and intensity in determining the pace at which regeneration of vegetation occurs given their effect on isolation and seeding distance. Further data collection aimed at characterising the current vegetation mosaic in response to recent fires, manipulation of current fire data, or fire experiments could be beneficial to exploring alternative mechanisms of the effects of fire on GDS.

Although skinks are unlikely to suffer direct mortality following a fire, it is important to consider the indirect agents of mortality. Given the apparent ubiquity of abandoned burrows in recently burnt areas, there is likely some relationship that is not being captured in the modelling process. The exposure of burrows after a fire, when spinifex no longer conceals the entrance, may create an easy target for predators. We hypothesise that predators could simply sit and wait for the skinks to emerge from their burrows, resulting in very high mortality in the immediate area around burrow after recent fires. Predators, such as the bustard, *Ardeotis australis*, and cat, *Felis catus*, are often attracted to recently burnt areas for this reason (Burrows et al. 2006a; Bird et al. 2013). If evidence of increased indirect mortality relating to fire were obtained, it would be possible to represent this process as a post-fire decrease in survival using existing functionality of RAMAS GIS. This could be represented as some functional shape, where mortality in the year of a fire is very high, and then decreases each year as spinifex and other vegetation returns. Burrows and colleagues (2006b) monitored ground cover in spinifex sand plains following fire, and found that the percentage of bare ground fell from 80% in the first 2 years to a stable 55% after approximately 6 years. Rains following fire led to faster re-growth, although the bulk of this was due to grasses, rather than spinifex (also in Driscoll et al. 2012). These findings supported those of Letnic and colleagues (2004), who identified spinifex cover as being below 10% in at least the first two years following a fire, and Griffin (1990) who describe the dominance of grasses and conversely low spinifex cover up to 15 years post-fire (depending on rainfall amounts). This non-linear increase in spinifex cover through time, while related to rainfall, may also be related to initial fire intensity, as less severely burnt plants are able to re-sprout and recover faster (Rice & Westoby 1999). This highlights the importance of incorporating some measure of fire intensity into the models, potentially as a proxy for initial burrow abandonment probability. Percentage of ground cover is likely to be highly correlated with the skinks’ ability to avoid predation, and particularly spinifex cover which is denser and more permanent than that of grasses and herbs (Driscoll et al. 2012; Griffin 1990). As such, this non-linear regrowth rate of spinifex could be used as a starting point for the estimation of a function for GDS mortality immediately following fire. Managers guess that approximately 90% of burrows are inactive immediately post-fire. While there have been similar findings in other spinifex-specialist species (Caughly 1985; Legge et al. 2008; Masters 1996), this is in
contrast to the findings of Driscoll and colleagues (2012) who found that a spinifex-specialist reptile species remained relatively abundant at recently burnt sites. They suggest that this inconsistency is both a result of species-specific responses to fire and increased detectability (reptiles increase their movements following fire, making them easier to trap). Currently at Newhaven, data is being collected on the movements of skinks after a fire directly burns their burrow (D. Moore unpublished data). Plots are either burnt completely, patchily burnt, or left unburnt, and the movements of GDS monitored in the following weeks. Preliminary data suggests that skinks are not emigrating from the burrows in burnt plots, implying that the previously observed inactive burrows may be a result of predation or a force other than local dispersal. This information may also help to determine the true relationship with time since fire, potentially lending credence one of the relationships described in the three candidate models, A, B or C, proposed in this study. Given this potential local patch extinction dynamic following fire, dispersal distances, probabilities and re-colonisation rates are likely to play an important role in determining the long-term persistence of the metapopulation. Further investigation of the direct effects of fire on GDS movements will shed light on the nature of the relationship, and allow better estimates of population persistence under changing fire regimes.
CONCLUSIONS

In this study, I investigated the variables that drive distribution and abundance of the GDS across part of its current range, explored fire regime scenarios, and provided recommendations about fire regimes that are the most compatible with an objective of securing the skink population of Newhaven. More specifically, I have:

- Characterised the most important drivers of GDS distribution as elevation, vegetation type, soil type and fire regime.
- Found that fire history can help explain the distribution of GDS across the sanctuary, and explored how best to characterise that influence with the given data.
- Accounted for model uncertainty by exploring the implications of basing predictions on a number of plausible competing models.
- Investigated how changes in fire regimes are likely to affect trajectory and extinction risk of the GDS population using simulations of long-term metapopulation dynamics under three different candidate models representing different GDS relationships with fire.
- Evaluated the sensitivity of those ranked fire scenarios to uncertainty in the three SDMs and other model parameters.
- Discussed the implications of my findings in terms of strategies for ensuring the long-term persistence of the population of GDS at Newhaven through fire management.

