

Cascades in the Desert: Interactions between lizards and mammalian apex predators.

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Tong, Nicholas

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Cascades in the Desert: Interactions between lizards and mammalian apex predators.

Nicholas W. Tong

Master of Philosophy

Centre for Ecosystem Science

University of New South Wales

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Other name/s: William

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Apex predators shape ecosystems through top down pressures which impact lower trophic levels through numerous interaction pathways. Lizard assemblages in arid Australia are driven by habitat structure, competition, and predation. The presence of mammalian predators in an ecosystem may influence the distribution of lizard species in Australian ecosystems. As lizards are ectotherms they are particularly sensitive to the changes in the thermal environment facilitated by climatic fluctuations, rainfall, herbivory and fire. The links between dingo control and lizard assemblages were explored using a natural experiment created by the Dingo Barrier Fence. Five years of data on predator activity and lizard assemblages from locations with a variety of management practices was used. The results showed that lizard assemblages reflected the differences in predator abundance and vegetation structure on either side of the Dingo Barrier Fence. Further investigation suggested a model where dingo control affects the abundances of lizard species via complex 4-link cascades. These findings suggest that there are winners and losers when dingoes are controlled: small lizards and geckoes benefit from dingo control while larger predatory lizards benefit from having dingoes in the ecosystem.

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Clockwise from top: Cameron's Corner Gate through the Dingo Fence © C. Spraggon; *Varanus gouldii* testing the air; Ghost Skink *Eremiascincus phantasmus* (prev. *E. fasciolatus*); Male tan coloured *Canis dingo*; Gecko *Lucasium* sp.; Juvenile *Menetia greyii*. © N.Tong.

Abstract

Apex predators shape ecosystems through top down pressures which impact lower trophic levels through numerous interaction pathways. Lizard assemblages in arid Australia are driven by habitat structure, competition, and predation. The presence of mammalian predators in an ecosystem may influence the distribution of lizard species in Australian ecosystems. As lizards are ectotherms they are particularly sensitive to the changes in the thermal environment facilitated by climatic fluctuations, rainfall, herbivory and fire. The links between dingo control and lizard assemblages were explored using a natural experiment created by the Dingo Barrier Fence. Five years of data on predator activity and lizard assemblages from locations with a variety of management practices was used. The results showed that lizard assemblages reflected the differences in predator abundance and vegetation structure on either side of the Dingo Barrier Fence. Further investigation suggested a model where dingo control affects the abundances of lizard species via complex 4-link cascades. These findings suggest that there are winners and losers when dingoes are controlled: small lizards and geckoes benefit from dingo control while larger predatory lizards benefit from having dingoes in the ecosystem.

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Chapter 1 General introduction

1.1 Thesis objectives

The two objectives of this thesis are to: 1) investigate the variation in lizard assemblages either side of the dingo fence incorporating varying forms of land use; and 2) to determine if differences in predator activity drives differences in the lizard assemblages in arid Australia; to better understand the depth and complexity of the ecological effect of the dingo, in the context of trophic cascades and mesopredator release theory.

In chapter 2 I investigate populations of lizard across the dingo fence on pastoral properties and National Parks, to compare and contrast lizard populations. I identify possible driving forces which correlate with the differences in the lizard assemblages including; dingo control, predator activity, land-use and habitat structure in the arid Australian desert.

In chapter 3 I sample a larger area than that considered in chapter 2, to determine if the trends identified in chapter 2 remained consistent across a larger area, in the Strzelecki Desert, Australia. The possible influences of predator activity and habitat structure on lizard abundances are explored. Lizard assemblages are used as a case study to illustrate the complexity of the cascading effects resulting from the control of the dingo in Australia.

In chapter 4 I provide a synthesis of the focal findings of the research, highlighting the contributions to current literature. This chapter will also include details of the limitations of the research and provide possible future avenues for predator research.

Chapter 1. General Introduction

1.2 Study Site

This study was conducted in the Strzelecki Desert in the Arid South East of Australia. The study region was dominated by East – West longitudinal dunes of red siliceous sand, separated by clay interdunal areas (swales) (Figure 1.1). The study made use of the dingo barrier fence, which provides the unique opportunity to study the effects of the absence of a top predator from an ecosystem, which is difficult to study classically due to ethical and logistical reasons. This study concentrates on the populations of lizards which occur on the sand dunes. In Chapter 2, 30 grids were sampled on six occasions across two pastoral stations and two National Parks properties from 2011 to 2014. In Chapter 3, 58 grids were sampled on two occasions across five pastoral stations and two National parks properties from 2014-2015.



Figure 1.1 Photo of dunes and swales.

1.3Chapter 2: Lizard assemblages across the dingo fence.

The aim of this chapter is to compare and contrast the lizard assemblages across the dingo fence and to identify factors which could be responsible for the differences in the lizard assemblages.

1.3.1 Driving forces of lizard assemblages

The vertebrate fauna of arid Australia is characterised by an incredibly rich assemblage of lizards (Pianka 1969, 1972, 1996, Pianka and Goodyear 2012). In particular the sand ridge deserts sustain very diverse communities of lizards with 20 or more sympatric species occurring on the dune tops (Pianka 1989). There are a number of different factors involved in shaping lizard assemblages in arid Australia, for example; wild fire, vegetation cover and vegetation structure (Dickman et al. 1999, Pianka and Goodyear 2012, Nimmo et al. 2013, Pastro et al. 2013, Smith et al. 2013). Grazing by herbivores, both domestic stock and indigenous species, can shape the vegetation structure and the cover of vegetation (James 2003, Ritchie and Johnson 2009, Read and Cunningham 2010). Wild fire is also an important process in shaping vegetation structure because it consumes vegetation and prompts succession in vegetation assemblages (Nimmo et al. 2013, Abom and Schwarzkopf 2016). The different habitat structures along a post-fire succession gradient supports different assemblages of lizard species (Pianka 1969, Driscoll and Henderson 2008, Nimmo

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et al. 2013, Abom and Schwarzkopf 2016). However, there are some species which do not appear to be affected by changes brought upon by fire and/or changes in habitat structure (Smith et al. 2012). There is a possibility that there are other, currently unidentified factors which could be shaping lizard assemblages in arid Australia.

1.3.2 Trends across the dingo fence

The Australian dingo barrier fence provides the opportunity to study the effects of the removal of the dingo, Australia's largest terrestrial predator. The dingo fence was constructed in 1908 along the NSW/SA and NSW/QLD borders, which arbitrarily follow the meridians 141° East and 29° South (Fitzwater 1972, Gordon and Letnic 2015). The dingo fence is not aligned with any natural geological boundaries in the region. The purpose of the dingo fence is to protect sheep-flocks, to the south and east of the dingo fence, from predation by the dingo. In the southern grazing lands "inside the dingo fence" sheep grazing is the primary pastoral industry and is accompanied by a decrease in apex carnivore activity, where the dingo is considered a pest species as they are responsible for the loss of stock (Fleming and Korn 1989). Thus, dingoes are subjected to intense lethal control methods, with the aim of extermination and as a result dingoes are rare in the region. To the north and west "outside the dingo fence" the principal pastoral industry is cattle, which are infrequently preyed upon by dingoes (Fleming and Korn 1989). Therefore, dingoes are not considered to be major pests outside the dingo fence, thus they are

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subjected to little or irregular control and are common (Letnic et al. 2009b, Gordon et al. 2015).

As there are no immediate geological structures or noted long term rainfall gradients divided by the dingo fence in the study region, the resulting ecological differences have been attributed to the difference in land-use and the associated difference in dingo abundance (Caughley et al. 1980, Newsome et al. 2001). Dingoes are key predators of large to medium sized mammals including kangaroos, the largest native herbivores in Australia. Thus, dingoes actively suppress kangaroos in regions where dingoes are common (outside the dingo fence) to a point where kangaroos are uncommon and inside the dingo fence, where dingoes are rare, kangaroos populations irrupt as they go regulated in the absence of dingoes (Caughley et al. 1980, Newsome et al. 2001). The abundances of foxes and feral cats follow the same population trends as kangaroos, as they are also suppressed by dingoes (Glen et al. 2007, Letnic and Koch 2010, Moseby et al. 2012). Foxes and cats are the foremost predators of small to medium sized mammals in Australia, resulting in many species becoming extinct or being threatened with extinction. As a consequence of predation by foxes and cats, small mammals are rare inside the dingo fence, where dingoes are rare and are common outside the dingo fence, where dingoes are common (Letnic et al. 2009b, Gordon and Letnic 2015).

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The structure and composition of vegetation also varies across the dingo fence, with a greater amount of shrub cover and reduced grass cover inside the dingo fence, where dingoes are rare (Letnic et al. 2009b, Gordon and Letnic 2015). Increased rainfall and drainage patterns are proposed as reasons for the differences in vegetation (Newsome et al. 2001, Letnic and Koch 2010). However, it is also plausible that herbivory and seed predation causes these differences. The differences in stock raised on either side of the fence may contribute to the difference in vegetation, as sheep farming is more intensive than cattle (Caughley et al. 1980). It has been suggested that predation of seeds by native rodents, specifically the Dusky Hopping Mouse, *Notomys fuscus*, may also be drives of the differences in vegetation evident across the dingo fence (Gordon and Letnic 2015). Outside the dingo fence, where they are common, *N. fuscus* are notable consumers of shrub seeds (Gordon and Letnic 2015). However, inside the dingo fence these rodents are rare to the point that their consumption of shrubs seeds is negligible. Thus it has been hypothesized that the consumption of shrub-seeds by rodents could be a driver of the differences in shrub cover across the dingo fence (Gordon and Letnic 2015).

1.4 Chapter 3: Population drivers of arid lizards

1.4.1 Effects of vegetation structure on lizard populations

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A widely accepted model which has been applied to lizard assemblages is a successional model, which predicted that a species will increase in abundance as the availability of its key habitat increases (Fox 1982, Letnic et al. 2004, Smith et al. 2013). The structure of vegetation and the availability of habitats such as leaf litter and open ground; are continually modified as a result of climatic events, rainfall, herbivory and fire (Read 2002, Letnic et al. 2004, Nimmo et al. 2012, Smith et al. 2013, Abom and Schwarzkopf 2016). Changes in vegetation structure can result in differing rates of solar insolation or influence the availability of basking sites. As lizards are ectotherms, they are sensitive to these changes, since basking is vital for thermoregulation (Schoener 1974, Tilman 1994). Burrowing and nocturnal lizard species appear to prefer open habitats, while litter-dwelling lizards prefer a closed shrub dominated habitat (Letnic et al. 2004, Nimmo et al. 2012, Smith et al. 2013). However, the ability of this habitat based model to predict the responses of lizards is limited and may be too simplistic to explain the structure of lizard assemblages as habitat structures are often patchy on a fine scale, providing niches for multiple species (Driscoll and Henderson 2008, Nimmo et al. 2012, Smith et al. 2013).

1.4.2 Dingo induced trophic cascades

Trophic cascades are relationships that result when a predator has effects that flow across more than one trophic link in a food web, either through direct predation or by altering behaviour through instilling fear (Pace et al. 1999, Estes et al. 2011, Colman et al. 2014, Ripple et al. 2014). The most commonly recognised trophic cascade is one in which apex

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predators control the abundance of herbivores, allowing plant biomass to flourish (Ripple and Beschta 2004, Colman et al. 2014). A famous example of this is the reintroduction of the grey wolf (*Canis lupus*) into Yellow Stone National Park, relieving trees/shrubs of browsing pressure due to the elk (*Cervus elaphus*) abundance (Ripple and Beschta 2004, Fortin et al. 2005, Ripple and Beschta 2007).

Another model of a top-down trophic cascade is known as the mesopredator release hypothesis. It proposes that predators at lower trophic levels (mesopredators) characteristically display temporal and spatial avoidance of the apex predator in the ecosystem (Crooks and Soulé 1999, Ritchie and Johnson 2009). A reduction in the apex predator's abundance releases mesopredators from suppression, thus causing irruptions in their abundance, amplifying their effects on lower trophic levels (Newsome et al. 2001, Colman et al. 2014, Ripple et al. 2014).

In the Australian arid zone, trophic cascades that are triggered by dingoes have been theorised (Caughley et al. 1980, Newsome et al. 2001, Letnic et al. 2009b, Visser et al. 2009, Gordon and Letnic 2015). Links that have been established between dingo removal in the region include increased abundances of the Red Kangaroo (*Macropus rufus*) and the Grey Kangaroo (*M. giganteus*) inside the dingo fence, where dingoes are rare, leading to a reduction in grass cover (Caughley et al. 1980, Letnic et al. 2009b). Also, where dingoes are rare there is an increased abundance of exotic foxes and cats, and a decrease in the

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small mammal abundance (Newsome et al. 2001, Letnic et al. 2009b, Letnic and Koch 2010, Gordon and Letnic 2015). Similar dingo induced cascades have been found in the forested environments of south eastern Australia (Colman et al. 2014). The current literature is limited in regards to the effect of dingo induced cascades on other classes of animals. For instance, there are no studies of dingo-induced trophic cascades on reptiles, however, there are studies of the effects of exotic mesopredators on reptiles. These studies have investigated the effects of foxes on the reduction in abundance of *Varanus gouldii*, *Ctenophorus pictus* and *Emydura spp.* (Read and Bowen 2001, Spencer and Thompson 2005, Read and Scoleri 2014).

Chapter 2 Lizard assemblages across the dingo fence

Chapter 2. Lizard assemblages across the dingo fence

2.1 Abstract

The abundance and distribution of lizards is determined by an assortment of abiotic and biotic factors. As ectotherms, lizards are particularly sensitive to changes in the thermal environment brought about by shifts in vegetation structure due to climatic fluctuations, rainfall, herbivory and fire. I investigated the effects of exclusion of dingoes, land-use and habitat structure on the composition of lizard assemblages. The study was conducted on pastoral properties and in National Parks across the dingo fence, in the Strzelecki Desert from 2011 to 2014. There was a difference in the lizard assemblages across the dingo fence. Lizard assemblages at sites where dingoes were common were dominated by predatory lizards, while the sites where dingoes were rare were dominated by small skinks and terrestrial geckoes. Lizard assemblages were also influenced by tenure, however, the effect of the dingo fence was greater than the influence of tenure.

