Nest predator abundance and its relationship with regent honeyeater (*Anthochaera phrygia)* nest success

by

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Candidate's Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author’s knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Daniel Gautschi Date: 03/06/2020

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Abstract

Woodland bird populations continue to decline in south-eastern Australia. As a result of habitat loss and fragmentation woodland birds now face novel threats, including elevated rates of nest predation. Nest predation presents a damaging selective pressure for threatened species, preventing recruitment to, and recovery of, small populations. It is the leading cause of nest failure for the critically endangered regent honeyeater (*Anthochaera phrygia*), which has already experienced rapid population decline. A number of common avian and mammalian species have been observed depredating regent honeyeater nests in recent studies. I surveyed diurnal and nocturnal nest predators in key regent honeyeater breeding areas to develop an understanding of the distribution and predictors of nest predators and to examine the impact of predator abundance and species richness on regent honeyeater nest success.

I surveyed 12 species of nest predators at 246 study sites between August and November 2019. I used repeat point-count surveys for diurnal and nocturnal predators, and conducted scat surveys as an additional indicator of common brushtail possum (*Trichosurus vulpecula*) presence. Results showed that predator abundance and predator species richness were significantly higher at sites near water, with high hollow abundance and where short grass was the dominant ground cover. Predator species richness was also higher at sites with moderate (15 – 30%) canopy cover. Both predator abundance and species richness were slightly elevated at regent honeyeater nest sites, although these results were non-significant.

I used data from 115 regent honeyeater nests from the last five years to examine the impact of predator abundance and predator species richness on nest survival. Predator abundance and predator species richness were positively related to nest success, indicating that high levels of predator abundance were not associated with regent honeyeater nest failures. While unexpected, these results suggest that other factors may be causing variation in nest predation rates, including regent honeyeater anti-predator strategies, resource availability and / or differing rates of learned predatory behaviour across sites. Despite a positive correlation between regent honeyeater nest survival and nest predators, nest success was low (31.6%). Further research is required to identify the most significant drivers of nest predation rates, in order to better understand variances in regent honeyeater nest success and inform effective manage of the species.

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List of acronyms and abbreviations

AIC	Akaike information criterion
AICc	Second order Akaike information criterion
AWS	Automatic weather station
DSR	Daily nest Survival Rate
EPBC Act	Environment Protection and Biodiversity Conservation Act 1999
GAM	Generalised additive model
GLM	Generalised linear model
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IUCN	International Union of Conservation of Nature
NRHMP	National Regent Honeyeater Monitoring Program
NRHRT	National Regent Honeyeater Recovery Team
NSW	New South Wales
OBPSR	Occupancy Based Predator Species Richness
PA	Predator Abundance
SE	Standard error
PSR	Predator Species Richness

Glossary and Terms

Aggregation	A group of separate but spatially proximate nests of the same species
Anthropogenic	Caused by human activity
Arboreal	Living in trees
Avian	Relating to birds
Biodiversity	Variety of plant and animal life
Call-playback	Playing recorded bird calls to invoke a reaction
Captive-bred	Born in captivity
Colour-banded	Previously fitted with a coloured band for identification purposes
Conspecific	A member of the same species
Detectability	The probability that an individual is detected
Diurnal	Day-time
Ecosystem	A community of organisms and the environment in which they occur
Habitat fragmentation	The break-up of a large area of habitat into smaller, disconnected fragments
Interspecific	Occurring between different species
Intraspecific	Occurring between members of a single species
Mammalian	Relating to mammals
Mesopredator	A mid-trophic level predator
Nectarivorous	Predominantly feeding on nectar
Nocturnal	Night-time
Parsimonious	Used to describe a model that has the least assumptions and variables (lowest complexity), but the greatest explanatory power
Point-count	A tally of all birds visually or aurally detected at a fixed location
Predator community	All predators, regardless of species
Scat	Animal faecal matter
Species richness	The number of different species in a specified area
Trophic level	A hierarchical level within an ecosystem, comprising organisms which have a similar role in the food-chain

1 Introduction

Biodiversity is crucial to ecosystem functioning, facilitating ecosystem processes and promoting ecosystem stability (Cardinale et al., 2012). It is the result of millions of years of evolutionary processes (Mace et al., 2012), leaving ecosystems exposed to serious disruption or even collapse should species be removed (Cardinale et al., 2012). At least 680 vertebrate species have gone extinct since the 16th century, and approximately one million plant and animal species are now threatened globally (Díaz et al., 2020). Australia is no exception to this trend, with 54 species of fauna listed as extinct and 454 endangered or vulnerable (Commonwealth of Australia, 2020). Birds make up the largest proportion of threatened fauna in Australia (Commonwealth of Australia, 2020).

Australian woodland birds are among the most at-risk, as a large proportion of their natural habitat has been converted to pasture since European Settlement (Ford et al., 2001). With dwindling populations and reduced habitat, woodland birds now rely upon small habitat remnants, resulting in the rise of novel threats (Ford et al., 2001). One such threat is nest predation, which is understood to have increased as a result of habitat fragmentation (Fulton, 2018). Nest predation occurs at a crucial time in avian life history, hindering the proliferation and recovery of threatened species (Ibáñez-Álamo et al., 2015). Nest predation has gained increasing focus among avian ecologists, however its drivers and the role of nest predators themselves are still not completely understood (Ibáñez-Álamo et al., 2015; Fulton, 2018).

1.1 Under threat - the regent honeyeater

The regent honeyeater (*Anthochaera phrygia*) is classified as critically endangered under *International Union for Conservation of Nature* (IUCN) criteria, having undergone a population decline of more than 80% since the 18th century (Commonwealth of Australia, 2016; BirdLife International, 2018). A steep decline of the population in the last 50 years has been driven by ongoing habitat loss and fragmentation (Kvistad et al., 2015). As a result of the specialised breeding habitat of the species (Geering and French, 1998), few breeding areas remain, predominantly occurring in heavily fragmented woodlands (Franklin et al., 1989). Primary management objectives include the regeneration and protection of woodland habitats and an ongoing captive-breeding program (Commonwealth of Australia, 2016). However, habitat regeneration will take time - possibly more than the species can afford, and upon release captive-bred birds are limited by the same threats facing the wild population (Taylor et al., 2018). As a result, research and management of the indirect effects of habitat loss is needed alongside habitat restoration (Mortelliti et al., 2016). Currently, poor nesting success is inhibiting the proliferation and recovery of the species (Crates et al., 2019b), partly attributable to an already depleted population (Ford et al., 1993; Crates et al., 2017a) and high rates of nest predation (Taylor et al., 2018; Crates et al., 2019b).

Nest predation is the main known cause of nest failure for regent honeyeaters (Crates et al., 2019b), making it an urgent area for further research. The impact of the predator community on regent honeyeater nest success has not yet been explored, despite a number of species being observed depredating regent honeyeater nests and the significant negative impact of nest predation on regent honeyeater recruitment (Taylor et al., 2018; Crates et al., 2019b).

1.2 Study aims, overview and hypotheses

1.2.1 Study aims

This thesis seeks to develop an understanding of the distribution of nest predators and its impact on nest success in key breeding areas of the regent honeyeater. The ultimate goal is to better inform predator management techniques to reduce the rate of regent honeyeater nest predation and facilitate recovery of the wild population. I undertook a landscape-scale study of nest predators to address two primary research aims:

1) Develop an understanding of the distribution of nest predators in a key regent honeyeater breeding region.
2) Examine the impact of predator abundance and predator species richness on regent honeyeater nest success.

1.2.2 Study overview and hypotheses

I collected nest predator data at 246 study sites within the Capertee and Goulburn River Valleys (New South Wales (NSW), Australia). I selected sites that represented potential regent honeyeater breeding habitat, while ensuring variation in landscape features. I conducted repeat diurnal and nocturnal point-count predator surveys, a scat survey and recorded habitat variables at each site. I used the data to model predator distribution and examine relationships between habitat features and predator abundance / species richness. I also used the data to generate predator predictions at historic regent honeyeater nest sites (2015 – 2018) to examine the relationship between nest success and predator abundance / species richness. I developed three main hypotheses:

1) Certain habitat features will predict predator abundance at a species and community level.
2) Predator abundance / species richness will be higher near regent honeyeater nest sites and at sites with habitat features favoured for regent honeyeater nesting.
3) Nest success will be lower at sites with higher predator abundance / species richness.

1.3 Thesis structure

Chapter 1 provides an overview of the research, including aims and hypotheses.

Chapter 2 comprises a review of relevant literature, with a focus on biodiversity, contemporary nest predation research and the regent honeyeater.

Chapter 3 explains the methods employed for data collection and statistical analysis.

Chapter 4 presents the results of the study.

Chapter 5 examines the key findings and outlines implications for future research and management.

Chapter 6 provides closing remarks on the thesis.

2 Literature Review

2.1 Biodiversity and conservation

Biodiversity can be viewed at three different levels: intraspecific genetic diversity, species richness and ecosystem diversity (Mace et al., 2012). Of these, species richness is often considered the basic unit of biodiversity, despite both genetic and ecosystem diversity being of great significance (Mace et al., 2012). Numerous studies have highlighted the fundamental importance of biodiversity to ecosystem functioning and stability (Mooney et al., 2009; Cardinale et al., 2012; Hooper et al., 2012; Mace et al., 2012; Loreau and de Mazancourt, 2013). Biodiversity is linked to improved efficiency in ecosystem processes, including the capture of vital resources and the production of biomass (Cardinale et al., 2012). This pattern is consistent across organisms of different trophic levels and between ecosystems, suggesting an important relationship between ecosystem processes and the make-up of the organic community (Cardinale et al., 2012). While the loss of a relatively abundant species logically suggests a greater impact, even the loss of rare species can affect these ecosystem processes (Gamfeldt et al., 2008; Hooper et al., 2012). In addition to facilitating ecological processes, biodiversity also creates ecosystem stability. Stable ecosystems are those in which ecosystem-level measures, such as overall species richness, remain stable through time (Ives and Carpenter, 2007). Stability is the result of evolutionary processes, and the removal of species may render ecosystems vulnerable to collapse (Cardinale et al., 2012; Loreau and de Mazancourt, 2013). To encourage the resilience of ecosystems to future change, maintaining and managing biodiversity is extremely important (Mooney et al., 2009).

With approximately one million plant and animal species threatened by extinction (IPBES 2019), biodiversity is declining faster than any time in human history (Díaz et al., 2020). Habitat loss and modification, harvesting of species, pollution, climate change and invasive species are the primary drivers of biodiversity loss, all of which have continued to accelerate environmental change over the last 50 years (Díaz et al., 2020). Human-driven habitat loss and degradation pose the greatest threats to mammalian and avian biodiversity (Tilman et al., 2017). Agricultural land clearing alone threatens approximately 80% of mammal and bird species globally (Tilman et al., 2017). Habitat-specialist birds have experienced particularly significant population declines in recent years due to anthropogenic change (Butchart et al., 2010).

In Australia the list of threatened, endangered and critically endangered species has continued to expand, primarily due to habitat loss, invasive species and climate change (Commonwealth of Australia, 2017). *The Environment Protection and Biodiversity Conservation (EPBC) Act List of Threatened Fauna* now contains 203 vulnerable species, 162 endangered species and 89 critically endangered species (Commonwealth of Australia, 2020). Within these three categories there are 134 bird species. Many Australian woodland birds have experienced substantial population declines due to ongoing habitat loss and further deterioration of remaining habitat; particularly in riparian zones with highly fertile soils (Ford, 2011; Fulton, 2018). Indirect effects of habitat fragmentation further exacerbate the impact of habitat loss on woodland birds. Many woodland species are not adapted to disperse long distances between the remaining habitat fragments, restricting their spread and proliferation (Ford et al., 2009; Bennett and Watson, 2011). Furthermore, aggressive competitor species such as the noisy miner (*Manorina melanocephala*) and mesopredators such as butcherbirds (*Cracticus spp.*) thrive in fragmented landscapes, creating competition for resources and increasing the risk of nest predation (Fulton, 2018). While a number of factors, such as exposure to the elements and disease, can lead to nest failures, nest predation and resource accessibility are considered to have the largest impact on the success of nests (Ford, 2011; Fulton, 2018).

2.2 Nest predation

Nest predation is one of the most significant selective pressures for avian species (Martin, 1993; Ibáñez-Álamo et al., 2015), and the leading cause of nest failure for Australian woodland birds (Fulton, 2019). Nest predation is particularly harmful to threatened species as it occurs at a critical stage of the avian life-cycle, limiting the ability of birds to reproduce and bolster the numbers of future generations (Fulton, 2018). Studies suggest that nest predation rates in Australia have increased since the 1970s, with the proliferation of key predator species believed to be the main cause (Remeš et al., 2012). The introduction of non-native species can increase nest predator abundance and subsequent nest predation rates. For example, predation of swift parrot *(Lathamus discolour)* nests has drastically increased following the introduction of the sugar glider (*Petaurus breviceps*) to Tasmania (Heinsohn et al., 2015). Overabundance of native nest predators, such as the pied currawong (*Strepera graculina*), can also increase the risk of nest predation to woodland bird populations (Ford et al., 2001). Mesopredator release (the proliferation of middle trophic level predators (Soulé et al., 1988)) has been facilitated by the removal of large predators and human induced habitat modification, which enables species to expand their range and abundance due to increased habitat suitability (Andren, 1992; Fulton, 2018). An example of this phenomenon from south-eastern Australia is the expansion in the range of currawongs (*Strepera* spp.), butcherbirds (*Cracticus* spp.) and corvids (*Corvus* spp.) due to the fragmentation of woodland habitats and loss of large predator species (Fulton et al., 2008; Fulton, 2018).