While PVA models tend to suffer from considerable uncertainty in predictions about population trajectories and extinction risks, the real value of these models is in explicitly teasing out the sources and form of that uncertainty, highlighting what is possible and not possible under explicitly stated assumptions, coarsely ranking options with explicit reference to risk, and providing a defensible strategy for prioritizing the collection of new data to improve knowledge about sensitive parameters (Burgman 1993; Lindenmayer & Possingham 1996; Wintle et al. 2005a). In the face of these uncertainties, we have nonetheless recommended that risk-averse management actions would focus on maintaining fires at the current levels and to invest effort in clarifying the relationship between GDS occupancy and fire history at a finer scale than can currently be achieved. Further refinement of the fire mapping technique would help to reduce uncertainty about GDS’ response to fire, but it is not the whole story. Given the short foraging and dispersal distances of GDS, it is likely that small-scale fire mosaic patterns are important in determining suitable habitat for the skinks. Research on the immediate responses of skinks to direct and indirect burning of the vegetation surrounding their burrows is currently being conducted. These experiments will shed valuable light on the direct effects of fire on GDS mortality rates, as well as helping to determine the true nature of the relationship between the probability of GDS occurrence and fire.
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application: A review. Impact Climate Group, CSIRO Impact Group, CSIRO Marine and Atmospheric Research.


APPENDICIES

Appendix 1: Vegetation and geological features at Newhaven wildlife sanctuary, NT.

Figure A1. Map of Newhaven wildlife sanctuary showing the vegetation classes in the original GIS variable layer provided by the AWC.
Figure A2. Map of Newhaven wildlife sanctuary showing the grouped vegetation classes used in the variable for fitting the species distribution models ‘vegnew’. A value of 1 represents water bodies and hills; 2 represents soft spinifex sand plains and open saltbush flats; and 3 represents all other vegetation classes described in figure A1 above.
Figure A3. Map of Newhaven wildlife sanctuary showing the geological classes used in the variable for fitting the species distribution models ‘geology’.
Appendix 2: OpenBUGS code for estimating the individual observer-level detection probability for GDS latrines

model
{
meanfeocontent <- mean(feocontent[]) 
meannften <- mean(nften[]) 
meanternery <- mean(ternery[]) 
meantsf <- mean(tsf[]) 

for( i in 1 : 45 ) # for each of the 45 sites
{
lp[i] <- max(-99, min(99, a[1] + a[2]*(feocontent[i]-meanfeocontent) + a[3]*(nften[i]-meannften)+a[4]*(nften[i]-meannften)*(nften[i]-meannften) + a[5]*(ternery[i]-meanternery) + a[6]*(tsf[i] - meantsf) )) # same as the normal logistic regression line above only now including a truncation on the logit to help stability
logit(p[i]) <- lp[i] 
pres[i] ~ dbern(p[i]) # is the species is there? 1/0 - this lines allows this to vary across sites - redundant when there are no habitat variables considered
pr_sight[i] <- d*pres[i] # prob of seeing it depends on whether it is there
Obs[i] ~ dbin(pr_sight[i], Visits[i]) # number of observations drawn from a binomial distribution with number of trials = number of visits
}
d ~ dunif(0, 1) # prior for detectability
for(i in 1:6)
{
a[i] ~ dnorm(0.0, 0.001) # priors for regression parameters for occupancy
}
}

Inits
#
list(a = c(0,0,0,0,0,0), d=0.5)
list(a = c(0.5,0.5,0.5,0.5,0.5,0.5), d=0.8)
list(a = c(0,0,0,0,0,0), d=0.2)
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END
Appendix 3: Schematic representation of RAMAS Landscape and Repeater program processes

Figure A4. Conceptual flowchart of RAMAS Landscape sub-programs, including the wrap-around program RAMAS Repeater. This figure is adapted from Gordon et al. 2012, with permission.
Author/s: CADENHEAD, NATASHA

Title: The role of fire in the distribution and persistence of the great desert skink, Liopholis kintorei, under climate change

Date: 2013

Persistent Link: http://hdl.handle.net/11343/52492

File Description: Main article