2.2 Introduction

The abundance and distribution of lizards is determined by an assortment of abiotic and biotic factors (Pianka and Goodyear 2012, Pastro et al. 2013). As ectotherms, lizards are particularly sensitive to changes in the thermal environment brought about by shifts in vegetation structure due to climatic fluctuations, rainfall, herbivory and fire. (Read 2002, Letnic et al. 2004, Nimmo et al. 2012, Pianka and Goodyear 2012, Pastro et al. 2013, Abom

Chapter 2. Lizard assemblages across the dingo fence

and Schwarzkopf 2016). Changes in vegetative structure can alter the thermoregulatory environment available to lizards, by increasing or decreasing the amount of solar insolation or by influencing the availability of basking sites and shade, which lizards use to regulate their body temperature (Schoener 1970, Tilman 1994).

While many studies of lizard ecology have focused on how lizards respond to shifts in their thermal environment, manipulative studies which have excluded putative competitors and predators of lizards have demonstrated that biotic interactions such as inter-specific and intra-specific competition and predation are also important factors that shape lizard assemblages (Menge and Sutherland 1976, Pacala and Roughgarden 1982, Olsson et al. 2005). Competition can result in the abundance of weaker-competitors being suppressed or result in species occupying divergent niche space (Schoener 1974, Lister 1976). Similarly, predation can result in suppressed abundances of species that are vulnerable to predation (Menge and Sutherland 1976, Carothers and Jakšić 1984, Olsson et al. 2005).

In many ecosystems; the strong suppressive effects of predators on the abundance of their prey, results in cascades of indirect effects; that become manifest as shifts in the demography of species, which may have only weak interactions with predators (Estes et al. 2011). Such cascades of indirect effects can occur, if for example, the populations of the prey or competitors of predators' prey species, are themselves released from either predation or competition by the prey species. Due to the fact that they tend to have strong

Chapter 2. Lizard assemblages across the dingo fence

interactions with prey and competitor species, the removal of mammalian predators from ecosystems can induce particularly strong cascades of indirect effects (Ripple et al. 2014).

Apex predators have been documented as shaping ecosystems via ecological cascades, arising simultaneously from both their suppressive effects on herbivores and their suppressive effects on smaller predators (mesopredators) (Colman et al. 2014). Trophic cascade theory predicts that herbivore populations will irrupt following the removal of apex predators, which in turn will result in the depletion of plant biomass, by the over-abundant herbivores (Schmitz et al. 2000). The mesopredator release hypothesis predicts that removal of apex predators will release mesopredators from competition and result in the decline of the prey of mesopredators due to an increase in mesopredator abundance and impact (Letnic et al. 2009b, Letnic and Koch 2010, Sutherland et al. 2011, Read and Scoleri 2014).

The dingo, *Canis dingo* (Crowther et al. 2014), is Australia's apex predator and its removal from arid ecosystems is thought to have engendered ecological cascades (Letnic et al. 2012). Irruptions of kangaroos and red foxes, and declines in the abundances of small mammals and grasses where dingoes have been removed from arid ecosystems are consistent with the predictions of trophic cascade theory and the mesopredator release hypothesis (Caughley et al. 1980, Pople et al. 2000, Letnic et al. 2009b). The presence or absence of dingoes has also been linked to shifts in humans' livestock grazing practices, in

Chapter 2. Lizard assemblages across the dingo fence

particular sheep are rarely grazed in the presence of dingoes due to the likelihood of attacks (Letnic et al. 2012). The removal of dingoes has been linked to increases in the abundance of herbivores and introduced mesopredators that frequently prey on lizards (Cooper 1957, Read and Bowen 2001, Paltridge 2002, Olsson et al. 2005, Moseby et al. 2009b, Read and Scoleri 2014). It is also conceivable that dingo removal could affect lizard assemblages by influencing habitat structure and predation risk.

In this study I compared and contrasted the lizard assemblages across the dingo fence and identified the possible driving forces for the observed differences. The properties in the study region are situated so that there is a pastoral property and a conservation reserve in areas with similar landforms and climate on either side of the Dingo fence. Dingoes are rare on one side of the dingo fence and common on the other side (Fleming and Korn 1989, Letnic and Koch 2010). This contrast in the management of the dingo provides an ideal situation to compare and contrast the assemblages of lizards found in the presence or absence of the dingo as top predator. I used multivariate analyses to identify correlations of exclusion of dingoes, pastoral grazing and physical habitat properties, with the composition of lizard assemblages. I predicted that lizard assemblages will vary across the landscape due to heterogeneity of habitat at spatial scales and predator distributions.

2.3 Materials and methods

Chapter 2. Lizard assemblages across the dingo fence

2.3.1 Study area and climate

The study area was situated in the south-eastern Strzelecki Desert. The Strzelecki Desert has a mean annual temperature of 19-21 °C, with a summer maximum of 46-48 °C and a winter minimum of -3-0 °C (source: Australian Bureau of Meteorology). The annual rainfall in this region averages from 150-200 mm per year and is highly unpredictable, however, it has a pronounced higher incidence of rainfall during summer (Figure 2.3). The dominant landforms in the study region are longitudinal dunes of red siliceous sand, separated by clay plan swales. The dunes vary in height from 2-10 m and are spaced 50-500m apart (Figure 2.1). The dunes are predominately covered in a sparse low tree canopy (*Acacia aneura*, *Acacia ligulata*, *Cassia artemisioides*, *Dodonaea viscosa*, *Hakea leuconota*) and a ground cover of grasses (*Aristida contorta*, *Aristida browniana*, *Zygochloa paradoxa* and other grasses), forbes and ephemeral herbs (NPWSSA 2002).

Chapter 2. Lizard assemblages across the dingo fence



Figure 2.1 Dunes of red siliceous sand © C. Spraggon.

The study was conducted across 4 sites, within a conservation reserve and a pastoral property on each side of the dingo fence, which follows the New South Wales (N.S.W.) and South Australian (S.A.) border (Figure 2.2). The NSW/SA dingo fence follows the meridian 141° east. The NSW/SA border is an arbitrary boundary that does not reflect any natural geographic boundaries and was declared by a decree from King William IV in 1835 prior to the region's exploration. Dingoes are rare on the NSW side or "inside" of the fence due to intensive control activities and are common on the SA or "outside" side of the dingo fence. Two of the sites studied were pastoral; Coonanna bore (Quinyambie) ($29^{\circ} 48' \text{ S}$, $140^{\circ} 49' \text{ E}$) outside the dingo fence and Winnathee ($29^{\circ} 47' \text{ S}$, $141^{\circ} 9' \text{ E}$) inside the fence. Two of the sites studied were conservation reserves which have not experienced livestock grazing for more than 20 years prior to the study; Sturt National Park ($29^{\circ} 9' \text{ S}$, $141^{\circ} 2' \text{ E}$) inside the

Chapter 2. Lizard assemblages across the dingo fence

fence and Strzelecki Regional Reserve (29° 24' S, 140° 33' E) outside the fence (NPWSNSW 1996, NPWSSA 2002).

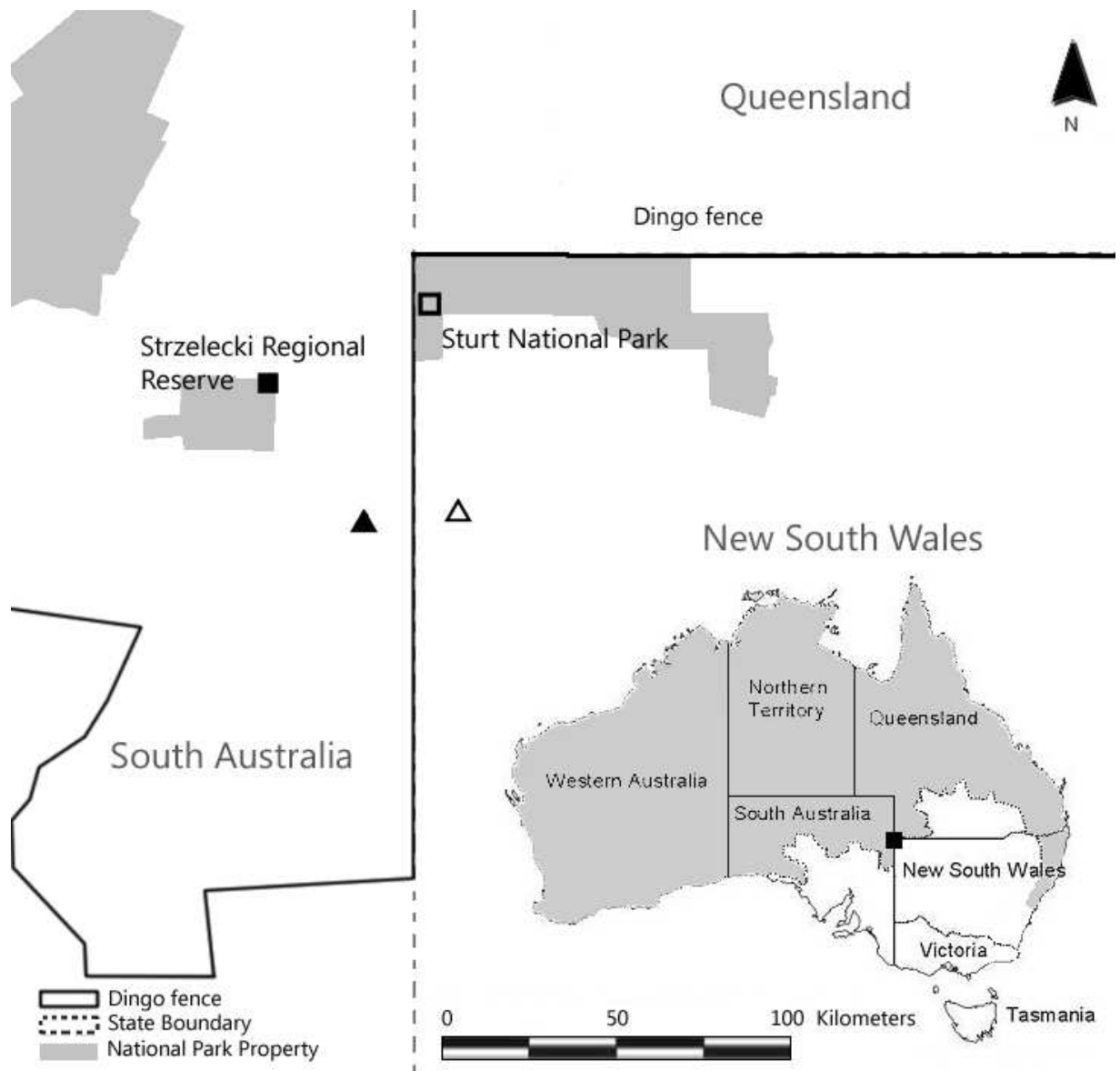


Figure 2.2 Map of the study region showing the four study regions (Coonanna bore, Strzelecki Regional Reserve, Sturt National Park, Winnathee). Squares represent sites in conservation reserves and triangles represent sites on pastoral properties. Hollow symbols are locations where dingoes are rare and solid symbols represent locations where dingoes are common. The blackline represents the Dingo fence, the broken line represents the State borders and the greyed areas are conservation reserves.

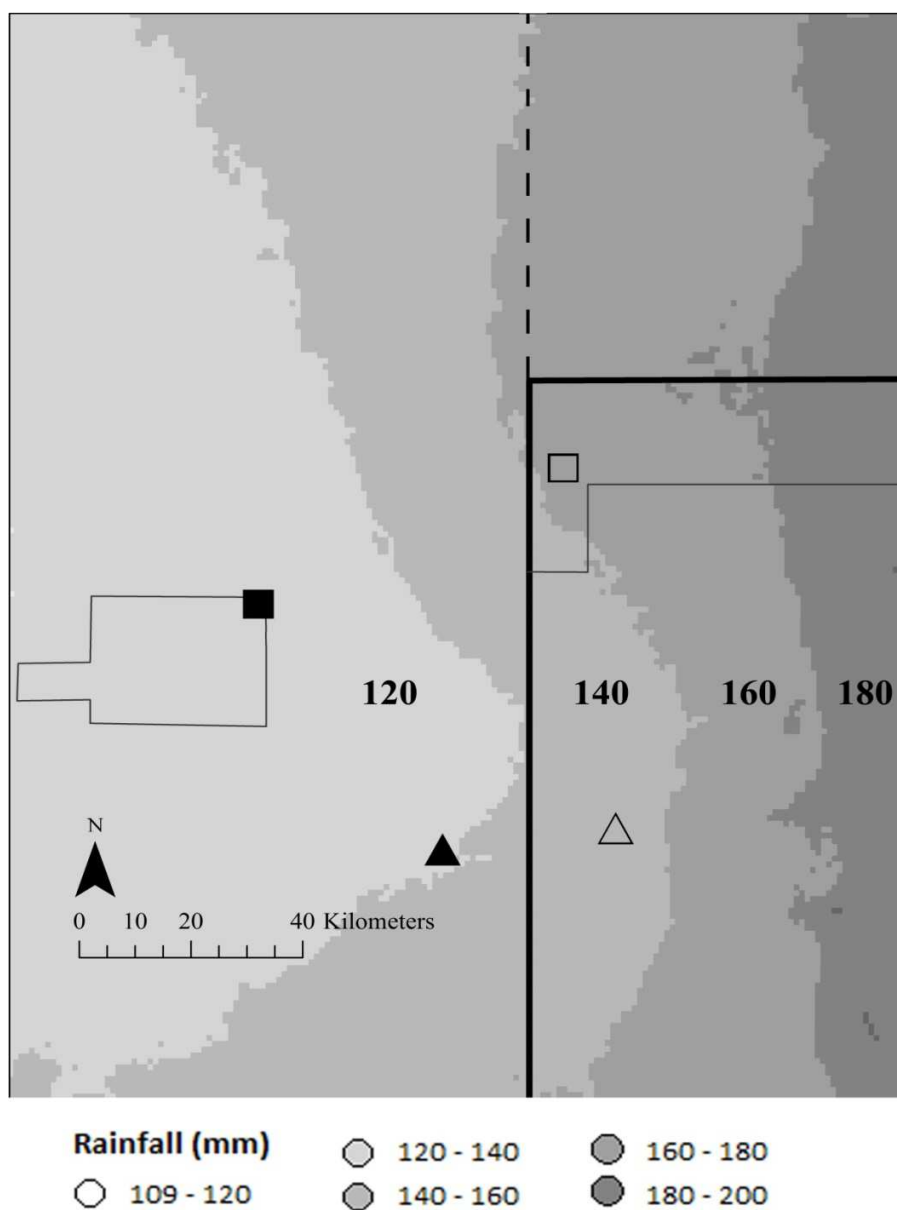


Figure 2.3 The mean annual rainfall (mm) in the region (source: Australian Bureau of Meteorology). Squares denote study sites located with conservation reserves and triangles denote study sites located on pastoral land. Shaded symbols indicate sites where dingoes are common and open symbols indicate sites where dingoes are rare.