Contemporary nest predation research has focused on identifying the causes of interspecific variation in nest predation rates. Species size has been linked to predation risk, with smaller-bodied species experiencing higher rates of nest predation (Remeš et al., 2012). Differences in nest characteristics, such as nest type, nest height and nest concealment, impact predation rates by altering the nest's accessibility and detectability to predators (Colombelli-Négrel and

Kleindorfer, 2009; Remeš et al., 2012; Hollander et al., 2015; Fulton, 2018). Anti-predator strategies and parental activity may also impact nest predation rates by deterring predators or alerting them to the location of the nest (Martin et al., 2000; Ibáñez-Álamo et al., 2015; Fulton, 2018). Despite extensive research on the topic, much of the interspecific variation in nest predation remains unexplained (Remeš et al., 2012).

Researchers have also tried to explain intraspecific variation in nest predation rates. Substantial interest surrounds the impact of habitat fragmentation on nest predation, commonly referred to as the edge-effect (Wilcove, 1985; Paton, 1994; Lahti, 2001; Boulton and Clarke, 2003; Batáry and Báldi, 2004). The edge-effect was first examined by Gates and Gysel (1978), and describes how nest predation rates are higher at nests that are closer to the edge of a habitat patch. While evidence of an edge-effect has been found across multiple continents (Paton, 1994), studies of Australian species have revealed mixed results (Fulton, 2018). This may reflect the different interactions between predator species and fragmented habitats (Cox et al., 2012). Nest predation rates can be influenced by parental behaviour, both in the form of behaviours that deter predators (Ibáñez-Álamo et al., 2015) and activity that may attract predators to nests (Martin et al., 2000). Parental behaviour has also been found to change in response to perceived predatory threat (Fontaine and Martin, 2006a; Fontaine and Martin, 2006b; Zanette et al., 2011; Hollander et al., 2015; Ibánez-Alamo and Soler, 2017). A study of 12 North American species found an increase in incubation rates when predation risk was high, and an increase in time off the nest when predation risk was low (Fontaine and Martin, 2006b). Many studies have shown a positive correlation between predator abundance and nest predation (De Santo and Willson, 2001; Boulton et al., 2008; Macdonald and Bolton, 2008) and an increase in nest success is often experienced when predators are excluded or suppressed (Section 2.2.1). However, some studies have found that the relationship between nest predation and predator abundance is not so clear. Red-backed shrike (*Lanius collurio*) nests in Belgium were found to be more successful in areas of higher predator abundance. This was subsequently explained by increased nest concealment in areas of high predator abundance (Hollander et al., 2015). In addition, a study of the predatory behaviour of American red squirrels (*Tamiasciurus hudsonicus)* showed that nest predation was a learned behaviour (only utilised by some individuals), suggesting nest predation risk is not determined by nest predator abundance, but rather by the presence of a repeat offender (Pelech et al., 2010). Many predictors of nest predation have been proposed and explored, however the dynamics of nest predation are not yet well-understood and require further research (Ibáñez-Álamo et al., 2015; Fulton, 2018).

2.2.1 Predator exclusion and suppression

Predator exclusion and suppression are implemented to manage overabundant predator species and involve the use of various measures, including fences (Malpas et al., 2013), trunk guards and nest boxes (Berris et al., 2018), nest cages (Debus, 2006) and the removal of predators through baiting and culling (Fulton and Ford, 2001; Baines et al., 2004; Armstrong et al., 2006). Largely, predator exclusion and suppression studies have shown a short-term increase in nest success following the reduction of predator abundance.

Predator exclusion and suppression have been widely used in Australia, with the aim of reducing nest predation rates and supporting threatened species. Berris et al. (2018) reported significant increases in nest success, from 23% to 31 - 68%, among the endangered Kangaroo Island glossy black-cockatoo *(Calyptorhynchus lathami halmaturinus)* population, when trunk guards where implemented to protect nests from predation by common brushtail possums (*Trichosurus vulpecula*). Debus (2006) found that nest cages significantly increased the nesting success of scarlet robins (*Petroica boodang*) and eastern yellow robins (*Eopsaltria australis*) from 20% to 86%. Some studies have been unable to find a clear relationship between nest success and predator exclusion and suppression. Fulton and Ford (2001) used artificial nests in eucalypt woodlands to explore the impact of pied currawong culling on nest predation rates. The time to failure of nests increased significantly following the cull, however no noticeable difference in nest success was experienced. Debus (2006) recorded a 19% increase in the nesting success of robins following a similar cull. Discrepancies between these findings may result from the use of artificial nests in Fulton and Ford's 2001 study, which has come under scrutiny due to findings that suggest artificial nests are not representative of natural processes (Major and Kendal, 1996; Zanette, 2002; Thompson III and Burhans, 2004). Artificial nests may result in increased predation rates as no parental defence is available and scent lines may enhance a nest's detectability to predators (Zanette, 2002; Fulton, 2018).

Another possible explanation for the lack of a clear relationship between culls and nest success is compensatory nest predation, a phenomenon in which another predator species fills the role of nest predator when one predator species is removed (Rayner et al., 2007; Oppel et al., 2014). Beggs et al. (2019a) observed a 28% reduction in noisy miner abundance following culls in NSW, however no reduction in nest predation was found. It was found that the noisy miner only accounted for 18% of predation events, and five other predator species were identified, suggesting a possible compensatory predation phenomenon.

2.2.2 Nest predators in Australian woodlands

By analysing 177 Australian studies, Fulton (2019) identified 94 nest predator species; predominantly birds. The top five predator species by number of prey species were the pied currawong, the square-tailed kite (*Lophoictinia isura),* the tiger snake (*Notechis scutatus*), the laughing kookaburra (*Dacelo novaeguineae*) and the grey shrike-thrush (*Colluricincla harmonica*).

Beggs et al. (2019) used artificial nests to study compensatory nest predation, identifying the Australian magpie as the key predator. The noisy miner, white-winged chough *(Corcorax melanorhamphos)*, pied butcherbird *(Cracticus nigrogularis)*, Australian raven *(Corvus coronoides)* and grey butcherbird *(Cracticus torquatus)* were also identified as regular nest predators (Beggs et al., 2019a).

Guppy et al. (2017) recorded predator identity of woodland birds through the use of motion-activated cameras across 10 hectares over a three-year period. This study looked at the nests of 26 species and identified 16 nest predators (Guppy et al., 2017). The study found that the fan-tailed cuckoo (*Cacomantis flabelliformis*) and eastern whipbird (*Psophodes olivaceus)* were the key nest predators. Among the 16 nest predators identified were the pied currawong, laughing kookaburra and sugar glider.

The role of the sugar glider as a generalist nest predator has been confirmed, with a number of studies observing the predation of woodland bird nests by sugar gliders (Guppy et al., 2014; Guppy et al., 2017). The sugar glider is the primary nest predator of swift parrots in Tasmania, where it was introduced from mainland-Australia (Stojanovic et al., 2014; Heinsohn et al., 2015). Despite being considered largely insectivorous, the squirrel glider (*Petaurus norfolcensis*) has also been identified as an opportunistic nest predator, taking both eggs and adult birds on the nest (Winter, 1966; Holland, 2001).

The predatory role of the common brushtail possum in New Zealand is well documented, however the species' role in an Australian context is yet to be examined to the same extent (Fulton, 2017). Its role as a nest predator in Australia is still evident, having been identified as the key predator of the arboreal nests of the endangered Kangaroo Island glossy black-cockatoo (Garnett et al., 1999; Berris et al., 2018). A recent artificial ground-nest study also observed common brushtail possum predatory behaviour in Western Australia (Fulton, 2017).

2.3 The regent honeyeater

The critically endangered regent honeyeater is a highly mobile, nectarivorous passerine, endemic to the woodlands of south-eastern Australia (Commonwealth of Australia, 2016). In recent years the species' range has contracted, with only three known breeding regions remaining: the Greater Blue Mountains (NSW), Bundarra-Barraba (NSW) and the Chiltern region of Victoria (Commonwealth of Australia, 2016). Despite being identified and described by George Shaw in 1794, surprisingly little was known about the bird's life history until the late 1980s (Shaw, 1794; Franklin et al., 1989). And now, with approximately 100 breeding pairs left to be studied (Kvistad et al., 2015), the species is in need of urgent conservation attention. Increasingly, efforts have been directed towards the management of the remaining regent honeyeater population. However, highly mobile species are heavily impacted by habitat loss, and their reliance on multiple regions at different times makes their conservation a complex undertaking (Runge et al., 2014).

The decline of the regent honeyeater population is attributable to a number of factors, and compounded by the ecology and breeding biology of the species. Key threats include habitat loss and fragmentation, habitat degradation, tree dieback and stress on nectar-producing trees due to drought and climate change (Commonwealth of Australia, 2016). The regent honeyeater has a predisposition to nest in aggregations and display aggressive behaviour (Ford et al., 1993), which may exclude larger-bodied competitors and therefore increase the likelihood of successfully fledging young. This behaviour could also provide protection from nest predators if multiple nesting pairs engage in predator mobbing. Due to the already depleted population size, the species is unable to establish aggregations, amplifying the impact of competition and nest predation (Crates et al., 2017a). Furthermore, habitat modification has facilitated the proliferation of aggressive competitor species such as the noisy miner (Commonwealth of Australia, 2016) and predator species such as the pied currawong (*Strepera graculina*) (Fulton and Ford, 2001), adding stress to the regent honeyeater population. The significance and contemporary nature of these threats contributes to the critically endangered status of the species and the need for further research and management.

2.3.1 Contemporary management and research

The *National Recovery Plan for the Regent Honeyeater* was updated in 2016 and aims to halt population decline, promote a viable breeding population and improve the quality of regent honeyeater habitat (Commonwealth of Australia, 2016). As part of this effort, the *National Regent Honeyeater Recovery Team* (NRHRT) was established to coordinate the recovery efforts and includes members from State Governments, BirdLife Australia, Taronga Zoo, Community Groups and Universities (Commonwealth of Australia, 2016). As part of NRHRT efforts, yearly monitoring of key breeding regions is conducted to examine nest success, breeding behaviour and distribution of the species. In addition, Taronga Zoo heads a captive-breeding program to raise birds for release, with the aim of increasing the size of the wild population (Commonwealth of Australia, 2016).

In the late 1980s and 1990s regent honeyeater research was largely focused on the species' ecology and behaviour, breeding biology and nesting success (Franklin et al., 1989; Ford et al., 1993; Geering and French, 1998; Oliver, 1998; Oliver et al., 1998). While population decline and range contraction was already documented (Geering and French, 1998), research predominantly aimed to improve understanding of the species and establish a foundation of knowledge. In more recent years, focus has shifted towards the distribution of the species and habitat selection, establishing habitat characteristics associated with regent honeyeater occupancy (Oliver and Lollback, 2010; Crates et al., 2017b) and refining monitoring techniques in order to target better direct management of the remaining population (Crates et al., 2017b). The population structure of the species has also come to attention, with studies finding consistently low genetic separation throughout the species' range (Kvistad et al., 2015; Crates et al., 2019a). The shift in focus to distribution and genetic structure can be seen as a response to the increasing concern regarding the species' small population size. Another contemporary focus is the unique interspecific song-learning displayed by the species (Roderick, 2014; Veerman, 2016; Crates, 2019), which may be caused by extremely low population densities (Crates, 2019).

Only recently has the contribution of low reproductive success to population decline been considered in more depth. Two studies have revealed lower rates of nesting success in the current population of regent honeyeaters (Taylor et al., 2018; Crates et al., 2019b). Between 1994 and 1997 in the Bundarra-Burraba region, nesting success was 38% (Oliver et al., 1998), similar to the 38.7% success rate found in the Capertee Valley in 1995 (Geering and French, 1998). These success rates fell into the normal range for Australian passerines (Ford, 1989). In contrast, Crates et al. (2019) found nesting success to range from 9 - 34%. Of nests where cause of failure was discernible, 89% failed due to nest predation. Significant variance in daily survival rate of nests between study regions was noted (Crates et al., 2019b). In addition, nest monitoring cameras identified six species depredating regent honeyeater nests: the pied currawong, noisy miner, pied butcherbird, laughing kookaburra, sugar glider and common brushtail possum. A study of captive-bred regent honeyeater nests in the Chiltern region of Victoria found less than 20% of nests were successful and that 50% of monitored nests failed due to nest predation (Taylor et al., 2018). This study also utilised nest-monitoring cameras, observing predation events by the sugar glider, squirrel glider, Australian magpie and house sparrow (*Passer domesticus)*. While a natural phenomenon, the impact of nest predation on the regent honeyeater has likely been amplified due to habitat loss and fragmentation (Fulton, 2018) and an already depleted breeding population (Crates et al., 2017a).

2.4 Research gaps

Nest predation research plays a crucial role in informing the conservation management of avian species (Fulton, 2019). A great deal is still to be understood regarding the role and identity of nest predators themselves (Ibáñez-Álamo et al., 2015; Fulton, 2018). Taylor et al. (2018) showed the impact of nest predation on the regent honeyeater through video-monitoring of nests, however conclusions were based on just 10 nesting attempts in a population of captive-bred birds. The small sample size and the fact that the anti-predatory strategies of captive-bred birds may differ from wild birds (Griffin et al., 2000; Carrete and Tella, 2015) calls for further study into regent honeyeater nest predation. Furthermore, the study only identified nest predators, making no attempt to explain high predation rates.

Predator abundance studies tend to focus on only a single predator species, rather than the entire predator community, despite recent research showing the impact of compensatory nest predation (Rayner et al., 2007; Oppel et al., 2014; Beggs et al., 2019a). A number of diurnal and nocturnal species have been observed depredating regent honeyeater nests, and many have been identified as regular nest predators in south-eastern Australian woodlands. The role of nest predators must be understood in order to conserve threatened species (Ibáñez-Álamo et al., 2015; Fulton, 2018). Without improved nest success rates among wild birds, it is unlikely that the species can be brought back from the brink of extinction.

2.5 Research questions

I developed three research questions based on the research gaps identified during a review of the literature.

There is little understanding of which habitat features predict the abundance of regent honeyeater nest predator species and how they are distributed at a landscape-scale, leading to the first research question:

1. **Which habitat features predict localised predator abundance / species richness?**

It is unclear whether the high rates of nest predation and nest failure in the regent honeyeater population are explained by concentrated predator activity around nest sites, or whether the predator activity is uniform throughout the breeding region. In addition it remains unclear why the regent honeyeater nest survival is lower than many other honeyeater species, leading to the second research question:

2. **Do regent honeyeaters nest in areas of high predator abundance / species richness?**

Finally, there is a lack of evidence of how community-level predator abundance and predator species richness affect the success of regent honeyeater nests, leading to the third research question:

3. **Can spatial variation in regent honeyeater nest survival be explained by spatial variation in predator abundance / species richness?**

3 Methods

3.1 Study areas

The study areas encompass 80% of known wild regent honeyeater breeding activity since 2015 (Crates et al., 2019b and 2019 field observations) (Figure 3).

Capertee Valley: The Capertee Valley study area covers approximately 460 km$_2$ of fragmented woodland 50km north of Lithgow, NSW (Figure 1). The Capertee Valley is one of the key breeding areas for the regent honeyeater, and is dominated by box-gum (*Eucalyptus spp.*) woodland on low lying slopes and river-oak (*Casuarina cunninghamiana*) gallery forest along the Capertee River (Geering and French, 1998). The valley floor is approximately 300 - 400 m in elevation (Geering and French, 1998). Average minimum and maximum temperatures range from 3 - 17°C in August to 12 - 27°C in November and mean annual rainfall is 644.5 mm (Bureau of Meteorology, 2020a). Within the Capertee Valley, I defined five regions (Figure 2), based on geographically distinct regent honeyeater nesting areas identified by Crates et al. (2019b).

Goulburn River: The Goulburn River study area covers 7 km$_2$ of largely cleared river flats within the Goulburn River National Park, NSW (Figure 1) (Crates et al., 2018). The area is dominated by box-gum woodland and river-oak gallery forest and is approximately 300 m in elevation. The area is also an important regent honeyeater breeding area, with colour-banded regent honeyeaters known to move between the Goulburn River and the Capertee Valley (Crates et al., 2019b). Average minimum and maximum temperatures range from 3 - 18°C in August to 13 - 28°C in November and mean annual rainfall is 600 mm (Bureau of Meteorology, 2020b). I considered all sites in the Goulburn River to be part of the one discrete region due to their proximity to each other (Figure 2).

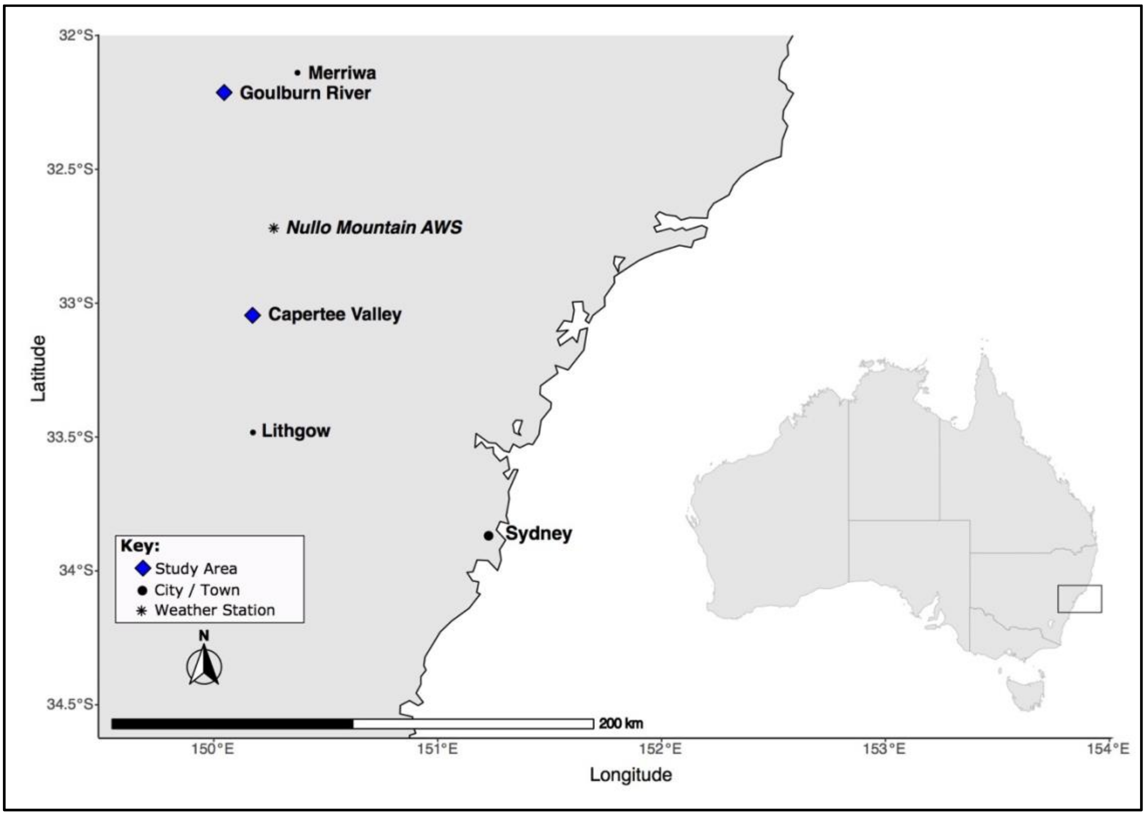

Figure 1: Map showing the broader location of the study areas.

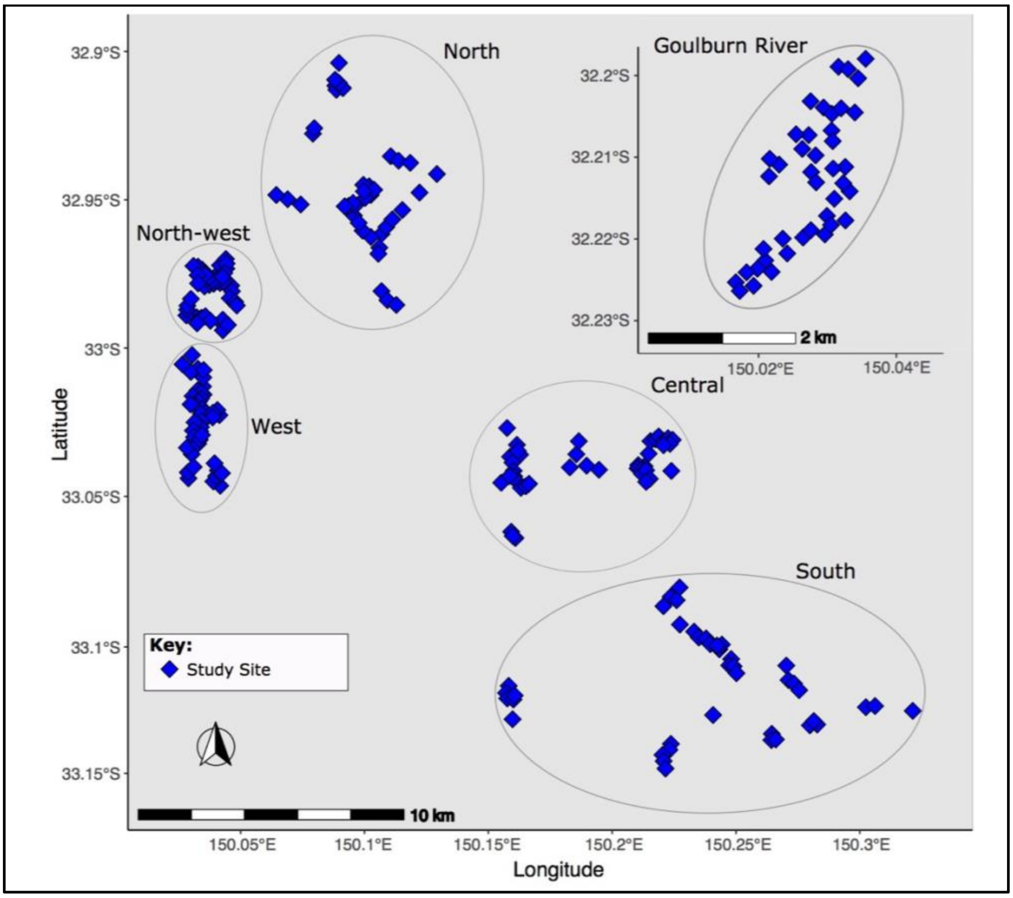

Figure 2: Map of study regions and study sites (n = 246). The Goulburn River Map is inset within the larger Capertee Valley Map.

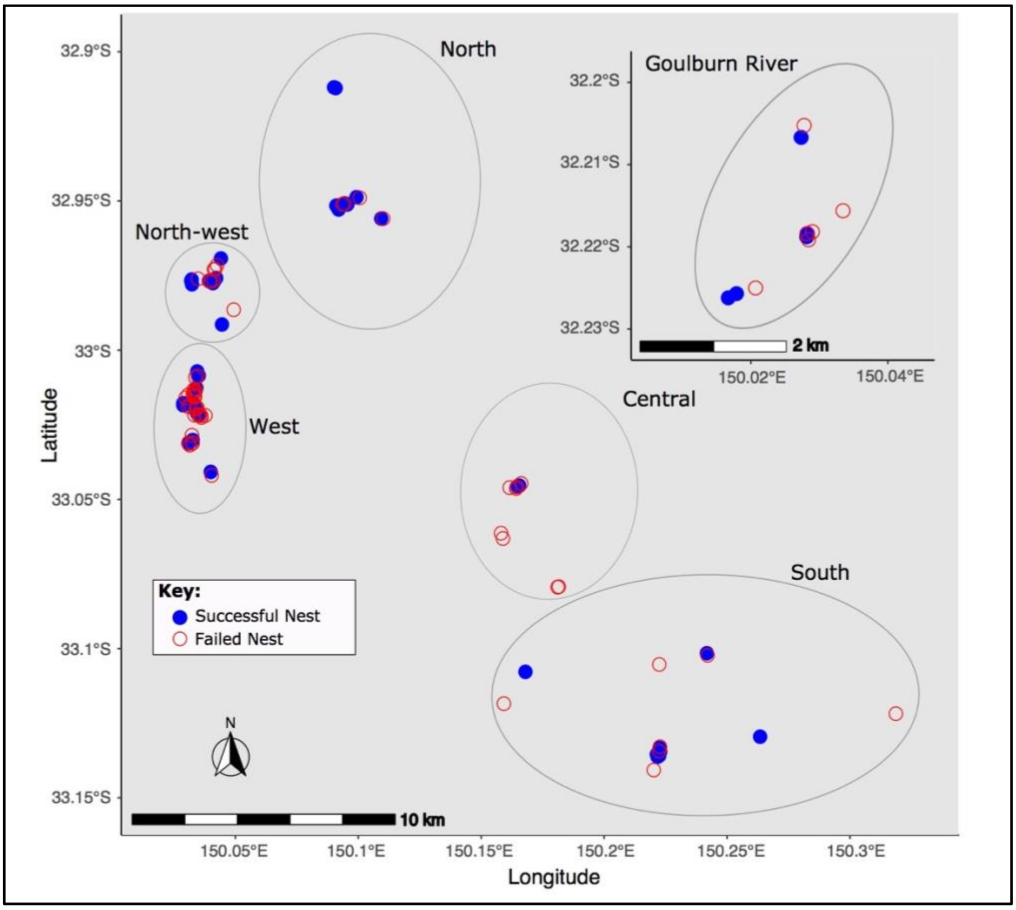

Figure 3: Regent honeyeater nests (n = 115) within the study regions between 2015 and 2019. The Goulburn River Map is inset within the larger Capertee Valley Map.

3.2 Survey protocol

I defined a study site as a 50 m radius surrounding a pre-determined survey point. In total, I selected 246 sites with 40 - 43 sites per region. Some sites in the Capertee Valley (n = 126) were existing sites from the *National Regent Honeyeater Monitoring Program* (NRHMP), and I added 79 new sites to increase sampling stratification across habitats and locations. In the Goulburn River study area I selected a subset of sites (n = 41) used for a multi-season noisy miner study (Crates et al., 2018). Study sites were located on National Park, public, crown and private land. Further details of study sites are available in Appendix 1.

To maximise spatial coverage whilst maintaining detectability of the entire predator community I conducted three diurnal and two nocturnal surveys at each site (MacKenzie et al., 2017). I also conducted a survey for animal scats at each site as an additional indicator of common brushtail possum presence (Wayne et al., 2005b). To capture predator distribution during the regent honeyeater breeding season, I conducted surveys over a three-month period between mid-August and mid-November 2019 (Crates et al., 2019b). Where possible, I included two diurnal visits conducted as part of the NRHMP surveys, which used the same survey protocol. Due to the

2019 Gosper's Mountain Bushfire, I was unable to undertake a third diurnal survey at 17 sites, nocturnal surveys at 19 sites and scat surveys at 12 sites.