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2.3.2 Trapping

Lizards were live captured at 30 trapping grids, 7-8 per site, each covering 0.01 km² across the 4 sites. Each grid consisted of 6 pitfall traps in two lines of three, spaced 20 m apart, at least 20m from the road. The pitfalls were placed running parallel to the dunes, so that one row of pitfalls ran along the crest and the other was on the side of the dune. The grids were located a minimum of 1 km apart. The pitfall traps consisted of a length of PVC pipe (16 cm diameter, 60 cm deep) buried flush with the ground with a 10 m length of fly screen fence positioned over the pipe (Figure 2.4). Fly screen was also placed at the bottom of the pitfall to stop animals from escaping. A total of 3,240 trap nights were conducted. Trapping was conducted in February/March and in October/November from October 2011 – March 2014, with a total of 6 trapping sessions. The traps were removed at the end of each trapping session. The abundance at each grid was calculated as the number of individuals per 100 trapping nights.



Figure 2.4 Fence of flyscreen across the top of the pitfall traps.

2.3.3 Vegetation surveys

Vegetation cover was sampled using a step-point method; at each point the vegetation cover was classified as bare, grass, forb, litter or shrub (Landsberg 2003, Letnic et al. 2013). On each grid, at each trapping session, three 100 m transects were sampled at 1 m intervals, giving 300 points per grid. The transects were conducted longitudinally along the dunes and were situated so that the sampling occurred at the top, middle and base on one side of the dunes.

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2.3.4 Statistical analyses

Due to low overall capture rates in this study, lizard abundances have been pooled over trapping sessions and grids (individual dunes) have been used as repeated measures. The number of captures was used as an index of relative abundance, lizards were marked with a non-permanent mark (Sharpie) and recaptures within the same survey were excluded. Captures were expressed as the number of captures/100 trapping nights.

A zero-adjusted Bray-Curtis dissimilarity matrix was constructed and the species abundances were square-root transformed to down-weight the contribution of the dominant species. Analyses were conducted using PERMANOVA+ add-on package for PRIMER v6 (Anderson et al. 2008).

A two-way mixed model PERMANOVA (maximum permutations = 9,999) was used to test the assemblages of lizards, with tenure and dingo control as factors. The relationships among sites were visually depicted using Non-Metric Multidimensional Scaling (nMDS).

Canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) is a constrained technique based on principal coordinates, used to find patterns in a cloud of multivariate points. CAP was also used to identify the lizard species correlating with the differences between sites, determine how habitat characteristics correlate with lizard communities in the Strzelecki Desert (Pastor et al. 2013).

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The number of principal coordinate (PCO) axes (m) used in the CAP model was determined using a leave-one-out (LOO) residual sum of squares cross validation method (Anderson et al. 2008). This method assisted in preventing the identification of false trends, while maximizing the predictive capability of the model and minimizing the number of axes (m). The strength of the association between the multivariate data cloud and the hypothesis of group differences is indicated by the size of the first two canonical correlations (δ), which varies between 0 and 1 (Anderson and Willis 2003, Anderson et al. 2008). When discrete groups were identified within the data cloud, Pearson correlations (r) were calculated for the variables contributing to those CAP axes. Variables *with* $r > 0.5$ were perceived as responsible for the observed effect of the axes and were traced over the plot as vectors (Anderson and Willis 2003, Pastro et al. 2013).

The CAP performs a permutation test to check for significant differences between multivariate groups in multi-dimensional space. The test statistic is a representation of the sum of the canonical eigenvalues or the trace of the matrix $Q_m^0 ' H Q_m^0$, which is an indication of the strength of the effect (Anderson and Willis 2003). The relative position of the grids compared to each other, on the two dimensional representation, give an indication of the similarity or dissimilarity of the lizard assemblage that they contain.

2.4 Results

A total of 341 lizards were caught representing 21 species (Table 2.2). 196 individuals were caught where dingoes were rare and 145 individuals were caught where dingoes were common. *Lucasium damaeum* and *Lucasium stenodactylum* were pooled as *Lucasium spp.* as it is difficult to distinguish between these two species in the field.

2.4.1 Effect of dingo control and tenure

The composition of lizard assemblages in the region differed (Figure 2.5) with side of dingo fence ($F_{1,26} = 7.2893$, $p = .001$) and tenure ($F_{1,6} = 6.0378$, $p = .001$) (Table 2.1).

Table 2.1 Results of PERMANOVA for species assemblage with Tenure (Te) and Dingo Control (DC).

Factor	df	SS	MS	Pseudo-F	$p(\text{perm})$	Unique perms
Te	1	11351	11351	7.2893	0.0001	9961
DC	1	9402.4	9402.4	6.0378	0.0001	9947
Te x DC	1	3279.9	3279.9	2.1062	0.0628	9967
Res	26	40489	1557.3			
Total	29	64522				

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The vector overlay revealed that lizard assemblages at sites where dingoes were common were characterised as having greater abundances of larger lizards such as *Varanus gouldii* (800g) and *Eremiascincus phantasmus* (13 g), while sites where dingoes were rare, had greater abundances of smaller lizards *Menetia greyii* (1 g), *Ctenotus schromburgkii* (2 g) and *Lucasium* spp. (2 g). The assemblages were spilt by the abundance *Ctenotus taeniatatus* (2 g) where *C. taeniatatus* was most abundant at the pastoral site outside the dingo fence (Figure 2.6).

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Table 2.2 Species captures, mass and snout to vent length (SVL).

Species	Mass (g)	SVL (mm)	Captures inside fence	the fence	Captures outside fence	the fence	Total captures
Varanidae							
<i>Varanus gouldii</i>	1800	1600 (total)	0		11		11
Scincidae							
<i>Ctenotus leae</i>	3	60	0		2		2
<i>Ctenotus leonhardii</i>	5	70	0		1		1
<i>Ctenotus regius</i>	5	70	4		3		7
<i>Ctenotus schomburgkii</i>	2	45	26		13		39
<i>Ctenotus taeniatus</i>	2	50	17		24		41
<i>Eremiascincus phantasmus</i>	13	80	11		28		39
<i>Lerista aericeps</i>	1	50	2		0		2
<i>Lerista labialis</i>	1	60	35		24		59
<i>Menetia greyii</i>	1	30	15		5		19
<i>Morethia adelaidensis</i>	1	45	0		1		1
<i>Tiliqua rugosa</i>	600	250	1		0		1
Diplodactylae							
<i>Lucasium spp. (L. damaeum and L. stenodactylum)</i>	2	50	58		4		62
<i>Strophurus ciliaris</i>	6	85	2		0		2
Carphodactylidae							
<i>Nephrurus levis</i>	11	80	20		18		38
Gekkonidae							
<i>Heteronotia binoei</i>	2	50	1		0		1
Typlopidae							
<i>Ramphotyphlops bituberculatus</i>	2	300 (total)	2		0		2
Agamidae							
<i>Ctenophorus nuchalis</i>	27	100	1		1		2
<i>Ctenophorus pictus</i>	8	70	1		10		11
<i>Pogona Vitticeps</i>	500	250	1		0		1

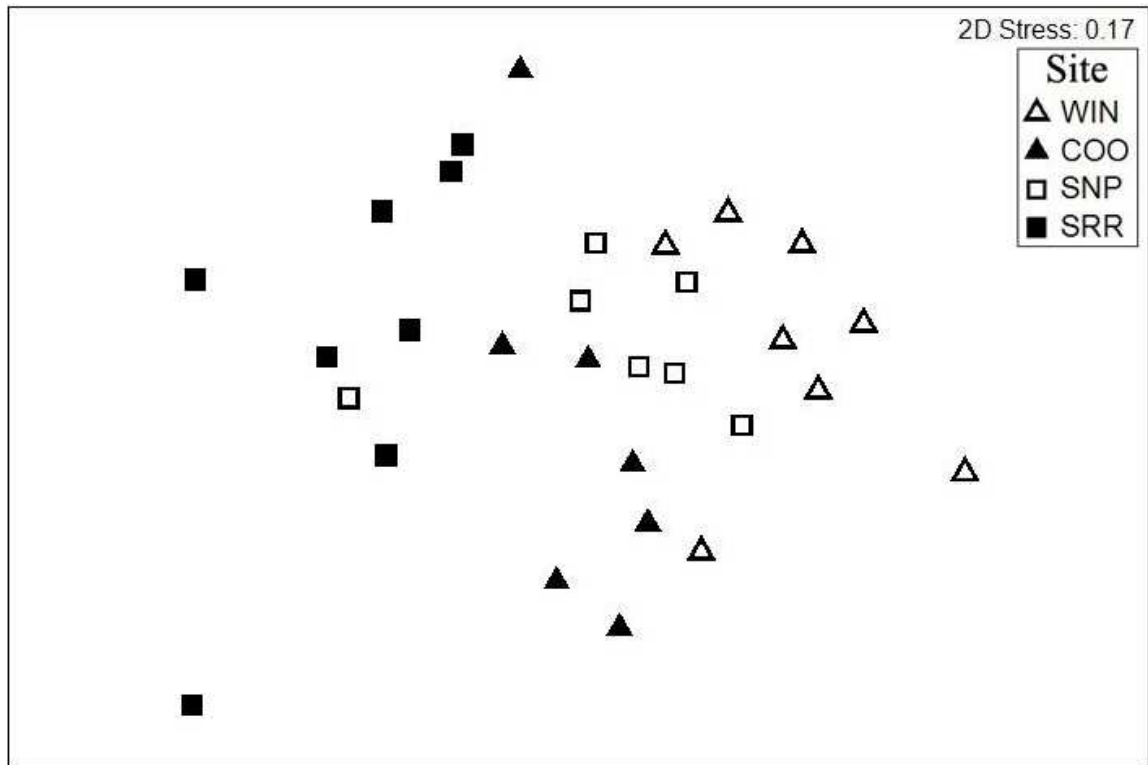


Figure 2.5 Results of the MDS indicate a difference in species assemblages at each grid across the study sites, the more similar the assemblages the closer the symbols they are. Shaded symbols denote grids where dingoes were common and open symbols indicate grids where dingoes were rare. Triangles indicate pastoral properties and squares indicate conservation reserves. The model is based on a zero-adjusted Bray-Curtis similarity matrix and species abundances have been square-root transformed.

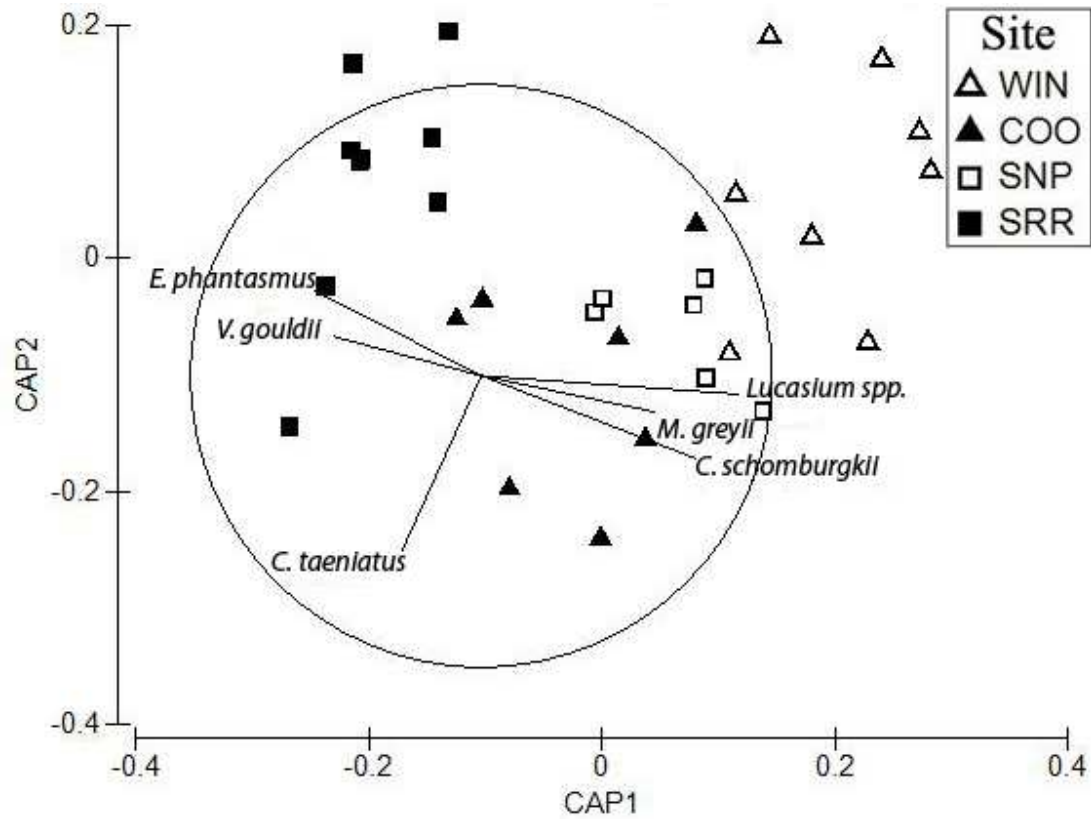


Figure 2.6 Results of the CAP analysis on the composition of lizard assemblages, in the Strzelecki Desert, the more similar the assemblages the closer the symbols they are. Shaded symbols denote grids where dingoes were common and open symbols indicate grids where dingoes were rare. Triangles indicate pastoral properties and squares indicate conservation reserves. The model is based on a zero-adjusted Bray-Curtis similarity matrix and species abundances have been square-root transformed. The CAP 1 axis separates the assemblages along the gradient of abundances of *Eremascincus phantasmus*, *Varanus gouldii*, *Menetia greyii*, *Lucasium spp.* and *Ctenotus schomburgkii*, and the CAP 2 axis separates the assemblages by the abundance of *Ctenotus taeniatus* as displayed by the overlay.