I sampled 12 nest predator species (nine diurnal and three nocturnal) for the purpose of the study, due to their observed predatory behaviour (see Section 2.2.2) and occurrence within the broader study region. The 12 predator species were: Australian magpie, Australian raven, common brushtail possum (henceforth referred to as possum), grey butcherbird, grey shrike-thrush, laughing kookaburra, noisy miner, pied butcherbird, pied currawong, squirrel glider, sugar glider and white-winged chough. I combined sugar glider and squirrel glider as 'Glider spp.', because rapid identification to species level was not always possible in the field at night.

I utilised a five-minute point-count for diurnal surveys, following Crates et al. (2017b). I recorded the maximum count of each predator species detected visually or aurally within 50 m of the site centroid. I considered bird species detected flying below canopy level to be occupying sites. For the infrequent cases in which I detected three or more individuals of a species on a site (2% of observations), I recorded these count data as 3+ to produce ordinal data with a fair spread across the four abundance levels. I also recorded Date, Time, Visit Number, Blossom Abundance, Wind Speed and Temperature during each diurnal visit (Table 1).

I used a six-minute point-count for nocturnal surveys, which involved three complementary methods: spotlighting - a standard detection method for arboreal marsupials (Wayne et al., 2005b), thermal imaging (Cilulko et al., 2013) and southern boobook (*Ninox boobook*) call playback to increase sugar glider detectability (Allen et al., 2018). The first five minutes of the survey required two observers: one spotlighting using a 600 lumen headlamp, and the other operating a thermal imaging camera (*InfRec Thermo Gear G100*). I operated the thermal camera for all nocturnal surveys, and a total of five observers operated the spotlight. After the initial five minutes, I broadcast six seconds of southern boobook call (from *Morcombe's Birds of Australia App*) over a portable Bluetooth speaker (*JBL Clip 3*) and listened for sugar glider responses for the remainder of the final minute of the survey. I recorded juvenile possums if seen unattached to the mother, as I considered this an indicator of their ability to act as an independent predator. Additional visit-level covariates I recorded at night were Moon Phase and Spotlighter Identity (Table 1).

For scat surveys, I adapted the *Spot Assessment Technique* used for koala (*Phascolarctos cinereus*) detection (Phillips and Callaghan, 2011). I searched for possum scat within 1 m of the base of the five most suitable trees within sites, based on diameter at breast height, visible hollows and / or food source presence (McElhinny et al., 2006). I terminated the survey when I found possum scat or after I had searched all five trees without detecting scat. I used scat only to infer presence or absence of possums, as scat-based abundance estimates rely upon multiple factors beyond the scope of my study (Ellis et al., 2013).

3.2.1 Covariates

Habitat Covariates: I recorded all static habitat covariates prior to the first diurnal predator survey (Table 1). I recorded Blossom Abundance at all predator surveys and used these observations to determine an overall blossom score.

Detectability Covariates: I recorded covariates that were likely to affect detectability during each diurnal and nocturnal predator survey (Table 1). For diurnal surveys (n = 235) conducted as part of the NRHMP (Capertee Valley only) I determined Temperature and Wind Speed from half-hourly dry-bulb temperature and wind speed / direction from Nullo Mountain (Bureau of Meteorology, 2020c), which is located 20 - 45 km from all Capertee Valley study sites (Figure 1). I compared wind speed estimates and the Bureau of Meteorology data to validate the Wind Speed ranges used.

Table 1: Habitat and detection covariates recorded in surveys of regent honeyeater nest predators in the Capertee and Goulburn River Valleys.

Level	Covariate	Description	Justification
Habitat Covariates	*Vegetation Community*	Dominant vegetation community, grouped to separate vegetation based on value to nesting regent honeyeaters. Four level factor: *Eucalyptus melliodora, E. blakelyi, E. camaldulensis, E. sideroxylon and Angophora floribunda* (Yellow-box / mugga ironbark), *E. albens* (White-box), *Casuarina cunninghamiana* (River-oak), Other *(e.g. E. crebra, E. punctata)* (Other)	Vegetation communities support different avian assemblages (Major et al., 2001). Regent honeyeaters prefer river-oak and yellow-box / mugga ironbark vegetation communities for breeding. Favoured to a lesser extent is white-box, while "other" is least preferred by regent honeyeaters for breeding (Crates et al., 2019b).
	Water Proximity	Linear distance from the centre of site to water source based on conditions at the time of assessment. Three level factor: On site (0), 50 - 200 metres (1), >200 metres (2)	Riparian habitats support a greater range of avian species in higher abundance, in part due to water availability (Palmer and Bennett, 2006). Regent honeyeaters have a strong positive association with water (Crates et al., 2017b).
	Nest Proximity	Linear distance from the centre of site to nearest known regent honeyeater nest, based on nest data from Crates et al. (2019) and nest monitoring during the 2019 season. Distances measured using *Google Earth*. Three level factor: On site (0), 50 - 200 metres (1), >200 metres (2)	Used to address research question 2; *Do regent honeyeaters nest in areas of high predator abundance / species richness?* The core territory areas of mammalian predators are unlikely to exceed a 200m radius (Quin, 1995; Ball et al., 2005).
	Blossom Abundance	Maximum blossom abundance level across repeat surveys. Three level factor: None (0), Mild (1), Heavy (2)	Nectar is a key resource for both birds and arboreal mammals in eucalypt forests (McElhinny et al., 2006).

Level	Covariate	Description	Justification
	Mistletoe Abundance	Number of mistletoe clumps on site. Three level factor: None (0), 1 - 10 clumps (1), >10 clumps (2)	Mistletoe is a keystone species for biodiversity and some nest predator species may rely upon mistletoe to supplement their diet (Watson, 2001; Watson and Herring, 2012).
	Hollow Abundance	Number of tree hollows on site assessed through ground-based estimation. Three level factor: None (0), 1 - 3 hollows (1), >3 hollows (2)	Hollows provide nesting locations for possum and glider species (Gibbons and Lindenmayer, 2002; McElhinny et al., 2006).
	Woody Debris Abundance	Abundance of woody debris on site. Three level factor: Low (0), Medium (1), High (2)	Woody debris support mammalian and avian biodiversity (Mac Nally et al., 2001; Lindenmayer et al., 2002).
	Canopy Cover	Percentage of canopy cover on site, visually estimated. Three level factor: 0 - 15% (0), 15 - 30% (1), >30% (2)	Habitat modification and fragmentation is associated with increased mesopredator abundance in Australian woodlands and high abundance of noisy miners (Clarke and Oldland, 2007; Fulton, 2018).
	Shrub Cover	Percentage of shrub cover on site. Three level factor: 0 - 15% (0), 15 - 30% (1), >30% (2)	Understorey vegetation has been found to impact noisy miner populations (Major et al., 2001; Lindenmayer et al., 2010; Montague-Drake et al., 2011).
	Ground Cover	Dominant ground cover on site. Three level factor: Bare / leaf litter (0), Short grass (1), Long grass / low shrub (2)	Ground cover type may influence the abundance and occupancy of a number of potential predators (Manzer and Hannon, 2005; Martin et al., 2006).
	Spatial location	Wgs84 latitude / longitude, modelled as a smoothed bivariate term. *s(Lat,Long)*.	Necessary to account for spatial autocorrelation between sites (Legendre, 1993).
Detection Covariates	*Visit Number*	Visit number. Diurnal (1 - 3), Nocturnal (1 - 2)	May impact detectability due to change in activity levels (e.g. vocalisation), or improvement in surveyor observations through time.
	Time of day	Period of the day / night in which survey took place. Diurnal three level factor: Before 10am (0), 10am to 4pm (1), after 4pm (2) Nocturnal two level factor: Within 2 hours of sunset (0), >2 hours after sunset (1)	Avian vocalisation varies with time of day (Brown and Handford, 2003), and survey start time may impact possum detection (How et al., 2004).
	Wind Speed	Estimated wind speed at time of survey. Surveys did not take place if wind was above a moderate speed. Three level factor: None (0), Light (1), Moderate (2)	Wind speed may impact the aural detection of birds and sugar gliders (Allen et al., 2018) and may disguise movement.

Level	Covariate	Description	Justification
	Temperature	Approximate temperature at time of survey. Nocturnal categories chosen due to observed impact on thermal imaging camera's operating ability. Three level factor: Diurnal: <10°C (0), 10 - 20°C (1), >20°C (2) Nocturnal: <15°C (0), 15 - 20°C (1), >20°C (2)	Temperature may impact vocalisation in avian species (Thomas, 1999) and possum detection (Wayne et al., 2005a). In addition, ambient temperature may impact the operating ability of the thermal imaging camera.
	Moon Phase	Moon phase observed at time of nocturnal survey. Four level factor: None (0), Small Crescent (1), Large Crescent (2), Full (3)	Moon phase may impact possum detectability (Wayne et al., 2005a).
	Spotlighter Identity	Identity of the spotlighter aiding the thermal camera operator during the surveys. Five-level factor	Ability of spotlighters may vary (Wayne et al., 2005a)

3.3 Statistical analysis

Statistical analysis involved four complementary stages: Occupancy Modelling, Development of Aggregate Predator Measures, Spatial Modelling and Nest Survival Modelling (Figure 4).

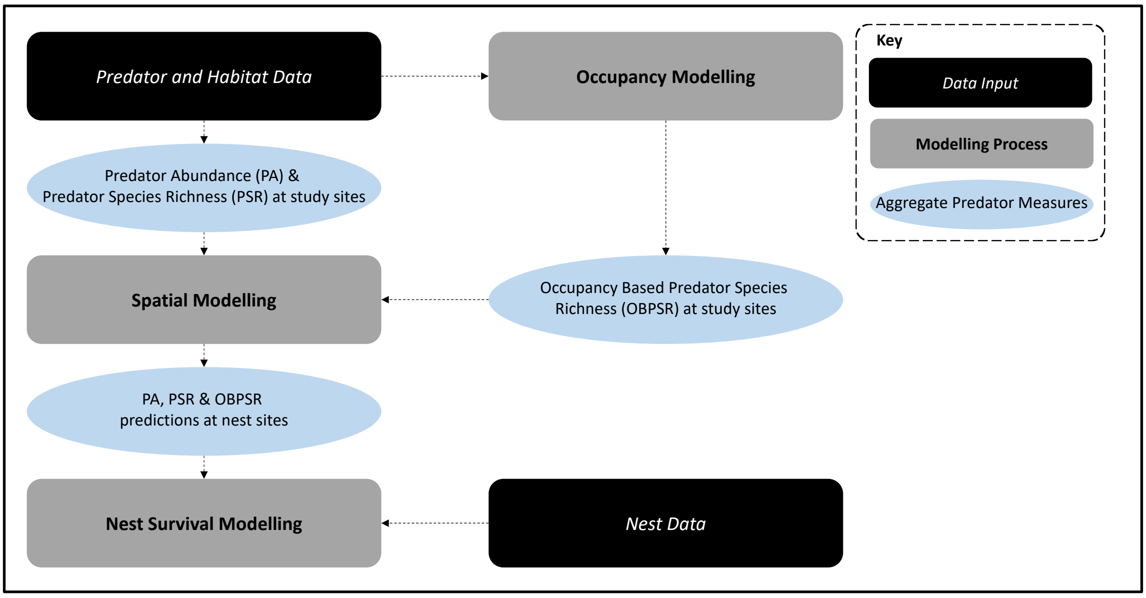

Figure 4: Workflow diagram showing the linkage between each stage of the statistical analysis.

3.3.1 Occupancy Modelling

I created single-season, single-species occupancy models to answer research question 1: *Which habitat features predict localised predator abundance / species richness?* I used occupancy models to account for the imperfect detection of predators in ecological surveys (MacKenzie et al., 2002; MacKenzie et al., 2005). I used the statistical program, R v3.6.2 (R Core Team, 2020) and the package *unmarked* v0.13.1 (Fiske and Chandler, 2011) to build the models. For each species I first created a null model and a set of models which included single habitat or single detectability covariates, with predator species presence / absence as the binomial response variable. I used Akaike Information Criteria (AIC) to estimate the strength of univariate models relative to each other, with the lowest AIC indicating the most parsimonious model (Burnham and Anderson, 2002). I then included covariates, identified via the single-term models that were more parsimonious (smaller AIC) than the null model, in a saturated model for each predator species. This allowed me to test a smaller set of variables, avoiding over-fitting of the data. I used *MuMIn* v1.43.15 (Bartoń, 2019) to test all combinations of covariates within the saturated model. I ranked the models by AICc, an AIC measure adjusted for model complexity (Burnham et al., 2011).

3.3.2 Aggregate Predator Measures

I generated aggregate predator measures for each study site in order to examine different predator measures throughout the rest of the statistical analysis. I used predator abundance and predator species richness measures in order to test which had a greater impact on nest success. The three aggregate predator measures are as follows:

- **Predator Abundance (PA)**; sum of the maximum number of each predator species observed across repeat visits to a site (excludes possum scat detections).
- **Predator Species Richness (PSR)**; the number of predator species detected across repeat visits to a site (includes possum scat detections).
- **Occupancy Based Predator Species Richness (OBPSR);** modelled number of predator species at a site when adjusted for imperfect detection (includes scat detections).

At this stage I adjusted both predator species richness measures (PSR and OBPSR) to include data from scat surveys. I considered possums to be present at sites where scat was detected, even if possums were not detected during nocturnal surveys.

To calculate Occupancy Based Predator Species Richness (OBPSR) I used the most parsimonious occupancy models to generate occupancy probability predictions for each predator species at each site. To adjust for false absences (i.e. non-detections at occupied sites), I used the mean predicted value at sites where I detected each predator species as a prediction threshold. I changed the occupancy status of sites in which each species was not detected from “Unoccupied’ to “Occupied” if the predicted occupancy value at that site exceeded this threshold (Figure 5).

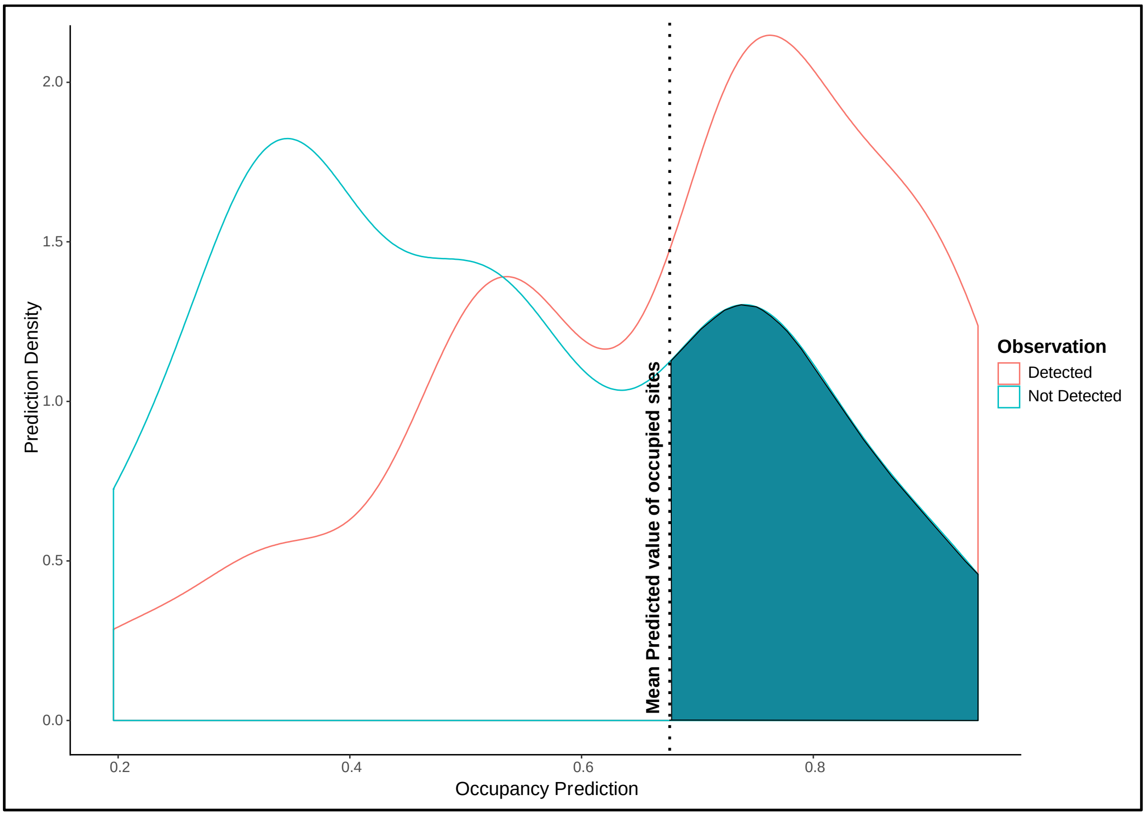

Figure 5: Example of prediction distribution, showing threshold at which sites without survey detections were adjusted to show presence. The area with dark blue fill represents sites where I did not detect the target species, but the model's occupancy probability exceeded the mean predicted occupancy value at sites where the target species was detected. Hence, I changed the occupancy status of these sites from Unoccupied to Occupied.

3.3.3 Spatial Modelling

I created spatial models for Predator Abundance (PA) and Predator Species Richness (PSR) to account for spatial autocorrelation, a phenomenon in which the presence of a species or habitat covariates at one location can be at least partly predicted by the presence of a species at neighbouring locations (Legendre, 1993). I did not create a spatial model for Occupancy Based Predator Species Richness (OBPSR) to avoid artificially amplifying the relationship between habitat features and the predator measure, as occupancy modelling had already accounted for the influence of habitat features on predator species presence.

I developed saturated generalised additive models (GAMs) using the package *mgcv* v1.8.31 (Wood, 2011), with PA and PSR as the response variables. I created these saturated GAMs using three different distribution types: Gaussian, Poisson and negative binomial. I tested the fit and residual spatial autocorrelation of the distributions using AIC values, the function *gam.check* in *mgcv* and package *ncf* v1.2.9 (Bjørnstad, 2020). I used the most suitable distribution based on these diagnostics for the rest of the spatial modelling process. The saturated GAMs included all habitat covariates (Table 1) and a smoothed spatial covariate, *s(Lat, Long)*. I used *MuMIn* to test all combinations of covariates within the saturated models, identifying the most parsimonious model (lowest AICc) for both predator measures.

Once I had identified the most parsimonious spatial models, I individually included covariates associated with regent honeyeater nesting suitability into each model to answer research question 2: *Do regent honeyeaters nest in areas of high predator abundance / species richness?* If not already part of the most parsimonious model, I added Vegetation Community and Blossom Abundance to the model individually. These are key defining characteristics of regent honeyeater nests sites, as regent honeyeaters favour sites with high blossom abundance and yellow-box / mugga ironbark or riparian vegetation communities (Crates et al., 2017b). White-box vegetation is lower preference but still more favourable than "Other" vegetation. I also added Nest Proximity to the model separately, as it acts as a further indicator of regent honeyeater nesting suitability. I used the package *visreg* v2.6.0 (Breheny and Burchett, 2017) to visualise the relationship between the site-level Predator Abundance / Predator Species Richness and the indicators of suitability for regent honeyeater nesting.

3.3.4 Nest Survival Modelling

I obtained historic regent honeyeater nest data (2015 – 2018) from Crates et al. (2019b) in addition to nest data collected by Dr Ross Crates and Liam Murphy during the 2019 breeding season. This data enabled me to address research question 3; *Can spatial variation in regent honeyeater nest survival be explained by spatial variation in predator abundance / species richness?* I measured nest survival in two ways:

- **Nest Fate:** The binomial survival of the nest (success or failure). Success was defined as the fledging of one or more young.
- **Daily nest Survival Rate (DSR)**: The probability that an egg / nestling will survive from any given day to the next.

While nest fate is the ultimate measure of nest success, it does not account for failed nests that remain undetected, creating a biased nest success rate (Johnson et al., 2007). Daily nest Survival Rate was included in my analysis as it accounts for this bias (Mayfield, 1961; Mayfield, 1975; Johnson, 1979).

I derived aggregate predator predictions for 115 nest locations from the most parsimonious GAMs of Predator Abundance (PA) and Predator Species Richness (PSR) using the function *predict* in *mgcv*. I derived an Occupancy Based Predator Species Richness (OBPSR) prediction for each nest site using the most parsimonious GAM for PSR. I based predictions on smoothed location data from survey sites (drawing upon weighted observations from all nearby sites) and complementary habitat covariates from each nest location.

3.3.4.1 Nest Fate Models

I created logistic regression models of Nest Fate (binomial response of success / failure) using the package *lme4* v1.1.21 (R Core Team, 2019). I included nest covariates that were previously found to predict nest success (Crates et al., 2019b) in a saturated GLM. These covariates were nest height (metres from ground), nest position (position within tree crown), nest concealment (percentage of surrounding vegetation) and presence of conspecifics (number of active regent honeyeater nests within 100m) (Crates et al., 2019b). I used *MuMIn* to test all combinations of covariates within the saturated model and identify the most parsimonious model based on lowest AICc. I then added the aggregate predator measures separately to the most parsimonious model, to test the relationship between predator abundance / species richness and nest success, whilst controlling for the other covariates known to impact nest success.

3.3.4.2 Daily Survival Models

I created models of Daily nest Survival Rate (DSR) using the package *RMark* v2.2.7 (Laake, 2013). I created single-term models for nest covariates (presence of conspecifics, nest concealment, nest position and nesting year) and aggregate predator measures, with DSR as the response variable. I used AIC to estimate the relative strength of univariate models. I then created multivariate models using combinations of the single terms that were more parsimonious than the null model. I only included one predator measure in each multivariate DSR model. The models were then ranked by AICc to determine the most parsimonious models overall and the most parsimonious models containing each aggregate predator measure.

I also compared the DSR of nests by study region, to determine if new nest data corrected or contributed to regional variation in DSR discrepancies found by Crates et al. (2019b).

4 Results

4.1 Species observations

The most frequently detected predator species was the common brushtail possum which I detected at 77% of sites. I detected possums more regularly through scat (57% of sites) than nocturnal surveys (48% of sites) (Appendix 2). The predator species I detected least frequently was the pied butcherbird (8% of sites) (Figure 6).

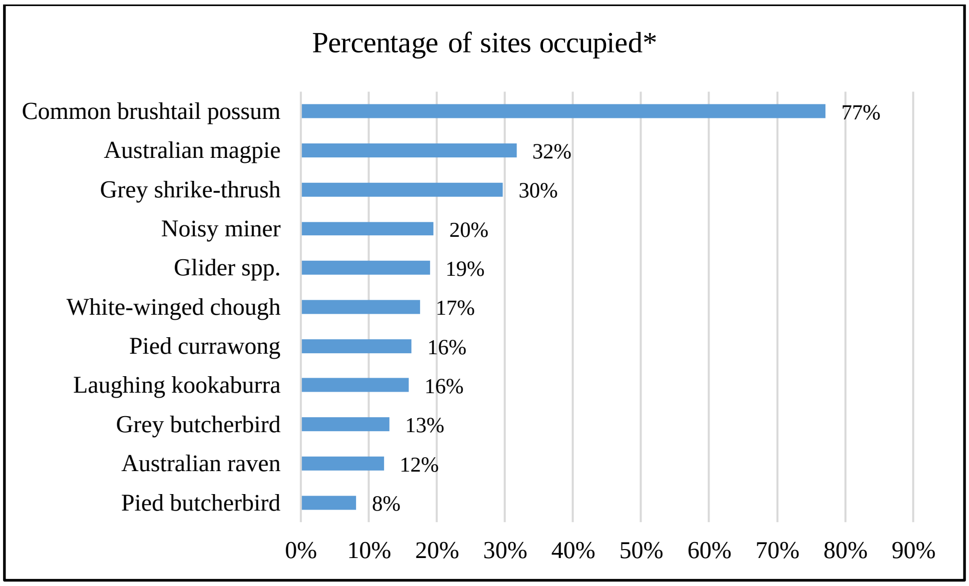

Figure 6: Percentage of sites where predator species were detected.
**Of 246 sites for diurnal species and 227 for nocturnal species*

4.2 Occupancy Modelling

Occupancy: For all predator species, except the grey shrike-thrush, one or more occupancy (habitat) covariates were included in the most parsimonious model (Table 2). Shrub Cover was included in the model for the Australian magpie, noisy miner and pied butcherbird. Woody Debris Abundance was included in the model for the Australian raven, common brushtail possum and white-winged chough. Blossom Abundance was included in the model for the common brushtail possum, glider spp. and noisy miner. Vegetation Community was included in the model for the pied currawong and white-winged chough. Hollow Abundance was included only in the model for the common brushtail possum and Ground Cover only in the model for the laughing kookaburra.

Detectability: For nine of the 11 predator species, one or more detectability covariates (dynamic variables) were included in the most parsimonious model. Wind Speed impacted the detectability of the most species (5), followed by Visit Number (4), Time of day (2) and Temperature (2). Detailed occupancy modelling results are provided in Appendix 3.

Table 2: Most parsimonious occupancy model for each predator species. ΔAICc shows is the difference between the AICc of the most parsimonious model and the second most parsimonious model. The Akaike weight (w_i) indicates the percentage (proportion) of variation explained by the model. *Ψ* precedes the occupancy covariates, while *p* precedes the detectability covariates.

Species	**Model**	**ΔAICc**	**w_i**
Australian magpie	*Ψ*(shrub).*p*(wind)	0.52	0.44
Australian raven	*Ψ*(wood).*p*(visit)	2.40	0.62
Common brushtail possum	*Ψ*(hollows + blossom + wood).*p*(1)	1.16	0.36
Glider spp.	*Ψ*(blossom).*p*(wind)	0.16	0.30
Grey butcherbird	*Ψ*(hollows).*p*(temp + visit)	0.41	0.28
Grey shrike-thrush	*Ψ*(1).*p*(time + visit + wind)	0.22	0.25
Laughing kookaburra	*Ψ*(ground).*p*(1)	0.12	0.52
Noisy miner	*Ψ*(blossom + shrub).*p*(temp)	1.76	0.43
Pied butcherbird	*Ψ*(shrub).*p*(time + wind)	0.22	0.25
Pied currawong	*Ψ*(vegetation).*p*(visit)	0.39	0.48
White-winged chough	*Ψ*(shrub + vegetation + wood).*p*(wind)	0.09	0.29

4.3 Spatial Modelling

Predator Abundance: I defined Predator Abundance (PA) as the sum of the maximum number of each species observed at a site, excluding scat detections. PA varied across the study areas (Figure 7), ranging from 0 - 14 with a median of 3. The most parsimonious PA model (ΔAICc = 0.61, Akaike weight w_i = 0.203) had a Poisson distribution, and included the following terms:

Predator Abundance ~ ground cover + hollows + mistletoe + shrub cover + water + *s(Lat,Long)*

PA showed a significant positive relationship with Hollow Abundance, Water Proximity and Ground Cover. PA also showed a significant negative relationship with the extent of Shrub Cover and a strong relationship with the smoothed spatial term (Table 3).