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2.4.2 Effect of habitat on lizard assemblages

The habitat characteristics were divided by site ($Q_m^0 \text{ 'H}Q_m^0 = 1.1853, p = .01, m = 2$) (Figure 2.7). The habitat characteristics contributing to the separation were divided so that sites where dingoes were common were characterised by low shrub and grass cover, and greater bare ground and forb cover. Sites where dingoes were rare were characterised by greater shrub, leaf litter and grass cover. The sites on the outside of the dingo fence were separated by the proportion of bare ground to forb and grass cover (Figure 2.7).

The composition of lizard assemblages were correlated with the habitat structure of the dunes ($Q_m^0 \text{ 'H}Q_m^0 = 1.2864, p = .016, m = 3$). *V. gouldii* and *E. phantasmus* were positively associated with bare ground. *V. gouldii* was also positively correlated with forb cover. *Lucasium spp.*, *C. schomburgkii*, *C. nuchalis* and *M. greyii* were positively correlated with grass cover; while *C. taeniatus* and *V. gouldii* were negatively associated with shrub cover (Table 2.3).

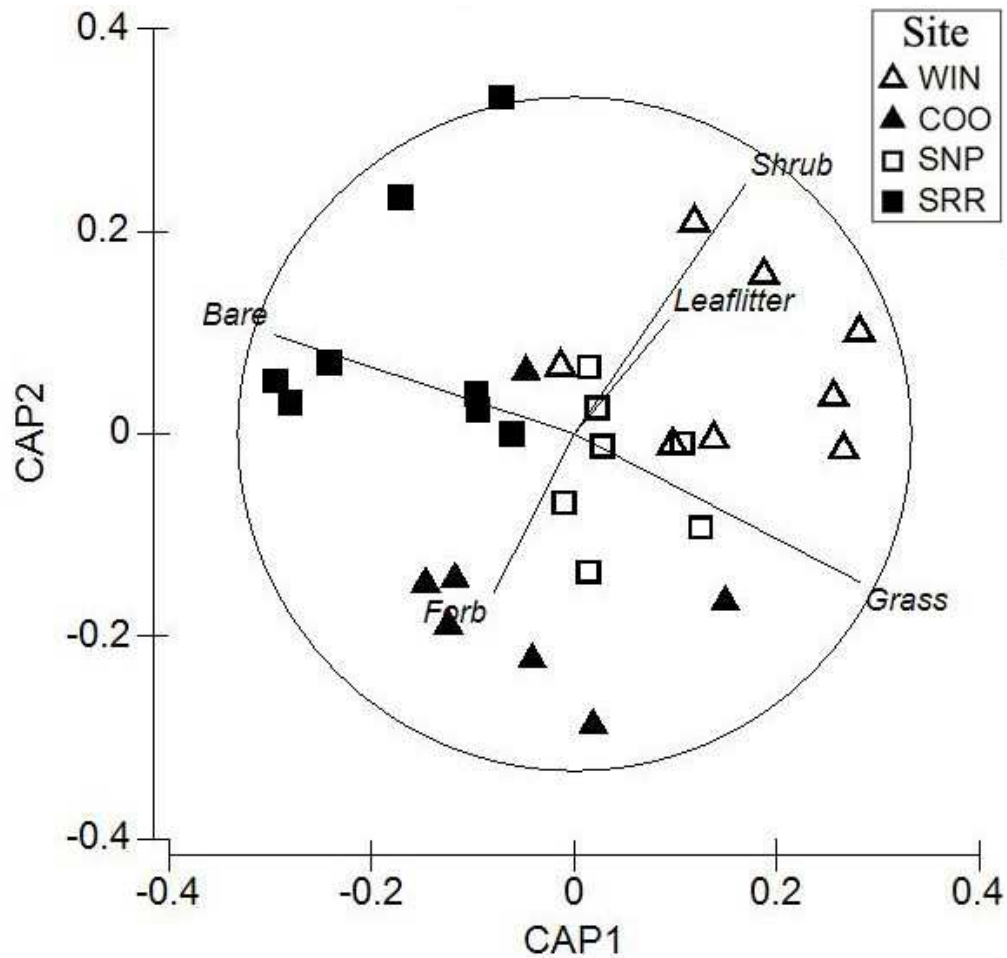


Figure 2.7 The habitat available at each site in Strzelecki Desert, as determined by CAP analysis. The Coonanna bore (Quinyambie) sites are represented by solid triangles, Strzelecki Regional Reserve by solid squares, Sturt National Park by hollow squares and Winnathee by hollow triangles. The model is based on a Euclidean distance similarity matrix and habitat variables have been normalised. The CAP 1 axis separates the grids by the amount of bare ground and grass cover, while the CAP 2 axis separated the grids by the amount of forb and shrub cover.

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Table 2.3 Correlations of species captured with habitat variables measured on each dune.

Habitat Variable	Bare ground	Leaf litter	Grass	Forb	Shrub
Species	r	r	r	r	r
<i>Ctenotus leae</i>	.261	-.196	-.250	.273	-.181
<i>Ctenotus leonhardii</i>	.060	-.378*	-.012	.218	-.199
<i>Ctenotus regius</i>	-.151	.054	-.031	.351	.224
<i>Ctenotus schomburgkii</i>	-.540**	.032	.683**	-.048	.171
<i>Ctenotus taeniatus</i>	.098	-.137	-.120	.140	-.541**
<i>Ctenophorus nuchalis</i>	-.436*	.149	.381*	.165	.157
<i>Ctenophorus pictus</i>	.321	-.261	-.323	.117	-.285
<i>Eremiascincus phantasmus</i>	.437*	-.049	-.575**	-.023	-.060
<i>Heteronotia binoei</i>	-.115	-.028	.148	-.094	.290
<i>Lerista aericeps</i>	-.080	.370*	.038	-.281	-.071
<i>Lerista labialis</i>	-.016	.170	-.091	.084	-.258
<i>Lucasium spp.</i>	-.450*	.298	.416*	-.270	.267
<i>Menetia greyii</i>	-.386*	-.115	.460*	-.041	.078
<i>Morethia adelaidensis</i>	.057	.237	-.167	.002	-.052
<i>Nephrurus levis</i>	.172	.016	-.285	-.119	.060
<i>Pogona Vitticeps</i>	-.177	-.112	-.122	-.121	-.114
<i>Ramphotyphlops bituberculatus</i>	-.083	.285	.027	-.034	-.145
<i>Strophurus ciliaris</i>	-.003	-.052	.049	-.174	.148
<i>Tiliqua rugosa</i>	.036	.299	-.110	-.218	-.071
<i>Varanus gouldii</i>	.468**	-.363*	-.274	.373*	-.391*

Note: *P < 0.05, **P < 0.01, n = 30

2.5 Discussion

There was a marked difference in habitat structure and lizard assemblages on either side of the dingo fence at sites where dingoes were common and rare. Sites where dingoes were rare had greater leaf litter, shrub and grass cover and were characterized by a greater abundance of the smaller lizards; *Lucasium* geckoes, *Menetia greyii* and *Ctenotus schomburgkii*. Sites where dingoes were common had more bare ground and forb cover; these sites were characterized by a relatively higher abundance of the larger lizards, *V. gouldii* and *E. phantasmus*. Could these differences in lizard assemblages be symptomatic of differences in the abundance of dingoes and differences in land-use?

Influences across the dingo fence on lizard assemblages

An important caveat to consider when interpreting the results of this chapter is that by necessity both the dingo and pastoral treatment effects were spatially segregated. For example, the dingo fence treatment was segregated east-west and the pastoral treatment was segregated north-south. Thus the differences in lizard assemblages on either side of the dingo fence and between conservation reserves and pastoral properties could be due to other factors.

One natural divide which coincides with the dingo fence, is the eastern edge of the natural distribution of *Ctenotus taeniatus*. The distribution of *C. taeniatus* encompasses all sites in

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this study, however they were absent a little way to the south and east of the study region. It is therefore possible that the abundance of *C. taeniatus* decreases with sites further to the south and east. This could explain why the Winnathee pastoral site, located where dingoes are rare, had the lowest abundance of *C. taeniatus*. The results indicate that the abundance of *C. taeniatus* is higher at the pastoral site, than at the conservation reserve located further north outside the dingo fence. This suggests that the results in this study are possibly an effect of tenure or another factor combined with the natural distribution of this species.

Other factors that could conceivably influence lizard abundances and assemblage composition in the study area include gradients in both long-term and short-term rainfall patterns and historical differences in land-use. For example, there is a general rainfall pattern where there is greater precipitation to the south and east of the study region (Figure 2.3). It is plausible that the greater precipitation in the south and east could result in a greater density of vegetation. This study found that there was greater shrub and grass cover on the New South Wales side of the fence (Figure 2.7). The greater abundance of *Ctenotus* and *Menetia* skinks on sites inside the dingo fence could be due to the greater abundance of shrub, leaf litter and grass over; as these species prefer habitats with leaf litter and ground cover (Wilson and Swan 2008, Cogger 2014). However, the association between *Lucasium* geckoes and shrub cover was unexpected because previous studies have found *Lucasium* geckoes to prefer open sandy areas (Pianka and Pianka 1976, Henle 1990, Smith et al. 2013, Cogger 2014).

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Consistent with previous studies Greer (1989), Wilson and Swan (2008), *Eremiascincus phantasmus* was more abundant at sites situated outside the dingo fence where the percentage of bare ground was higher than at sites situated inside the dingo fence. *E. phantasmus* require loose sand to bury in, dense leaf litter and vegetation to shelter under; however, they are more often found in more open areas (Greer 1989, Wilson and Swan 2008). The significant difference in abundance across the dingo fence suggests there is some factor related to the dingo fence which is suppressing the *E. phantasmus* populations where dingoes are rare.

Varanus gouldii occurs in a wide array of habitats across Australia, thus it would be expected that the abundance of *V. gouldii* should either not differ across the fence line, or be even higher on the low dingo, side due to the proposed greater productivity due to the rainfall gradient. However, the opposite was found. *V. gouldii* numbers were higher outside the fence, where dingoes are common, suggesting that further investigation is required to determine why *V. gouldii* abundances were starkly different either side of the dingo fence (Caughley et al. 1980, Newsome et al. 2001, Cogger 2014). Rainfall and habitat variations were found to be plausible explanations for the differences found in the distributions of some species, but were not found to be probable reasons for the differences in the distributions of others.

Influence of dingo control

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The control of dingoes in arid regions has been shown to have effects on lower trophic levels; either through the direct predation of macropods, rabbits and foxes or through indirect effects on small mammal abundance (Caughley et al. 1980, Newsome et al. 2001, Letnic and Koch 2010). The dingo is unlikely to have a direct affect on the abundances of most of the lizards in the assemblages, as dingoes prefer prey > 100g, well above that of most species recorded; with the exception of *V. gouldii* (Corbett and Newsome 1987, Paltridge 2002, Letnic et al. 2009b, Cupples et al. 2011). Lizards, on average, only make up about 11% of the dingo diet and the majority of that is comprised of larger Agamids and Varanids (Corbett and Newsome 1987, Paltridge 2002, Cupples et al. 2011).

A possible way that dingoes could affect the abundances of lizards indirectly is through mesopredator release. In this study, the abundance of *V. gouldii*, the largest predatory lizard in the region, was strongly correlated positively with dingo abundance. This was unexpected as *V. gouldii* is a known prey item of the dingo (Pianka 1970, Wilson and Swan 2008, Read and Scoleri 2014). A plausible explanation for the lower abundance of *V. gouldii* where dingoes were controlled is that they are subjected to higher rates of predation at those sites due to higher numbers of foxes and cats. *V. gouldii* falls within the preferred prey size of the foxes and cats, and it has been observed previously that *V. gouldii* abundances were lower in the presence of these introduced predators (Read and Bowen 2001, Paltridge 2002, Klocker 2009, Moseby et al. 2009b, Read and Scoleri 2014). It is possible that the abundance of *V. gouldii* is lower in the presence of foxes due to the direct predation by them. Also, foxes might have a greater impact on *V. gouldii* abundance than

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dingoes, possibly due to foxes occurring in greater densities? Thus, is it plausible that *V. gouldii* is being preyed upon on both sides of the dingo fence, but have a net benefit outside of the dingo fence, where dingoes suppress foxes.

Intriguingly, the abundances of *E. phantasmus* were higher at the sites where dingoes were common. It is possible that they are also being exploited by foxes and are not frequently preyed upon by either the Dingo or *V. gouldii*. Current research has found that skinks make up a component of the Varanid's diet, however, it is not known if *E. phantasmus* is preyed upon by *V. gouldii* (Pianka 1970, Shine 1986, Pianka 1995). Dietary studies have found that *Eremiascincus* sp. and other fossorial lizards are common prey items of fox and cats; so it is possible that *E. phantasmus* abundances could have been driven by predation from these mesopredators (Catling 1988, Read and Bowen 2001, Paltridge 2002).

The abundance of small skinks and *Lucasium* geckoes differed across the dingo fence, their abundances negatively correlated with the abundance of dingoes, *V. gouldii* and *E. phantasmus*. Due to their small size, it is unlikely that predation by dingoes was directly influencing the abundance of skinks and *Lucasium* geckoes. However, it is plausible that populations of small skinks and *Lucasium* geckoes were being driven by predation from *V. gouldii* and *E. phantasmus*. *V. gouldii* consumes skinks and geckoes (Pianka 1970, Losos and Greene 1988, Pianka 1995, Olsson et al. 2005). There is also evidence that *E. phantasmus* preys upon smaller skinks and possibly geckoes, as geckoes have been found in the gut contents of a congener *E. richardsoni* (James and Losos 1991).

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It is possible that the differences in lizard assemblages found either side of the dingo fence on both pastoral stations and conservation reserves, are a legacy of historical sheep grazing and cattle grazing in these areas. Sheep grazing still occurs on Winnathee and it occurred in Sturt National Park for over 100 years prior to being gazetted in the 1970's (NPWSNSW 1996). Overgrazing by sheep has been linked to changes in vegetation structure including the loss of grasses and increases in the cover of woody shrubs (Busack and Bury 1974, Read 2002). These impacts of sheep grazing may have produced an environment which is less hospitable to larger burrowing lizards, with lower levels of insolation and possibly a dense root mat (Tiver and Andrew 1997). Cattle grazing still occurs on Quinyambie and occurred in Strzelecki Regional Reserve prior to 1991. Cattle grazing enterprises tend to have less impact on vegetation than sheep grazing enterprises, so tend to have lower shrub cover than areas used for sheep grazing, which makes hunting prey easier and is preferable to larger predatory lizards (James 2003, Read and Cunningham 2010, Eldridge et al. 2016).

Influence of tenure

Lizard assemblages and abundances differed with grazing pressures due to recent land tenure; however, this effect was weaker than the effect of the dingo fence. The results indicate that there was a weak effect of tenure on lizard assemblages and the species most influenced by tenure was *C. taeniatus*. *C. taeniatus* were more abundant at sites situated on the pastoral property than the conservation reserve, outside the dingo fence. However, they were more abundant on conservation reserves than pastoral properties inside the dingo fence. The effect of tenure in this study was in essence an effect of contemporary livestock

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grazing, through the comparison of domestic herbivore free conservation reserves with pastoral properties. There is conflicting evidence as to how lizard abundances and species diversity are affected by livestock grazing (Read 1995, James et al. 1999, Read 2002, James 2003, Read and Cunningham 2010). However, the results suggest that the distribution of *C. taeniatus* is linked to the shrub cover at each site (Table 2.3). This is consistent with current literature on fenced enclosures (Olsson et al. 2005, Read and Cunningham 2010).

2.6 Conclusion

This chapter shows that there were distinct differences between lizard assemblages on either side of the dingo fence. The effect of the dingo fence was greater than that of tenure. Smaller lizards were more abundant where dingoes were rare, while larger lizards were more abundant where dingoes were common. I hypothesise that the differences in lizard assemblages either side of the fence may be due to differences in habitat structure and predator regime. In the next chapter I explore these hypotheses by conducting a larger scale survey of lizard assemblages, relating to their composition of predator activity and habitat structure.

Chapter 3 Predator activity a driver of arid lizard populations

3.1 Abstract

Apex predators produce top down pressures that impact lower trophic levels, through a myriad of interaction pathways via both direct and indirect effects. Lizard assemblages in arid Australia are shaped by habitat structure, competition and predation. I surveyed lizard assemblages on properties with varying degrees of dingo control, in the Strzelecki Desert during 2014-5. Generalised structural equation modelling was used to investigate the links between dingo control and lizard assemblages. The results of the GSEM provide evidence of dingo control causing cascading effects and hence, shaping lizard assemblages. The proposed cascading effects of dingo control on the structure of lizard assemblages, demonstrates how it is possible for multiple 4-link cascades to be initiated by the removal of a top predator.

3.2 Introduction

In chapter 1, I found that there was a difference in lizard abundances across the dingo fence and between properties used for livestock grazing and conservation reserves. Differences in lizard assemblages were correlated with the activity of predators and the vegetation structure available at each site, but the reason for the differences in the abundances of individual species could not be identified owing to the east-west spatial separation of sites. In this chapter, I conducted a survey of lizards across a larger area with the aim of

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increasing the replication of sites and conducting surveys both east-west and north-south across the dingo fence. The new survey period included the use of previously visited sites to the east and west, as well as new locations to the north and new locations between the sites examined in the previous chapter. I explore how reptile assemblages are affected by predator activity and habitat structure, providing possible driving forces for lizard assemblages and individual species.

Apex predators, whether terrestrial or aquatic, have consistently confirmed their ability to shape the ecosystem they inhabit. Apex predators produce top down pressures which impact lower trophic levels, through a myriad of interaction pathways via both direct and indirect effects (Estes et al. 2011, Colman et al. 2014, Ripple et al. 2014). Direct effects encompass predation and the fear which they instil in both their prey and other smaller predators.

Two of the models that have been proposed to explain how predators indirectly influence lower trophic levels are known as the Mesopredator Release hypothesis and Trophic Cascade Theory (Ritchie and Johnson 2009, Letnic and Koch 2010, Estes et al. 2011, Colman et al. 2014). The Mesopredator Release hypothesis states that when a top predator is removed from a system, this will “release” the smaller mesopredators from the fear, competition and direct killing by the top predator (Ritchie and Johnson 2009). This leads to an increase in their population and a change in their behaviour, thus resulting in a decrease

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in the population of the mesopredators' prey. Trophic Cascade theory describes how apex predators suppress herbivores, which benefits plants consumed by the herbivore (Ripple and Beschta 2007, Letnic and Koch 2010, Estes et al. 2011). An example of this is how the lethal control of the dingo results in irruptions of macropods, which in turn leads to a decrease in the structural complexity of the vegetation in that area (Colman et al. 2014).

The dingo (*Canis dingo*, 12-22 kg) is the top predator in Australia. Recent studies have highlighted the dingo's ability to shape Australia's ecosystems, from the temperate forests to the arid deserts (Letnic et al. 2009b, Colman et al. 2014). These studies provide evidence that dingoes suppress the exotic mesopredators, the red fox (*Vulpes vulpes*, 3.5-8 kg) and the feral cat (*Felis catus*, 2.5-6.5 kg), benefitting small mammals which are preyed upon by the mesopredators (Letnic et al. 2009b, Moseby et al. 2012, Gordon et al. 2015). Dingoes also suppress macropods, thus in regions where there dingoes are controlled, macropod abundances increase, thus increasing herbivory reducing grass cover (Letnic et al. 2012).

There are few previous studies on the impacts of dingoes on reptile populations. Current research illustrates the significant negative impacts that foxes have on the sand goanna (*Varanus gouldii*, 1.8 kg, 1.6 m (length)). Studies comparing goanna abundances in areas where foxes are baited and unbaited, found that the sand goanna is rare in places where foxes are common. The results of Chapter 2 were consistent with these findings (Olsson et al. 2005, Read and Scoleri 2014). Although *V. gouldii* are part of the diet of the dingo, in

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Chapter 2 the goanna was found in greater numbers in areas where dingoes were common (Cupples et al. 2011). In turn, small lizard numbers were found to be greater in the regions where goannas were rare. Given these findings I propose the following hypothesis; considering that dingoes suppress fox abundance (Glen et al. 2007, Letnic and Koch 2010, Moseby et al. 2012) and as foxes suppress goanna abundance (Olsson et al. 2005, Read and Scoleri 2014). It is plausible that the lethal control of dingoes results in an irruption of foxes, which suppress the *V. gouldii* population, reducing the rate of predation on smaller lizards and geckoes. It is therefore plausible that small lizard and gecko populations were being driven by predation from *V. gouldii* (Shine 1986, Sutherland et al. 2011).

Hence, I predict that the dingo is indirectly affecting the abundances of small arid zone lizards. More specifically, I hypothesise that lizard assemblages will differ consistently according to the findings described in Chapter 2 and that this will be consistent over a larger area. The abundances of individual species found at a site will be linked to the predator activity at that location and the habitat available.

3.3 Materials and methods

3.3.1 Study area and climate

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The study was conducted at eight sites surrounding the dingo fence which follows the New South Wales (NSW), Queensland (QLD) and South Australian (SA) borders (Figure 3.1). The dingo fence follows the meridians 29° S and 141° E. Both the NSW/SA and NSW/QLD borders are arbitrary boundaries that do not reflect any natural geographic boundaries. The NSW/SA border was declared by a decree from King William IV in 1835 prior to the region's exploration, the NSW/QLD border shortly after exploration and prior to settlement. Dingoes are rare on the NSW side or "inside" of the fence due to intensive control activities and are common on the SA and QLD side or "outside" side of the dingo fence due to varying intensities of control.

Six sites located on pastoral properties and two sites on National Parks were sampled. Five were outside the dingo fence; Coonanna/COO (Quinyambie) (29° 48' S, 140° 49' E), Tilcha/TIL (Quinyambie) (29° 39' S, 140° 36' E), Omicon/OMI (28° 52' S, 141° 9' E) and Bollards Lagoon/BOL (28° 49' S, 140° 42' E), and Strzelecki Regional Reserve/SRR (29° 24' S, 140° 33' E) and three inside the dingo fence; Winnathee/WIN (29° 47' S, 141° 9' E), Lake Stewart/LAK (29° 25' S, 141° 13' E) and Sturt National Park/SNP (29° 9' S, 141° 2' E) (Figure 3.1). Sites outside the dingo fence were located to the west and to the north of the sites within the dingo fence. Some of the sites sampled in this chapter had not previously been sampled, while some were previously sampled during the Chapter 2 study and were sampled again in 2014 and 2015. The sites were located in the South Eastern region of the Strzelecki Desert. The nearest weather station to the study area has a mean annual temperature of 19-21 °C, with summer maximum of 46-48 °C and a winter

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minimum of -3-0 °C (source: Australian Bureau of Meteorology, Tibooburra Post Office).

The annual rainfall in this region averages from 150-200 mm per year and it is generally highly unpredictable, but has a pronounced wet season during summer.

The most important landforms in the study area were dune fields, dominated by longitudinal dunes of red siliceous sand, separated by clay plan swales. The dunes vary in height from 2-10 m and are spaced 50-500m apart. The dunes are mostly covered in a sparse low tree canopy (*Acacia aneura*, *Acacia ligulata*, *Cassia artemisioides*, *Dodonaea viscosa*, *Hakea leucoptera*) and a ground cover of grasses (*Aristida contorta*, *Aristida browniana*, *zygichloa paradoxa* and *Tripodia basedowii*), forbes and ephemeral herbs (NPWSSA 2002).

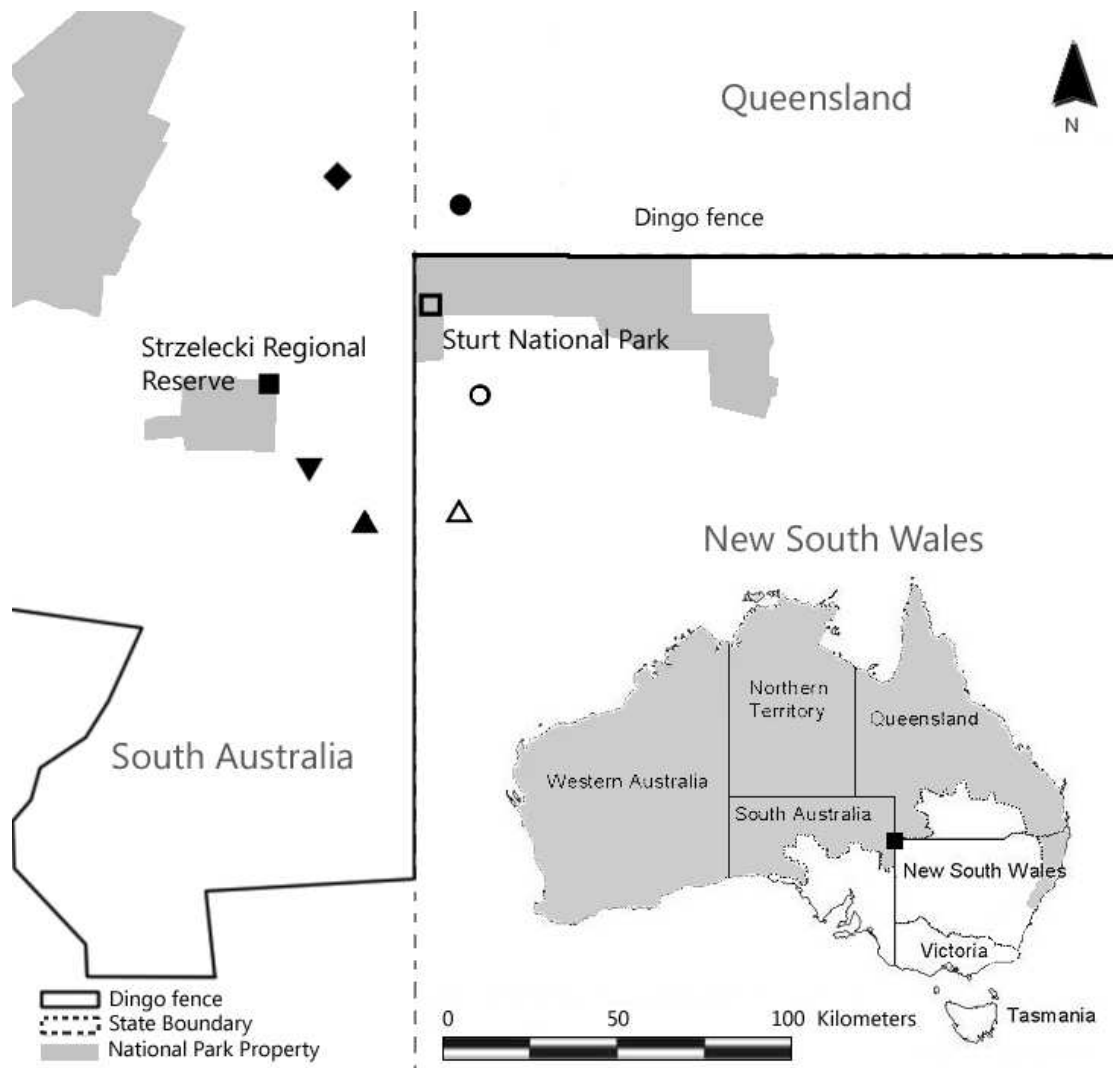


Figure 3.1 Study site locations in the Strzelecki Desert, Australia, including 4 additional sites. A number of the sites actively controlled dingoes through baiting and shooting (hollow symbols), the remaining sites dingoes were either not controlled or only incidentally controlled (solid symbols).