Predator Species Richness: I defined Predator Species Richness (PSR) as the number of predator species detected at a site, including detections through scat surveys. PSR varied throughout the study areas (Figure 8), ranging from 0 - 7 with a median of 2. The most parsimonious PSR model (ΔAICc = 0.82, w_i = 0.174) had a Gaussian distribution, and included the following terms:

Predator Species Richness ~ canopy + hollows + ground cover + water + *s(Lat,Long)*

PSR had a significant positive relationship with Hollow Abundance, and Water Proximity. PSR was higher at sites with short grass as the dominant Ground Cover and lower at sites with low Canopy Cover (0 - 15%). PSR also showed a strong relationship with the smoothed spatial term (Table 3). The frequency distribution of predicted aggregate predator measures at nest sites is available in Appendix 4.

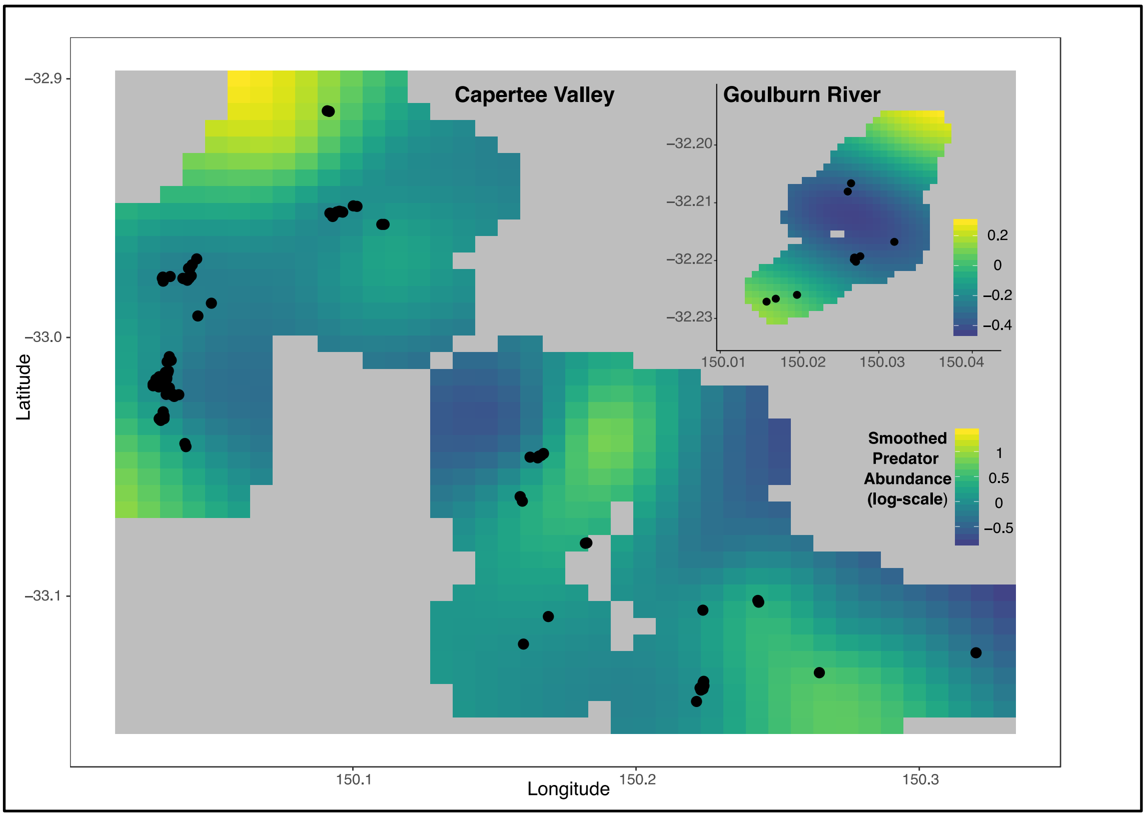

Figure 7: Logarithmic-scale smoothed predicted Predator Abundance (PA) surfaces across the Capertee Valley and Goulburn River. Predictions are derived from the most parsimonious Predator Abundance GAM. Black dots represent nest sites in the areas between 2015 and 2019.

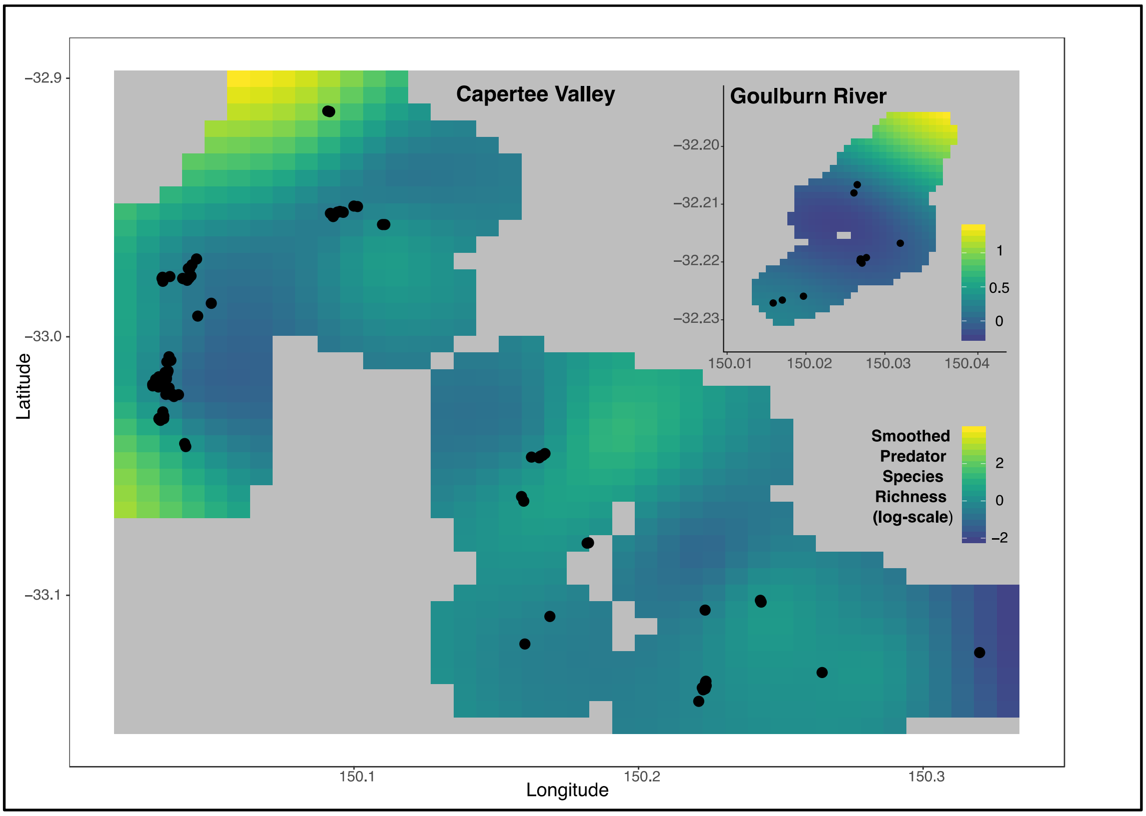

Figure 8: Logarithmic-scale smoothed predicted Predator Species Richness (PSR) surfaces across the Capertee Valley and Goulburn River. Predictions are derived from the most parsimonious Predator Species Richness GAM. Black dots represent nest sites in the areas between 2015 and 2019.

Table 3: Spatial model summaries showing the relationship between aggregate predator measures and habitat covariates. Significant effects ($p < 0.05$) are shown in bold. Beta (β) indicates the effect of the covariate level on the response variable. Standard Error (SE) indicates the statistical accuracy of an estimate. Estimated degrees of freedom (edf) indicates the number of values that are free to vary.

Measure	Covariate	Relative to	β	SE	z / t *	*p*
Predator Abundance	Ground Cover (Long grass / low shrub)	Ground (Short grass)	-0.32	0.14	-2.35	**0.019**
	Ground Cover (Bare / leaf litter)		-0.28	0.10	-2.87	**0.004**
	Hollow Abundance (1 - 3)	Hollow Abundance (None)	0.14	0.15	0.90	0.370
	Hollow Abundance (>3)		0.40	0.16	2.59	**0.010**
	Mistletoe Abundance (1 - 10)	Mistletoe Abundance (None)	-0.12	0.10	-1.22	0.223
	Mistletoe Abundance (>10)		0.11	0.10	1.09	0.274
	Shrub Cover (15 - 30%)	Shrub Cover (0-15%)	-0.04	0.09	-0.38	0.706
	Shrub Cover (>30%)		-0.46	0.14	-3.27	**<0.001**
	Water Proximity (50 – 200 m)	Water Proximity (On-site)	-0.27	0.12	-2.32	**0.020**
	Water Proximity (>200 m)		-0.31	0.11	-2.90	**0.004**
				edf	**X_2**	***p***
	s(Lat,Long)			24.53	90.84	**<0.001**
Predator Species Richness	Canopy Cover (15 - 30%)	Canopy Cover (0 - 15%)	1.24	0.44	2.82	**0.005**
	Canopy Cover (>30%)		1.04	0.44	2.37	**0.019**
	Ground Cover (Long grass / low shrub)	Ground Cover (Short grass)	-0.51	0.29	-1.78	0.077
	Ground Cover (Bare / leaf litter)		-0.77	0.21	-3.71	**<0.001**
	Hollow Abundance (1 - 3)	Hollow Abundance (None)	0.16	0.28	0.58	0.565
	Hollow Abundance (>3)		0.84	0.28	2.98	**0.003**
	Water Proximity (50 – 200 m)	Water Proximity (On-site)	-0.54	0.28	-1.94	0.054
	Water Proximity(>200 m)		-0.65	0.26	-2.49	**0.014**
				edf	**F**	***p***
	s(Lat,Long)			23.18	2.32	**<0.001**

**PA used z-value and X_2 (Poisson distribution), while PSR used t-value and F (Gaussian distribution)*

Study sites with high levels of blossom had marginally higher Predator Abundance (PA) and Predator Species Richness (PSR) than sites with mild or no blossom. Study sites with River-oak and White-box vegetation communities also experienced slightly higher levels of Predator Abundance and Predator Species Richness compared to sites with Yellow-box / mugga ironbark or "Other" vegetation communities. Study sites located on a current or historic nest site (within 50 m) experienced slightly higher levels of PA and PSR than sites located more than 50 m from a current or historic nest site. Despite these trends, all effect sizes were statistically non-significant (Figure 10 and Figure 11).

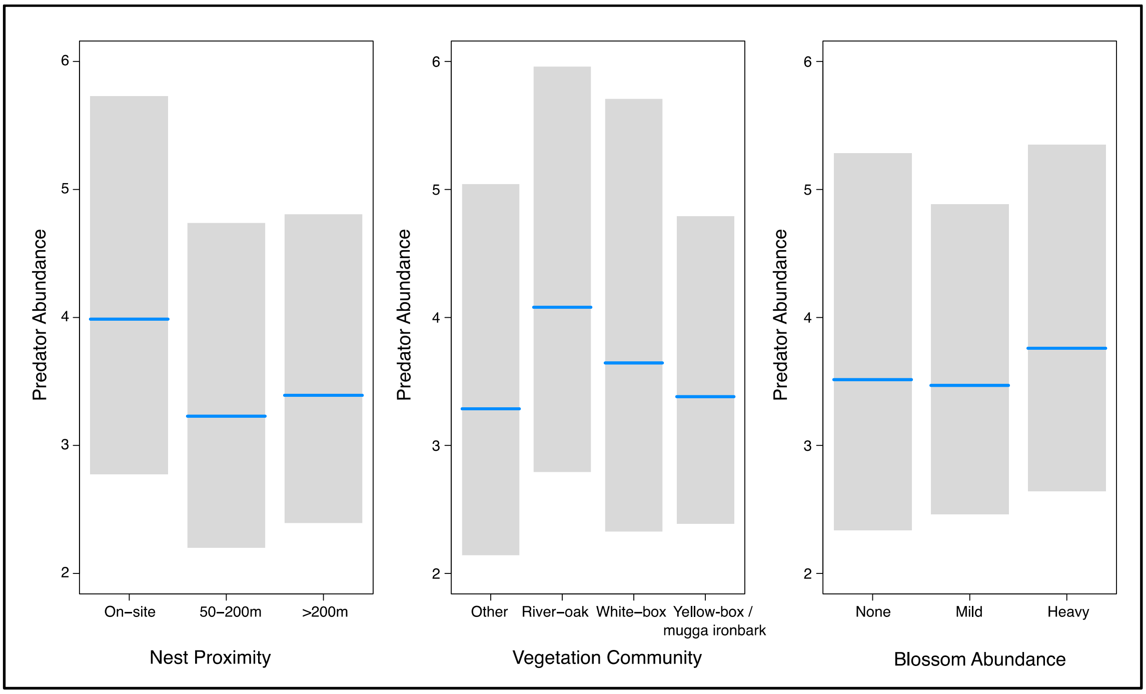

Figure 9: Relationship between key indicators of regent honeyeater nesting habitat (Nest Proximity, Vegetation Community and Blossom Abundance) and Predator Abundance. The shaded areas represent the 95% confidence interval.