3.3.2 Trapping

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Animals were live captured across the 8 sites, using 58 trapping grids, each covering 0.01 km² and consisting of 9 pitfall traps in lines of three spaced 20 m apart (Figure 3.1, Figure 3.2). The grids were located a minimum 1 km apart. The pitfalls were placed running parallel to the dunes, so that the centre row of pitfalls ran along the crest and the other two were on either side of the dune. Pitfall traps consisted of a length of PVC pipe (16 cm diameter, 60 cm deep) buried flush with the ground, with a 10 m length of fly screen fence positioned over the pipe. Fly screen was also placed at the bottom of the pitfall tube to allow drainage and prevent animals for digging out the bottom. Trapping was conducted as a separate experiment to the chapter 2 study, on two occasions, one in October/November 2014 and the second in February/March 2015. Over three consecutive nights at each site, a total of 354 trap nights were conducted. The traps were removed at the end of each trapping session.



Figure 3.2 Trapping grid consisting of row of pitfall and Elliot traps.

3.3.3 Predator activity

An index of the activity of predator species (*Canis dingo*, *Vulpes vulpes*, *Felis catus*, and *Varanus gouldii*) was obtained from individual tracks sets that did not intersect on each grid and the adjacent road using a 150 m x 1 m belt transect (Olsson et al. 2005, Read and Scoleri 2014). The belt transects were located so that they ran along the dune crest from the road through the trapping grid and each transect was swept clean after the tracks were recorded each day.

3.3.4 Vegetation surveys

Vegetation cover was sampled using a step-point method, at each point the vegetation cover was classified as either bare, grass, forb, litter or shrub (Landsberg 2003, Letnic et al. 2013). On each grid, at each trapping session, three 100 m transects were sampled at 1 m intervals, giving 300 points per grid. The transects were conducted longitudinally along the dunes and were situated so that the sampling occurred at the top, middle and base on one side of the dunes.

3.3.5 Statistical analyses

Reptile abundances have been averaged for each 'grid' (individual dunes). The number of captures per grid was used as an index of relative abundance and reptiles were marked with a non-permanent mark and recaptures within the same survey were excluded. Captures are expressed as the number of captures/100 trap nights. *Lucasium damaeum* and *Lucasium stenodactylum* were pooled as *Lucasium spp.* as it is difficult to distinguish between these two species in the field. *V. gouldii* activity was used as a surrogate measure of abundance (Bolton and Moseby 2004, Olsson et al. 2005, Read and Scoleri 2014).

3.3.5.1 Distance-based Redundancy Analysis (dbRDA)

Distance-based redundancy analysis was used to investigate spatial variation in the lizard assemblages, using a Bray-Curtis similarity matrix from square-root-transformed species-abundance data (Anderson et al. 2008). Key species were identified, according to abundances that were strongly correlated with predator activity and habitat structure when analysed using the Spearman rank correlation coefficients. Species with a Spearman rank correlation greater than 0.5 were classified as significant, as they are an indication of a strong relationship (Clarke and Warwick 2005). The analysis of the community structure of the lizards was conducted using Primer 6 (Clarke and Warwick 2005).

3.3.5.2 Generalized Structural Equation Modelling (GSEM)

GSEM, like classical Structural Equation Models (SEM), can be used to investigate direct and indirect interactions in multilevelled systems through the use of multiple regressions. The models are based upon *a priori* knowledge and justifiable biotic interactions. Unlike classical SEM, GSEM has the flexibility to allow for count data and variables that are not normally distributed. Estimates using this model were produced from variables which fitted either negative binomial or Poisson distributions. The initial model was constructed using the mean values for each grid (e.g. dingo activity, fox activity, cat activity, *V. gouldii* activity, *E. phantasmus* abundance, *Lucasium spp.* abundance, bare ground cover, shrub

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cover, leaf litter cover, forb cover and grass cover; n=58). The model was then simplified using a backwards, stepwise, elimination process whereby pathways which were not significant were removed from the model until only significant relationships remained (Colman et al. 2014). Standardised path coefficients were calculated using the relative range method and deviances were calculated for the model (Grace et al. 2012). Relationships between lizard abundances, predator activities and habitat structure were investigated using GSEM from STATA14 (StataCorp 2007).

3.3.5.3 Model

justification

A priori knowledge was used to hypothesise the relationship pathways between variables and included the following hypothesised pathways (Figure 3.6a). Lizard species which were included in the model were those identified by the dbRDA analysis, and their relationships with predator and habitat variables were derived from the Spearman rank coefficients (Figure 3.4, Figure 3.5). Dingo activity was hypothesised to negatively affect fox activity through direct predation or competitive segregation (Paltridge 2002, Letnic and Koch 2010, Letnic et al. 2012, Moseby et al. 2012). Cat activity should again be negatively affected by dingo/fox activity due to direct predation or competitive segregation by the larger predators (Catling 1988, Dickman 1996, Paltridge 2002, Letnic et al. 2009b, Moseby et al. 2012). *V. gouldii* abundances are hypothesised to be negatively affected by dingo/fox/cat activity, as *V. gouldii* is a known prey of all three predators (Catling 1988, Paltridge 2002, Olsson et al. 2005, Read and Scoleri 2014). *V. gouldii* was hypothesised to be negatively affected by

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shrub cover as this would reduce the available insolation and to be positively correlated with bare ground, as it is positively correlated with it in the region (Figure 3.5).

E. phantasmus abundance was predicted to be negatively associated with fox/cat activity (Figure 3.4) as these exotic mesopredators frequently prey on reptiles including *E. phantasmus* (Catling 1988, Read and Bowen 2001). I predict that *E. phantasmus* abundance is negatively associated by grass and shrub cover and positively by bare ground; as the grass and shrubs stabilise the ground, impeding the movement of the sand swimming skink (Figure 3.5)(Letnic et al. 2004, Pastro et al. 2013).

It was predicted that fox, cat and *V. gouldii* activity would negatively affect the abundances of the *Lucasium* geckoes, *M. greyii* and *L. labialis*; as they prey upon smaller lizard species (Shine 1986, Catling 1988, Cogger 2014, Read and Scoleri 2014). *E. phantasmus* was also hypothesised to negatively affect *Lucasium spp.*, *M. greyii* and *L. labialis*, as *Eremiascincus spp.* are predators of small lizards; while the majority of their diet is insects, when available they will take small vertebrates, including small skinks, geckoes, and even small mammals (Henle 1989, James and Losos 1991, Pianka 2011). *Lucasium spp.* and *M. greyii* abundances were hypothesised to be positively affected by shrub cover, forb cover and grass cover while being negatively affect by bare ground, as the vegetative cover reduces the risk of predation and stabilises the ground, thus assisting in the formation of burrows (Mayhew 1963, Burkholder and Walker 1973, Cogger 2014).

3.4 Results

3.4.1 Patterns of abundances, predators and habitat structure

The dbRDA identified a negative correlation between dingo and mesopredator activity (Figure 3.4). Sites with high dingo activity were also characterised by having high goanna activity and *E. phantasmus* abundance; as well as a few *Lucasium spp.*, and *M. greyii* (Figure 3.3, Figure 3.4). The ordination plot (Figure 3.3) revealed that the sites Omicron and Bollard's Lagoon, situated to the north of the dingo fence, had lizard assemblages and levels of dingo activity intermediate between those located to the east and west of the dingo fence. The sites with low dingo abundance were characterised by high fox and cat activity, high abundances of *Lucasium spp.* and *M. greyii*, as well as low goanna activity and *E. phantasmus* abundance (Figure 3.4, Table 3.1).

Habitat structure at each site did not display a distinct east-west pattern across the dingo fence (Figure 3.5), and did not appear to be related to geographic location, predator abundance or grazing practices. Winnathee was unique in having the greatest shrub cover. Tilcha and Coonanna were characterised by higher forb cover and bare ground, while Strzelecki Regional Reserve was characterised by more bare ground. Omicron, Lake Stewart, Bollard's Lagoon and Sturt National Park all had relatively high leaf litter coverage (Figure 3.5).

Table 3.1 Species captures per site.

Species	TIL (outside)	SRR (outside)	OMI (outside)	COO (outside)	BOL (outside)	WIN (inside)	SNP (inside)	LAK (inside)
<i>Varanus gouldii</i>	1	0	0	4	0	1	0	1
<i>Ctenotus leae</i>	2	4	0	0	0	0	0	0
<i>Ctenotus leonhardii</i>	0	0	1	0	0	0	0	0
<i>Ctenotus regius</i>	0	0	4	2	1	4	2	4
<i>Ctenotus schomburgkii</i>	0	0	13	11	0	9	5	7
<i>Ctenotus strauchii</i>	0	0	1	0	0	0	0	0
<i>Ctenotus taeniatus</i>	6	19	4	7	7	17	15	8
<i>Eremiascincus phantasmus</i>	22	30	5	36	28	3	0	2
<i>Lerista aericeps</i>	0	0	0	0	1	0	0	0
<i>Lerista labialis</i>	1	15	38	16	34	32	8	37
<i>Menetia greyii</i>	0	1	21	2	3	1	37	3
<i>Morethia adelaidensis</i>	0	1	0	0	0	0	0	0
<i>Tiliqua rugosa</i>	0	0	0	1	0	1	0	0
<i>Lucasium spp.</i>	1	5	4	2	7	24	13	25
<i>Diplodactylus tessellatus</i>	0	0	0	0	0	0	1	0
<i>Rhynchoedura eyrensis</i>	0	0	1	1	0	10	0	0
<i>Strophurus ciliaris</i>	0	0	0	1	0	0	0	3
<i>Nephurus levis</i>	0	6	5	7	5	8	3	3
<i>Gehyra versicolor</i>	0	0	0	0	0	2	0	1
<i>Ramphotyphlops endoterus</i>	0	0	1	1	2	1	0	0
<i>Ctenophorus nuchalis</i>	1	0	0	3	1	6	5	4
<i>Ctenophorus pictus</i>	0	2	0	5	0	0	0	0
<i>Pogona vitticeps</i>	0	0	0	0	0	1	1	2
<i>Diporiphora winneckeii</i>	0	0	0	0	1	0	0	0

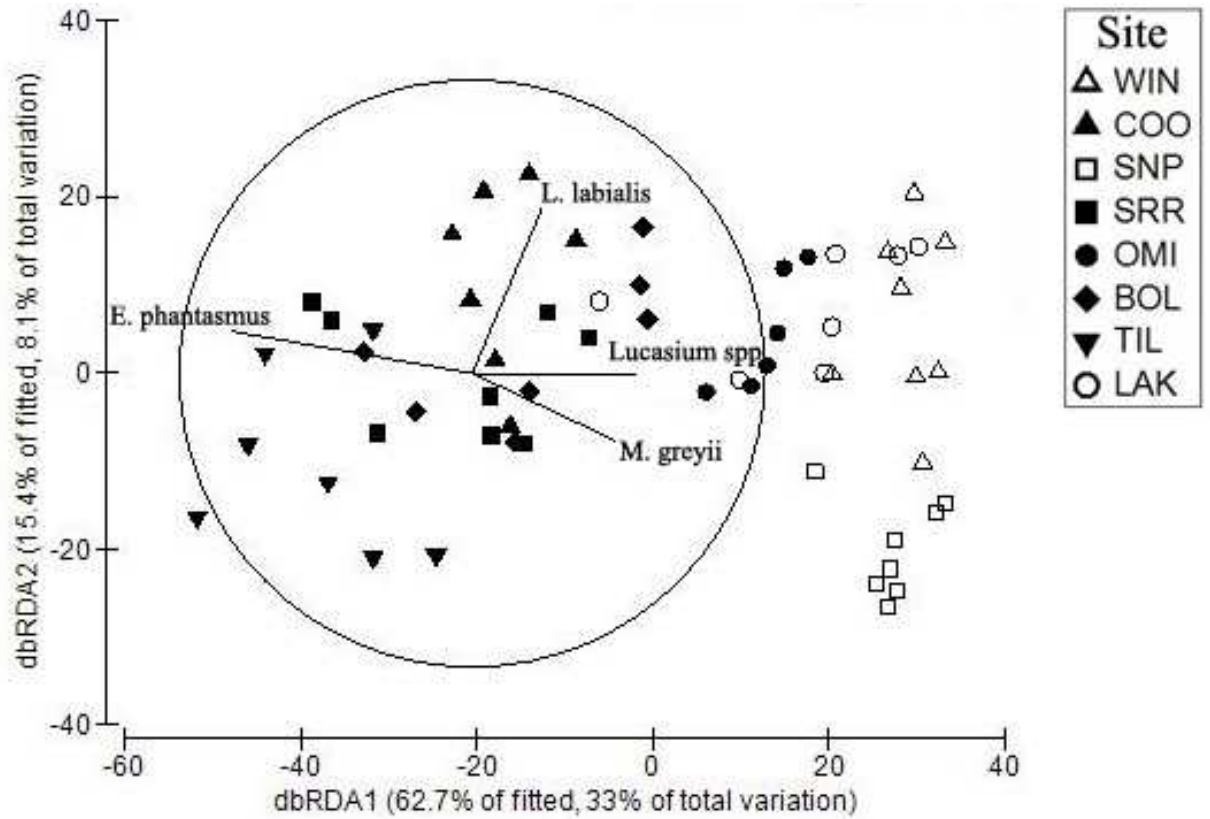


Figure 3.3 Results of the dbRDA of lizard abundances with predator activity and habitat variables. Open symbols denote sites where dingoes were rare and solid symbols indicate sites where dingoes were common. The vector overlay includes the lizard species with a Spearman's rank coefficient > 0.5 . The model is based on a zero-adjusted Bray-Curtis similarity matrix and species' abundances have been square-root transformed.