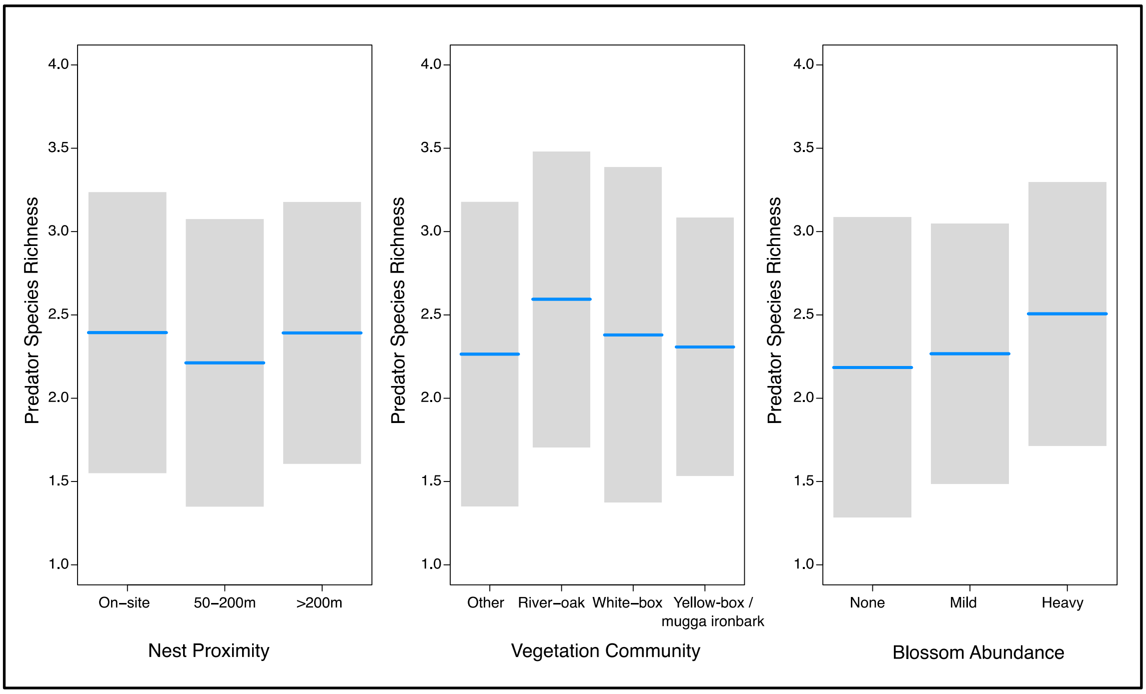

Figure 10: Relationship between key indicators of regent honeyeater nesting habitat (Nest Proximity, Vegetation Community and Blossom Abundance) and Predator Species Richness. The shaded areas represent the 95% confidence interval.

Table 4: Relationship between Nest Proximity, Vegetation Community, Blossom Abundance and Predator Abundance and Predator Species Richness. Beta (β) indicates the effect of the covariate level on the response variable. Standard Error (SE) indicates the statistical accuracy of an estimate. Significant effects (p < 0.05) are shown in bold.

Measure	Covariate	Relative to	β	SE	z / t *	*p*
Predator Abundance	Nest Proximity (50 – 200 m)	Nest Proximity (On-site)	-0.21	0.13	-1.57	0.116
	Nest Proximity (>200 m)		-0.16	0.12	-1.33	0.185
	Veg (River-oak)	Veg (Other)	0.22	0.18	1.18	0.239
	Veg (White-box)		0.10	0.18	0.58	0.560
	Veg (Yellow-box / mugga ironbark)		0.03	0.14	0.20	0.841
	Blossom Abundance (Mild)	Blossom Abundance (None)	-0.01	0.13	-0.10	0.921
	Blossom Abundance (Heavy)		0.07	0.14	0.47	0.636
Predator Species Richness	Nest Proximity (50 – 200 m)	Nest Proximity (On-site)	-0.18	0.33	-0.56	0.578
	Nest Proximity (>200 m)		0.00	0.30	-0.01	0.995
	Veg (River-oak)	Veg (Other)	0.33	0.40	0.83	0.407
	Veg (White-box)		0.12	0.38	0.31	0.760
	Veg (Yellow-box / mugga ironbark)		0.04	0.30	0.15	0.885
	Blossom Abundance (Mild)	Blossom Abundance (None)	0.08	0.27	0.30	0.765
	Blossom Abundance (Heavy)		0.32	0.32	1.02	0.308

**PA used z-value (Poisson distribution), while PSR used t-value (Gaussian distribution)*

4.4 Nest Survival Modelling

4.4.1 Nest Fate Models

Nest success was positively correlated with Predator Abundance (PA) and Predator Species Richness (PSR) (Figure 11). While the relationship between PA and nest success was non-significant, PSR had a significant positive relationship with nest success, indicating an increased probability of nest success in areas with more nest predator species. The most parsimonious model for Nest Fate included the presence of conspecifics and PSR (Table 6). There was no significant relationship between Occupancy Based Predator Species Richness (OBPSR) and nest success (Table 5).

Table 5: Relationship between aggregate predator measures and Nest Fate. Beta (β) indicates the effect of the covariate level on the response variable. Standard Error (SE) indicates the statistical accuracy of an estimate. Significant effects (p < 0.05) are shown in bold.

Measure	β	SE	z	*p*
Predator Abundance	0.16	0.13	1.23	0.218
Predator Species Richness	0.48	0.24	2.02	**0.044**
Occupancy Based Predator Species Richness	-0.07	0.14	-0.52	0.605

Table 6: Summary of the most parsimonious model for Nest Fate. Beta (β) indicates the effect of the covariate level on the response variable. Standard Error (SE) indicates the statistical accuracy of an estimate. Significant effects (p < 0.05) are shown in bold.

Covariate	Relative to	β	SE	z	*p*
Conspecifics (Present)	Conspecifics (Absent)	1.09	0.40	2.70	**0.006**
Predator Species Richness		0.48	0.24	2.02	**0.044**

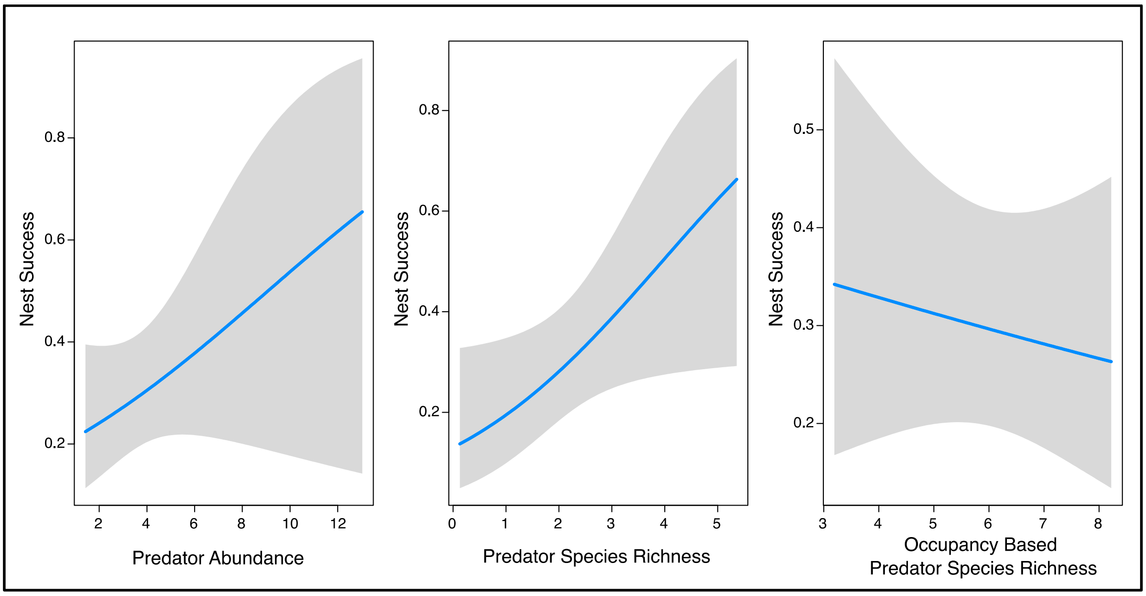

Figure 11: Relationship between aggregate predator measures and Nest Fate. The blue line represents the model estimate, while the shaded areas represent the 95% confidence intervals.

4.4.2 Daily Survival Models

Across the 115 nests, the modelled average nest success rate was 31.6% (95% confidence interval = 23.1 - 40.5%). The Daily Survival Rate (DSR) of nests was positively correlated with both PA and PSR, however the relationship between DSR and PA was non-significant. There was also no significant relationship between DSR and OBPSR (Figure 12). PSR had the strongest relationship with DSR, appearing in four of the top five models (Table 7). The most parsimonious model included PSR, conspecifics and nest position (Table 8). Analysis at a regional scale showed that there was no significant variation in DSR between study regions (Figure 13).

Table 7: The five most parsimonious Daily nest Survival Rate (DSR) models ranked by AICc. ΔAICc shows the difference between the AICc of the model and the AICc of the most parsimonious model. The Akaike weight (w_i) indicates the percentage (proportion) of variation explained by the model.

Model	ΔAICc	w_i
S(~Predator Species Richness + conspecifics + position)	0.00	0.40
S(~Predator Species Richness + position)	1.63	0.18
S(~Predator Abundance + conspecifics + position)	3.05	0.09
S(~Predator Species Richness + conspecifics)	3.63	0.06
S(~Predator Species Richness + conspecifics + year)	4.21	0.05

Table 8: Summary of the most parsimonious model for Daily nest Survival Rate (DSR). Beta (β) indicates the effect of the covariate level on the response variable. Standard Error (SE) indicates the statistical accuracy of an estimate. The lower confidence limit (lcl) and upper confidence limit (ucl) represent the 95% confidence intervals.

Covariate	Relative to	β	SE	*lcl*	*ucl*
Predator Species Richness		0.36	0.15	0.06	0.66
Conspecifics (Present)	Conspecifics (Absent)	0.51	0.27	-0.25	1.05
Nest Position (Mid)	Position (Inner)	0.73	0.37	-0.01	1.46
Nest Position (Outer)		1.13	0.39	0.36	1.90

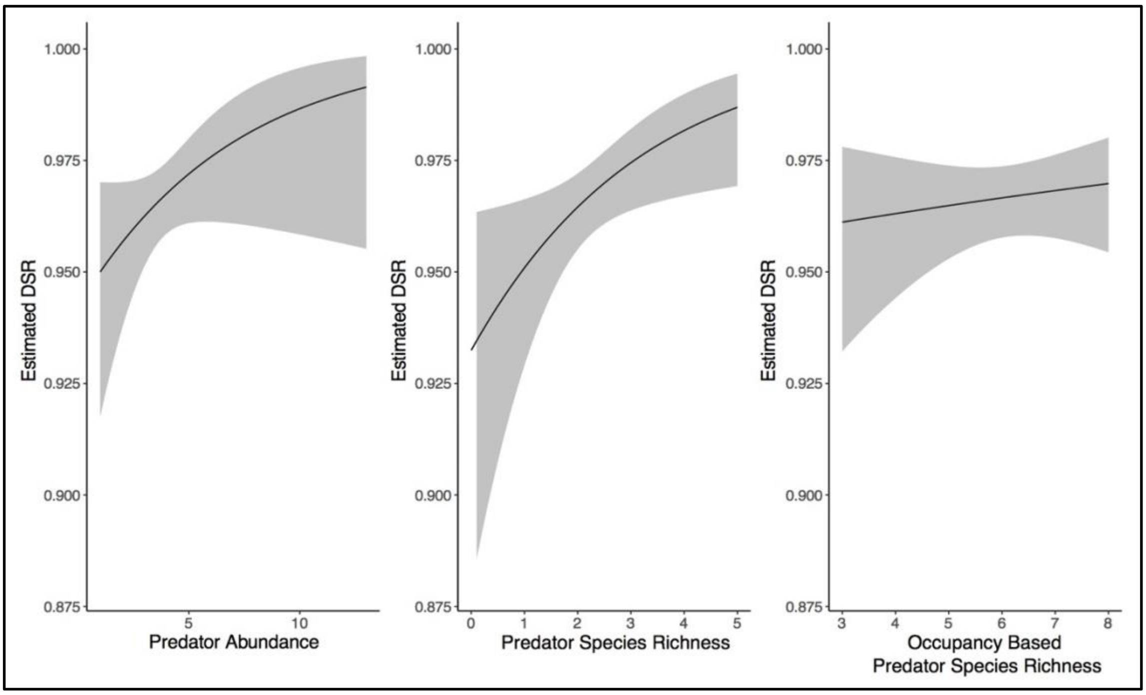

Figure 12: Relationship between aggregate predator measures and regent honeyeater Daily nest Survival Rate (DSR). The black line represents the model estimate, while the shaded areas represent the 95% confidence intervals.

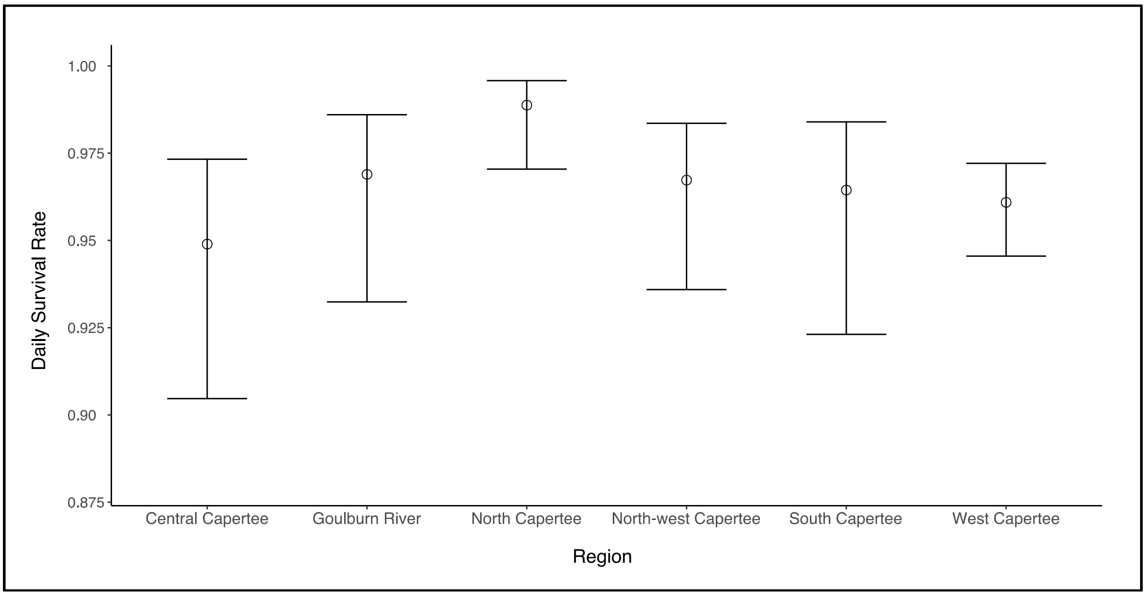

Figure 13: Average Daily regent honeyeater nest Survival Rate (DSR) by study region between 2015 and 2019. Error bars represent the 95% confidence intervals.