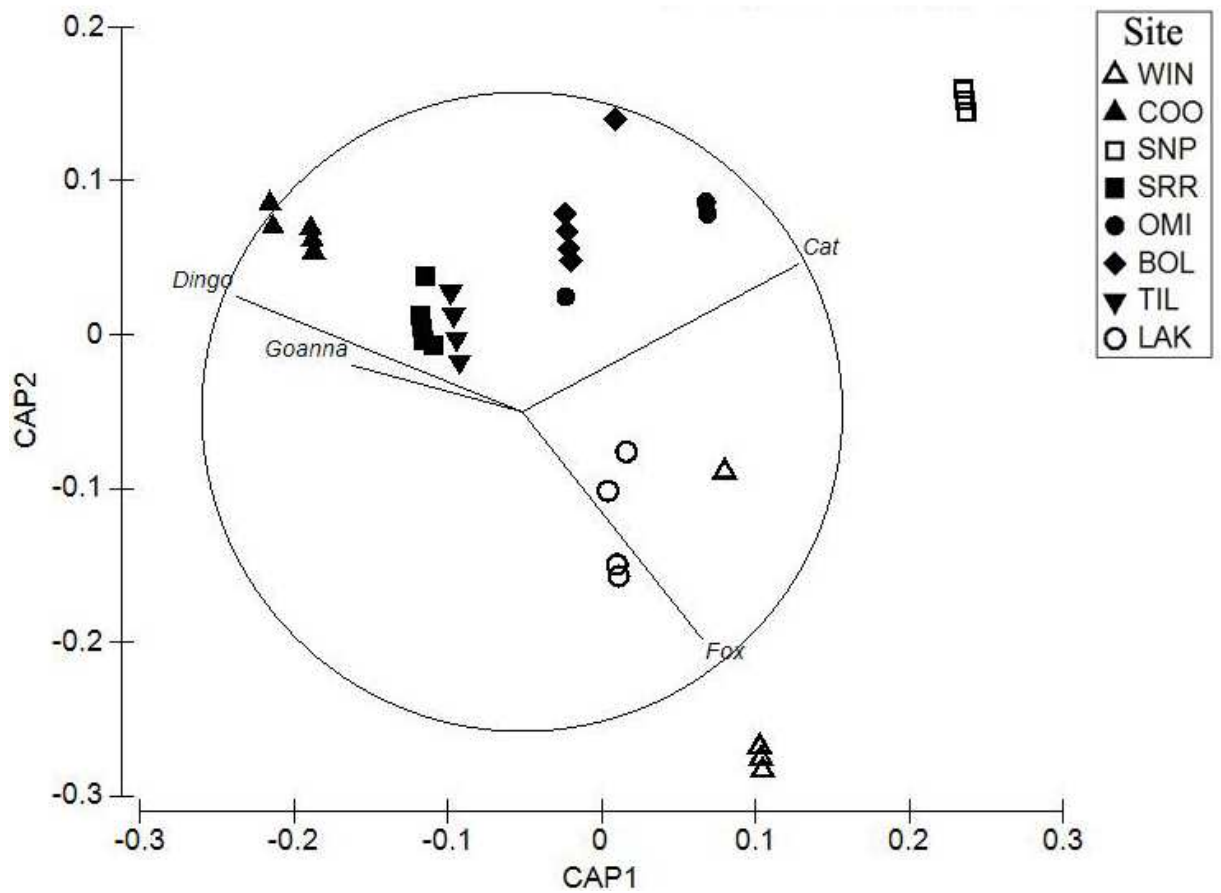


Figure 3.4 The activity of predators at each of the sites where lizard abundances were sampled. Open symbols denote sites where dingoes were rare and solid symbols indicate sites where dingoes were common. The vector overlay includes the predator at each site. The model is based on a Euclidean Distance matrix and where predator activity was normalised.

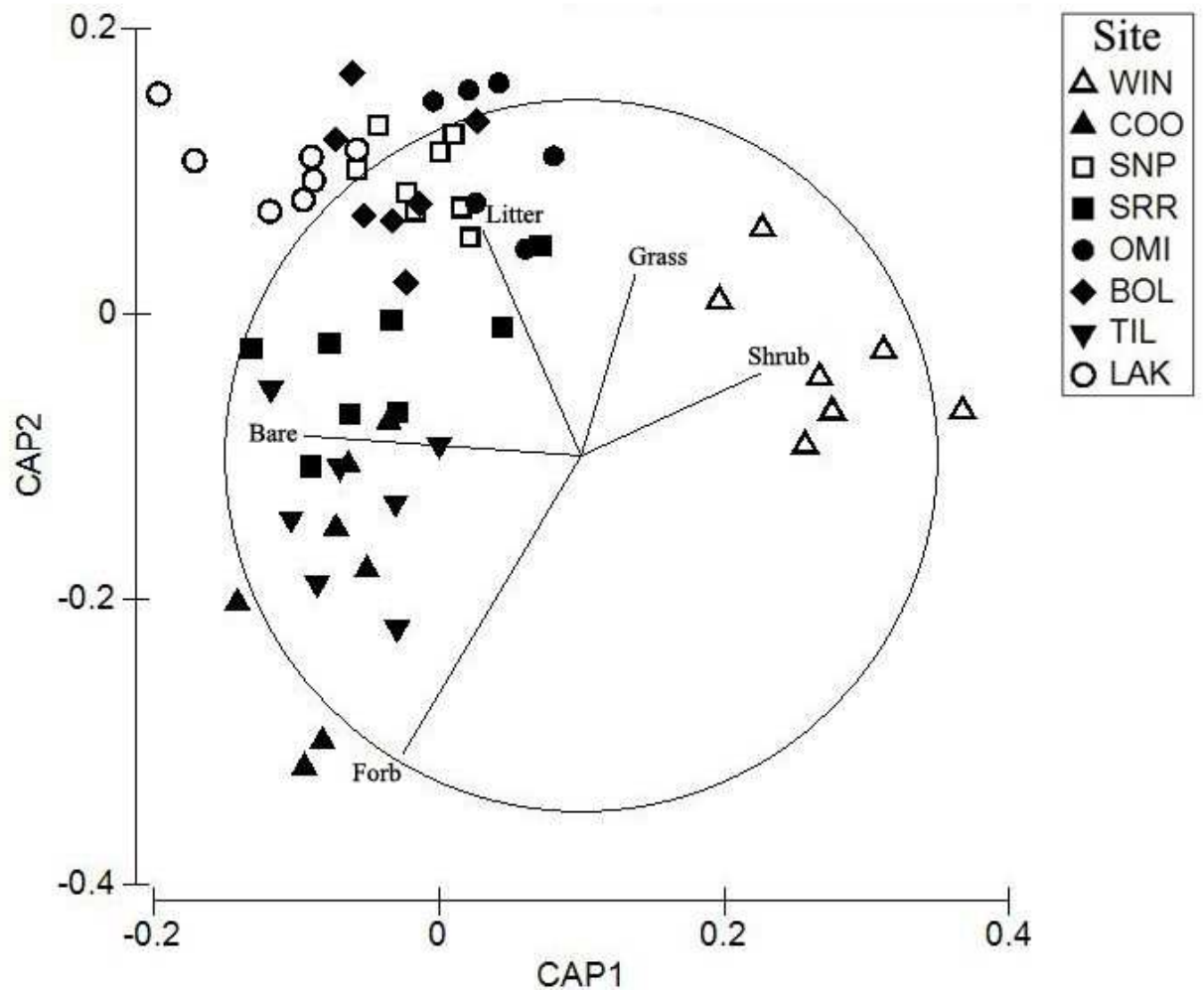


Figure 3.5 The habitat structure at each of the sites where lizard abundances were sampled. Open symbols denote sites where dingoes were rare and solid symbols indicate sites where dingoes were common. The vector overlay includes the predator at each site. The model is based on a Euclidean Distance matrix and where habitat variables were normalised.

3.4.2 Effects of predator activity and environmental factors on the abundances of small lizards

From the *a priori* model the following variables and pathways were excluded from the final GSEM model. The habitat variables; shrub cover, leaf litter and bare ground, were excluded as no significant pathways were identified from these variables. The following pathways were also excluded from the final model as they were non-significant; the pathways between *Lucasium spp.* abundance and dingo/ fox/ cat/*V. gouldii* activity/ grass/forb cover. The pathways between *E. phantasmus* and the following; dingo/cat/*V. gouldii* /grass/forb cover were also excluded. Pathways to *M. greyii* from dingo/fox/*E. phantasmus*/forb cover were excluded as well. The pathways to *L. labialis* from dingo/ fox/ cat/*V. gouldii* activity/ *E. phantasmus*/grass cover pathways were excluded from the final model as they were non-significant. The pathway between cat and *M. greyii* was excluded as it is more biologically appropriate that *V. gouldii* has a negative association, than cats have a positive association. The pathway between dingo and *V. gouldii* activity was also removed from the model in favour of keeping the fox activity and *V. gouldii* pathway as it was more biologically appropriate that foxes would have a negative impact on goannas, than a dingo would have a positive impact. Similarly the pathway from cat activity to *V. gouldii* activity was also excluded. All other variables were included in the final GSEM explaining lizard abundance (Figure 3.6b).

Dingo activity had a negative interaction with fox and cat activity, which is consistent with the *a priori* hypothesis and previous literature. Also in accordance with the *a priori* model,

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fox activity was negatively correlated with *V. gouldii* activity and *E. phantasmus* abundance. *E. phantasmus* was negatively associated with *Lucasium spp.* abundance, which was in line with the *a priori* model. Thus, according to the GSEM, dingoes conceivably have a negative, indirect effect on *Lucasium spp.* mediated through fox activity and *E. phantasmus*. Therefore, fox presence has a positive indirect effect on *Lucasium spp.*, facilitated via a reduction in the abundance of *E. phantasmus*. *V. gouldii* had weak negative correlation with *M. greyii*. Thus, the presence of dingoes has a weak indirect negative effect on *M. greyii* abundance, perhaps enabled through the suppression of the fox and release of *V. gouldii*. However, *M. greyii* abundance was more strongly correlated with grass cover. The GSEM indicated that *Lerista labialis* abundance was inhibited by forb cover and there were no significant interactions with any predators.

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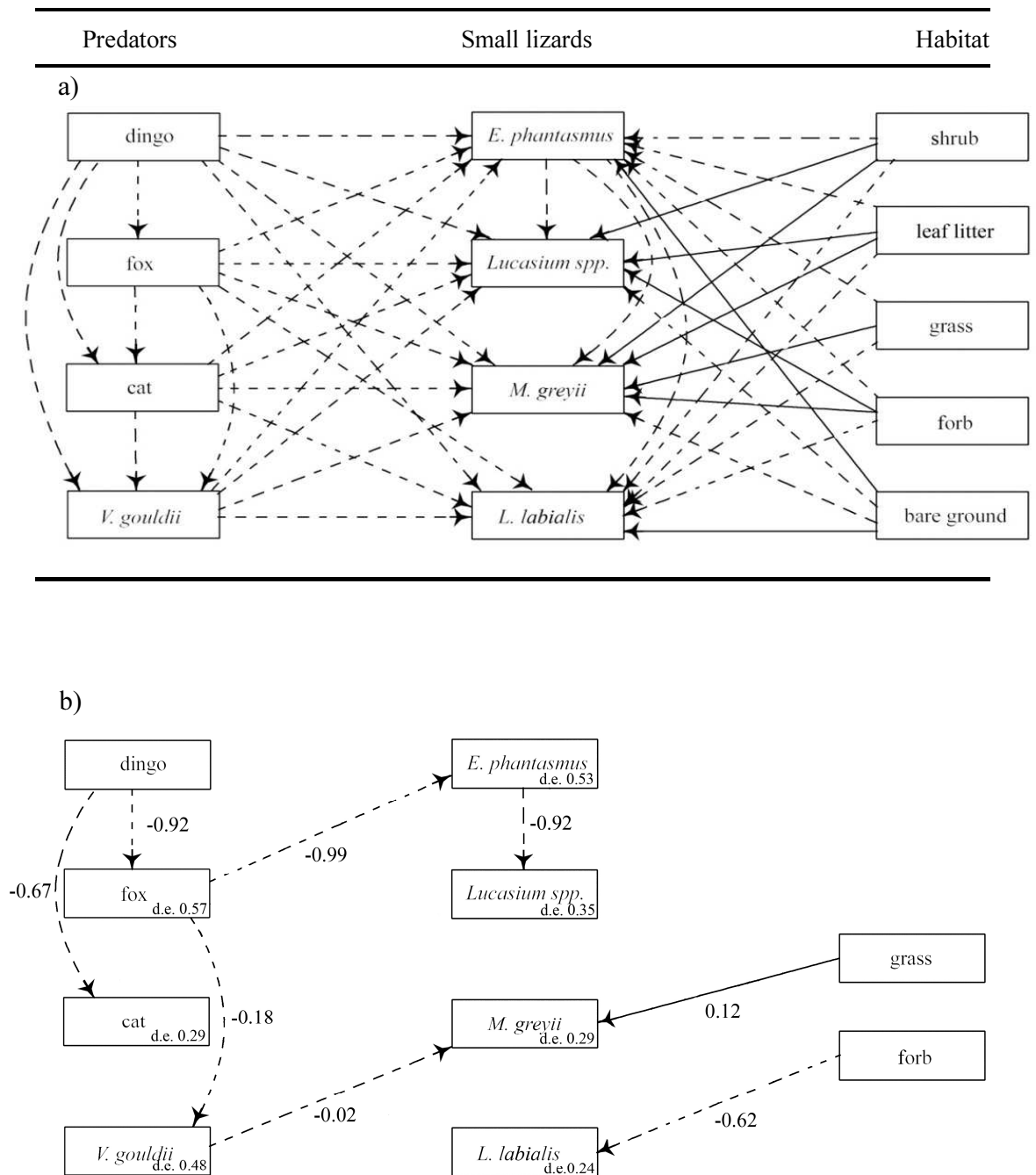


Figure 3.6 a) *A priori* generalised structural equation model describing arid lizard responses to the predatory structure and habitat availability. b) Most parsimonious generalised structural equation model showing direct and indirect relationship pathways

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influencing arid lizard abundance. Broken lines represent negative relationship pathways, and solid lines represent positive relationship pathways. Standardised path coefficients are displayed alongside the arrows and deviance explained (d.e) is displayed for all endogenous variables

3.5 Discussion

The results provide support for the hypothesis that dingo removal has complex cascading effects on lizard assemblages. The GSEM suggests two possible 4-link cascade pathways via which the removal of a top predator alters the lizard assemblages in the Strzelecki Desert. One of the identified cascades suggests dingo control can affect the small terrestrial geckoes, *Lucasium spp.* by releasing foxes from the suppression of dingoes, which results in increased abundances of foxes. The GSEM suggests that the increased abundance of foxes suppresses the abundances of *E. phantasmus* and in turn, the suppression of *E. phantasmus* by foxes releases *Lucasium spp.* from the effects of *E. phantasmus*. Another cascade pathway suggested by the GSEM is one in which dingo control indirectly influences the abundance of *M. greyii*. The presence of dingoes suppresses the fox abundances which allows the release of *V. gouldii*. The abundance of *V. gouldii* in the areas where dingoes were common appears to suppress the populations of *M. greyii*. Below I discuss, the evidence supporting the hypothesized interaction pathways supported by the GSEM.

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The results of this study confirm the results of previous studies, that the presence of dingoes has a negative effect on foxes (Letnic et al. 2009a, Colman et al. 2014). Gut contents studies have shown that *V. gouldii* are preyed upon by foxes, cats and dingoes (Catling 1988, Read and Bowen 2001, Paltridge 2002, Cupples et al. 2011). Previous studies have shown that sand goannas have a strong negative association with foxes, suggesting that foxes are their primary predator in the ecosystem and the results of this study were consistent with these findings (Olsson et al. 2005, Moseby et al. 2009b, Sutherland et al. 2011, Read and Scoleri 2014).

The polarity and differences of the effect sizes for dingoes, cats and foxes on goannas is consistent with the differences in the predators' body-sizes, and their prey preferences (Catling 1988, Paltridge 2002, Cupples et al. 2011). Even though dingoes, foxes and cats are predators of sand goannas, the results of this study indicated a positive correlation between dingoes and goannas (Read and Bowen 2001, Paltridge 2002, Cupples et al. 2011). The positive influence of dingoes on goannas is counter-intuitive. A plausible hypothesis to explain the positive relationship between dingoes and goannas is that goannas receive a positive net benefit from the presence of dingoes, due to dingoes suppressing foxes. Although there are no studies of the effects of dingo control on goanna abundance, there are a number of studies showing the goanna populations benefit from fox control (Olsson et al. 2005, Read and Scoleri 2014). A possible explanation for this is that *V. gouldii* is a better

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fit to the prey size preference of foxes than dingoes, or it may be foxes are more capable predators of goannas than dingoes.

Eremiascincus phantasmus abundances were negatively affected by foxes in our GSEM; this is consistent with predation by foxes (Catling 1988, Read and Bowen 2001, Paltridge 2002, Cupples et al. 2011). There was no significant effect of dingoes or cats on *E. phantasmus*; this was probably due to the sand-swimmers being outside the preferred prey size of dingoes and the inability of cats to dig them up (Catling 1988, Pettigrew and Whipp 1993, Cupples et al. 2011, Letnic et al. 2012, Moseby et al. 2012, Gordon et al. 2015). The GSEM suggests there was also no significant effect of *V. gouldii* on *E. phantasmus*, the largest lizard in the ecosystem and a known predator of *Eremiascincus* sp. A plausible reason for this is the different activity times of these two species; *V. gouldii* is diurnal, while *E. phantasmus* is nocturnal, also the diurnal burrows of *E. phantasmus* may be too deep for *V. gouldii* to excavate (Shine 1986, Cogger 2014). Thus, the observation that foxes have a greater effect on *E. phantasmus* abundance than other species could be due to a number of factors, including foxes being nocturnal, focusing their activity on dune crests, preferred prey size and their habit of digging for prey (Wood 1980, Paltridge 2002, Olsson et al. 2005, Moseby et al. 2009a, Cupples et al. 2011).

The abundance of *Lucasium* geckoes was negatively associated with *E. phantasmus*, I hypothesise that this negative correlation could be driven by predation (Figure 3.6b). This hypothesis is based upon the fact that *E. phantasmus* are predators and geckoes have been found in the gut contents of *Eremiascincus* sp. (James and Losos 1991). I found that no

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significant effect of *V. gouldii* activity on the abundances of *Lucasium* geckoes in this study, although other studies have shown geckoes make up a proportion of the sand goanna's diet (Shine 1986, Olsson et al. 2005). Thus, *Lucasium* geckoes are known to be preyed upon by both *V. gouldii* and *E. phantasmus*, but in this study only *E. phantasmus* abundance negatively correlates with *Lucasium spp.* abundance. It is possible that *E. phantasmus* has a stronger effect on *Lucasium* geckoes as they are both nocturnal and therefore active at the same time, providing opportunities for predation. In contrast *V. gouldii* are diurnal and therefore have to detect and excavate the geckoes from their day time burrows (Pianka 1970, Cogger 2014). Thus, it is plausible that the *E. phantasmus* affect *Lucasium spp.* abundance due to predation as they are both active at the same time, and *E. phantasmus* are predators of geckoes and small skinks (James and Losos 1991, Cogger 2014).

In the GSEM, *Lerista labialis* abundance was not associated with any hypothesized competition or predation pathways but was negatively associated with forb cover. *L. labialis* is a principally sand swimming species and thus, it is plausible, that the forbs are impeding the sand swimmer's ability to move through the sand (Greenville and Dickman 2009). However, if this is the case, then it is unclear why they are not negatively correlated with shrub and grass cover as well. One possibility is that the grasses have shallow root systems, while forb roots run deeper, presenting a larger impediment (Schenk and Jackson 2002). Shrub root systems are larger and sparse in distribution, thus there might still be sufficient free substrate for *L. labialis* to travel through.

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Menetia greyii abundance was weakly correlated with *V. gouldii* activity and grass cover in this study. These two driving factors appear to act as opposing forces, as *M. greyii* is negatively associated with *V. gouldii* abundance, while being positively associated with grass cover. The effects of *V. gouldii* activity are very weak; however, it is conceivable that the effect is due to predation, as *V. gouldii* preys upon *M. greyii* and skinks of similar sizes (Shine 1986, Pianka 1996). *M. greyii*'s positive correlation with grass cover is consistent with the grass providing shelter from heat and predation, as well as habitat for the invertebrate prey of *M. greyii* (Cogger 2014). Thus, the abundance of *M. greyii* in the eastern deserts of Australia could be the result of a “tug-of-war” between predation and habitat-based protection from predation. However, this only explained a small amount of the variation in abundances of *M. greyii* across the study region.

The results of this study provide support for the idea that there are cascading effects from dingo control to lizards at lower trophic levels and that these effects are conceivably the result of predation, it is not possible to guarantee that predation is the mechanism for these results, as this is a mensurative experiment. Therefore, it is necessary these pathways be confirmed through manipulative experiments. These experiments could include the use of exclosures to remove particular predators from a region. Even though the study doesn't provide definite proof of these mechanisms, this study along with current literature provides a conceivable theory of the effects of dingo control on lower trophic levels.

3.6 Conclusion

In this chapter, I proposed two novel 4-link trophic cascades, stemming from the control of apex predators. The proposed 4-link cascades, dingo – fox – *E. phantasmus* – *Lucasium spp.* and dingo – fox – *V. gouldii* – *M. greyii*, provides a mechanism for dingo control to indirectly affect the assemblages of lizards in an ecosystem. Predator induced 4-link cascades have also been proposed for ecosystems around the world, including Yellowstone National Park (Hebblewhite et al. 2005, Gibb 2012, Colman et al. 2014, Ripple et al. 2014). Dingo initiated multi-link cascades have also been proposed, as affecting the abundances of small and medium sized mammals in the forests of NSW (Colman et al. 2014).

The results of this study suggest that the removal of top predators can have far-reaching and unpredictable effects on an ecosystem. Few studies have provided evidence for 3 or more link ecological cascades (Hebblewhite et al. 2005, Gibb 2012, Colman et al. 2014, Ripple et al. 2014). I suggest that this is not because multiple-link cascades are rare, but rather, because they are difficult to detect.

Chapter 3. Predator activity a driver of arid lizard populations

Chapter 4 General discussion

4.1 Objective one: Variances in lizard assemblages

In Chapter 2, my objective was to investigate the variations in lizard assemblages across the dingo fence, with varying land-use. The dingo fence provided an opportunity to study the effects of dingoes on the ecosystem due to the differing rates of dingo control either side of the fence. This management, along with the location of a national park property on either side of the fence, provides a natural experiment of dingo control in the context of tenure. This is critical, as controlled experiments involving large carnivores are logically and ethically problematic (Borer et al. 2008).

Chapter 2 showed that lizard assemblages differed in composition in regards to both dingo control and tenure, however, the effect of dingo control was stronger than that of tenure. The effect of tenure was driven by the abundance of a single species; for which no pattern was observed across the dingo fence. The differences in assemblages across the dingo fence were driven by the abundances of five species. The results suggested that the distribution of the majority of these species was a result of the habitat structure, either as a result of land use or an underlying artefact (Read 2002, Letnic et al. 2004, Cupples et al. 2011, Nimmo et al. 2012, Smith et al. 2013). However, there were a few species; including *V. gouldii* and *Lucasium spp.*, whose distributions are difficult to explain by changes in habitat alone, suggesting that the distribution of these species are possibly being effected by other factors. I hypothesised that one of these factors was predation. Previous studies of the effects of

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predation on lizards and predator abundance were consistent with the results obtained across the dingo fence in this study (Olsson et al. 2005, Read and Scoleri 2014).

A shortcoming of Chapter 2 was the lack of spatial replication, with only a single national park property and pastoral property either side of the dingo fence. The properties were also located in such a manner as to have the national parks to the north of the pastoral properties and to have the sites where dingoes are rare to the east of the sites where dingoes are common. The differences in the assemblages on the pastoral properties were impossible to attribute solely to variations in dingo management, because the design does not allow the level of dingo control and the livestock on each property to be decoupled. Along with dingo control there are number of other factors that coincide with the east west design including: habitat availability, rainfall and species' natural distributions.

The possibility that these other factors were influencing these results can be uncoupled; by increasing the spatial replication of this study and removing the east-west divide (see Chapter 3). Others experimental designs which could conclusively determine the variations in lizard assemblages with dingo abundance include long-term temporal studies, either using the removal of dingoes from a currently populated location or the reintroduction of dingoes in a different location. These temporal manipulative experiments are expensive, as well as ethically and/or practically difficult.

4.2 Objective two: Effects of dingo activity on lizard abundances

The aim of Chapter 3 was to determine if dingo activity affects the lizard assemblages in arid Australia; in order to better understand the depth and complexity of the ecological role of the dingo in arid regions, in the context of trophic cascades and mesopredator release theory. I contrasted the predator activity, habitat structure and lizard abundance in arid regions with similar habitat but with varying degrees of dingo control. To reduce the extent of the spatial confounding which constrained the interpretation of results in Chapter 2, in Chapter 3 I conducted comparisons east-west and north-south across the dingo fence. My goal was to identify the direct and indirect effects of predator activity and vegetation cover on lizard abundances, chiefly in regards to the removal of the apex predator (Estes et al. 2011, Colman et al. 2014, Ripple et al. 2014).

Chapter 3 identified four key species that correlated with predator activity and habitat structure. I used generalised structural equation modelling to investigate direct and indirect pathways between the predator activities and habitat structure. The model was based on *a priori* knowledge, allowing me to quantify the influence of dingoes, the apex predator, and of trophic cascades. My findings suggest lizard assemblages are related to both dingo control and habitat attributes in arid ecosystems.

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A short coming of Chapter 3 is that, while the results are an indication of what could be occurring in the ecosystem, they are limited in their certainty, due to the snapshot design of this spatial study (Hargrove and Pickering 1992). Therefore, future experimentation is required to confirm the findings of this study. Classical or manipulative experiments could be used to test either the entire cascade or parts thereof. It is also possible for individual pathways to be explored using exclosure designs to verify the results that I found. Through the addition or exclusion of individual species, the direct effects could be observed and enable more definitive conclusions to be drawn (Moseby et al. 2009b).

Taken together the results of Chapters 2 and 3 suggest that dingo control has unintended cascading effects on the assemblages of lizards in the arid region. These 4-link tropic cascades have far reaching effects, on a variety of lizards, including carnivorous lizards; *V. gouldii* and *E. phantasmus*, diurnal, nocturnal and fossorial lizards. These finding suggest that dingo control has deep and complex unintended effects on lower trophic levels (Glen et al. 2007, Letnic et al. 2009b, Colman et al. 2014). It is therefore important to delve deeper into the unintended effects of dingo control, as it is likely that there are other parts of the ecosystem which are currently being affected by dingo control, the knowledge of which could assist in ecological conservation. Further study into the non-lethal management of dingoes is required, so that the ecological contributions of the dingo in ecosystems can be conserved, while minimising the harm they cause to livestock (Landry et al. 2005).

4.3 Conclusion

My results on the variation of lizard assemblages, are consistent with the knowledge found in current literature, which states that the dingo fence divides two ecologically distinct universes (Caughley et al. 1980, Newsome et al. 2001, Letnic et al. 2009b, Gordon and Letnic 2015). While supporting the theory that habitat availability is the driver for some lizard species; my findings also suggest that predator activity might contribute to the distributions of a number of species (Olsson et al. 2005, Sutherland et al. 2011, Read and Scoleri 2014). Through the use of field data, my findings on the ecological role of dingoes in arid Australia, demonstrate that in the absence of dingoes; as a result of lethal control; the ecosystems shifts to an alternate state dominated by exotic mesopredators, which is consistent with previous studies (Newsome et al. 2001, Letnic et al. 2009b, Sutherland et al. 2011, Moseby et al. 2012). As found by Read (2014) and Olsson (2005), mesopredator release drive population declines of the predatory lizard *V. gouldii* and the results of this study suggest *E. phantasmus* as well. I hypothesize that the suppression of predatory lizards reduces the regulation of small skinks and terrestrial gecko populations. My results suggest that there are winners and losers when dingo control is employed, the dingo appears to have a positive influence on predatory lizards, while negatively influencing smaller skinks and terrestrial geckoes. The ramifications of my study and the proposed cascades, suggest the effects of removing a top predator are deeper and more complex than is currently understood.

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