5 Discussion

Understanding the mechanisms driving nest predation is critical to the conservation of threatened avian species (Ibáñez-Álamo et al., 2015; Fulton, 2018). I modelled predator abundance and predator species richness across 80% of the contemporary breeding range of a critically endangered songbird. The key predictors of occupancy varied between nest predator species, but local predator community abundance and species richness were best explained by ground cover, shrub cover, water proximity, hollow abundance and canopy cover. Predator abundance and predator species richness were higher at nest sites and in riparian vegetation communities with high blossom abundance. While the relationships were non-significant, these characteristics are favoured for regent honeyeater nesting, suggesting regent honeyeaters do nest in areas of high predator abundance. Regent honeyeater nest success and daily nest survival rate were positively correlated with predator measures, suggesting that low rates of regent honeyeater nest success cannot be explained by predator community measures.

5.1 Predator distribution

Understanding the predictors and distribution of predators can help to inform the targeted management of nest predator species, maximising efficiency and minimising financial and ethical costs (Doherty and Ritchie, 2017). I found substantial interspecific variation in both predator distribution and site occupancy rates. A number of significant relationships were found between habitat features and species-level occupancy. A low degree of shrub cover was associated with Australian magpie occupancy. Noisy miner presence was associated with less extensive shrub cover and blossom abundance, consistent with findings that noisy miners are associated with woodland areas where understorey vegetation has been cleared (Lindenmayer et al., 2010; Montague-Drake et al., 2011). Common brushtail possums were strongly associated with high estimated hollow abundance - an important habitat feature for arboreal marsupials (Gibbons and Lindenmayer, 2002; McElhinny et al., 2006). White-winged chough presence was associated with a lower degree of shrub cover and woody debris abundance (Mac Nally et al., 2001).

Aggregate predator abundance and species richness measures were highly variable across both study areas. Spatial models revealed that predator abundance and species richness were both higher at sites near water, and with high hollow abundance and short grass as the dominant ground cover. Predator species richness was also higher at sites with moderate canopy cover. These habitat features are characteristic of highly modified agricultural landscapes bordering on riparian zones, where hollows are abundant in large old paddock trees; a landscape previously associated with elevated numbers of nest predators (Fulton et al., 2008; Ford, 2011; Fulton, 2018). Regent honeyeater nest sites and habitat features associated with regent honeyeater nesting, including riparian vegetation and blossom abundance (Geering and French, 1998), appeared to have been associated with higher predator abundance and predator species richness, although these results were non-significant. Nonetheless, the results show that regent honeyeaters do nest in areas of high nest predator abundance. Due to land clearing and habitat fragmentation it is likely that nest predator abundance in south-eastern Australian woodlands has increased (Fulton, 2018). Bird species have been found to select nesting sites that present lower predation risk (Fontaine and Martin, 2006a), however, with reduced breeding habitat, the regent honeyeater no longer has much choice.

Spatial models identified five habitat features with significant impacts on predator abundance and / or predator species richness, while occupancy modelling identified only four as significant species-level predictors. Predator species richness was significantly impacted by canopy cover, despite canopy cover appearing in none of the occupancy models. These discrepancies may be due to the inclusion of a smoothed spatial term to account for spatial autocorrelation between sites in spatial modelling, or because the abundance of each species is not accounted for in occupancy modelling (MacKenzie and Nichols, 2004).

5.2 Nest success

Sparsely populated, highly nomadic species are difficult to research due to their reliance on disconnected habitats and sporadic, resource-driven movements (Runge et al., 2014). The regent honeyeater population is small, nomadic and individuals rarely return to breed at the same nesting sites (Geering and French, 1998). As a result, targeted, time-intensive surveying of known breeding regions is required to study the breeding biology and nesting success of the species (Crates et al., 2019b). Due to recent monitoring of regent honeyeater breeding areas, I had five years of nest data to inform survey effort and test my hypotheses. Across the 115 nest sites, nest success was modelled at 31.6%, much lower than most honeyeater species (Crates et al., 2019b). Significant differences in regional DSR reported by Crates et al. (2019) were no longer evident following the inclusion of the 2019 nest data. This could signify an inconsistent threat from predators in space over time, altered resource availability between years (Crates et al., 2019b), or the correction of a Type I statistical error after the sample size was increased.

Contrary to my hypothesis, regent honeyeater nest failure was not associated with high predator abundance / species richness. Instead, regent honeyeater nest success and Daily nest Survival Rate (DSR) were positively correlated with Predator Abundance and Predator Species Richness. Occupancy Based Predator Species Richness did not show a significant relationship with nest success or DSR, potentially due to biases arising through the occupancy and spatial modelling framework (Section 5.3). The presence of conspecifics had the most significant positive relationship with Nest Fate and DSR, as found in the breeding ecology study conducted by Crates et al. (2019).

The positive relationship found between predator abundance and regent honeyeater nest success contradicts the results of many other predator abundance studies (Debus, 2006; Boulton et al., 2008; Heinsohn et al., 2015). A possible explanation lies in the regent honeyeater's anti-predator strategies. These strategies are the result of the selection pressure presented by nest predation, and imply that nest predation is not a new threat to the species. The propensity of regent honeyeaters to nest high in the outer canopy of large trees (Oliver et al., 1998) and in aggregations (Ford et al., 1993; Oliver et al., 1998) reduces the nest's accessibility to large-bodied predators, such as possums, and increases defences against predators through aggressive group behaviour. Similarly, nest concealment by regent honeyeaters acts to reduce the detectability of nests. Since anti-predator strategies may be triggered by perceived predatory threat, higher predator levels could actually encourage the survival of nests (Hollander et al., 2015). A North American study found that increased predator abundance resulted in a number of changes to breeding strategies in nesting birds, including increased time spent on the nest by females (Fontaine and Martin, 2006b). Furthermore, studies have suggested that nest predation risk may affect the conspicuousness of nests (Martin and Briskie, 2009), and ultimately may result in a disconnection between nest predation rates and nest predator abundance (Hollander et al., 2015).

While the main cause of nest failure among regent honeyeaters is nest predation, not all nest failures in the nest dataset used can be conclusively attributed to predation events (Crates et al., 2019b). As predator abundance / species richness is associated with resource availability, sites with higher predator abundance / species richness may have had better access to resources necessary for nest survival. Furthermore, parental foraging effort may have been minimised at these sites, reducing regular activity at the nest (Sofaer et al., 2012). In turn this could lead to increased defence of the nest, and reduced parental activity, decreasing the risk of nest predation (Martin et al., 2000).

Many species have been observed depredating regent honeyeater nests (Taylor et al., 2018; Crates et al., 2019b), however it remains possible that one species (or even one individual) may have a more significant impact than the entire predator community. A Canadian study found that the best predictor of predation by American red squirrels was prior experience, suggesting that predation was learned, rather than opportunistic, behaviour (Pelech et al., 2010). If this were the case among south-eastern Australian woodland nest predators, nest predation could occur mostly independent of predator abundance. The absence of a negative relationship between nest predator abundance and nest survival may be explained by the factors mentioned above, however further research is required to determine their true impact on regent honeyeater nest predation. Useful future studies directions include the surveying of nest predators at active regent honeyeater nests and the study of parental behaviour in response to perceived predatory threat.

5.3 Study limitations

I used repeat point-counts and a 50m radius detection zone around each site centroid to account for all 12 nest predator species. While this survey design enabled me to collect a large, spatially-extensive sample of the predator community, it may not have been the most thorough sampling method for each individual species. The home ranges of some species, such as the white-winged chough and Australian magpie are likely to exceed the 50 m site radius (Heinsohn, 1991; Cox and Bauer, 1997). However, the use of a 50 m site radius has been shown to be ecologically relevant for regent honeyeater (Crates et al., 2017b) and ensured compatibility with the NRHMP data. Furthermore, it enabled rapid surveys, allowing me to repeatedly assess a large sample of sites whilst minimising violation of the closure assumption (i.e. changes to the occupancy status of sites over the surveying period) (Rota et al., 2009). Despite the surveys being more suitable for certain species, its uniformity across all sites makes the data comparable. Techniques aiming to census an entire predator community will always face a trade-off between statistical power (number of sites), spatial coverage and detectability, and design decisions should be made based on the research questions and objectives (Eberhardt and Thomas, 1991; Bailey et al., 2007). I chose detection methods that were most appropriate to assess the whole predator community across a large area. I used multiple nocturnal detection methods (spotlighting, thermal imaging, call playback and scat surveys), some of which targeted individual species, to maximise detectability. This resulted in a somewhat disparate detection effort for different species. While consistent effort between sites makes spatial observations comparable, the relative abundance of a species in comparison with another should not be supposed.

In order to achieve a sufficient sample of nests, data from five breeding seasons (2015 – 2019) were included in the study. Due to repeat nesting across years and the regent honeyeater's predisposition to nest in aggregations (Ford et al., 1993; Oliver et al., 1998), many of the nest sites were geographically clustered and therefore not spatially independent of one another. To address this I employed spatial modelling, reducing the impact of spatial autocorrelation between sites. Only 10% of the nests were active in 2019, meaning that for the majority of nest sites, predators were surveyed after the actual nesting year. While nest predator occupancy may have changed between years, all predator species involved in the study are considered resident species, with the exception of the pied currawong, which in some cases may undertake partial migration (Chan, 2001).

As occupancy modelling aims to correct for imperfect detectability (MacKenzie et al., 2002; MacKenzie and Royle, 2005), some inaccuracies may have developed when I adjusted the occupancy status of sites (where I didn't detect a predator species, but the occupancy probability was above the average for sites where I did detect the species) (Welsh et al., 2013). By using occupancy predictions to develop Occupancy Based Predator Species Richness (OBPSR) predictions at nest sites, bias may have been induced. This is due to some habitat covariates, such as Hollow Abundance, being used for occupancy modelling and in the spatial model used to develop predictions at nest sites, potentially confounding the OBPSR predictions at nest sites. In addition, the uncertainty of occupancy predictions is not passed on to the spatial model and thus is not accounted for. There was a correlation of 0.45 between OBPSR and Predator Species Richness (PSR); relatively weak considering OBPSR is merely an adjustment of PSR. The lack of strong correlation between these measures highlights this potential bias and renders results associated with the OBPSR measure somewhat tentative. However, by inducing bias through 'double analysing' the data, bias caused by imperfect detection was reduced simultaneously through occupancy modelling (MacKenzie et al., 2002).

5.4 Novel findings & Implications for future research and management

I present a novel survey methodology and analytical framework to assess landscape-scale predator community distribution and abundance. This framework can be utilised for other conservation programs, and its stratified sampling design allows multiple research questions to be addressed by manipulating the data in different ways. While I found a positive relationship between predator abundance / species richness and nest survival, this is unlikely to be a direct causal relationship. As a result, predator distribution and abundance should still be considered when managing threatened woodland birds. An understanding of the landscape-scale distribution of nest predators enables the identification of landscapes of disproportionate concern, promoting more effective management of nest predators (Lindenmayer et al., 2008). Predator abundance / species richness were associated with short grass and less extensive shrub cover, suggesting that landscape regeneration could be used to reduce the abundance of potential nest predators. Regeneration of regent honeyeater habitat primarily focuses on restorative tree-planting on cleared river flats (Commonwealth of Australia, 2016); undoubtedly crucial to the entire woodland bird community (Bennett et al., 2014). Similarly the regeneration of native shrub cover and reduction in grazing may also benefit woodland birds by reducing nest predator abundance (Lindenmayer et al., 2010). The relationship between ground cover, shrub cover and the nest predator community should be researched further to determine the extent of association importance of these habitat features.

Many studies have examined the impact of species-level predator abundance on nest predation, rather than the impact of the entire predator community. My study addressed the predator community as a whole, which is important for species such as the regent honeyeater that are targeted by an array of nest predators. Nest survival modelling showed that regent honeyeater nest success was not negatively impacted by the overall abundance of nest predators within the Capertee Valley and Goulburn River study areas. Instead my findings point towards other factors, such as anti-predator strategies, resource availability and differing rates of learned predatory behaviour, as possible causes of variation in nest predation rates. Further research is required to properly understand the underlying dynamics of the predator-prey relationship for regent honeyeaters.

Currently, lethal predator suppression is used to support regent honeyeater breeding (Crates et al., 2018; Crates et al., 2020). The suppression of overabundant predator species, such as the pied currawong (Fulton and Ford, 2001; Debus, 2006) and noisy miner (Debus, 2008; Crates et al., 2018; Crates et al., 2020), has proved successful in providing short-term benefits to woodland birds. However, targeted culls may not be effective in the longer-term due to compensatory nest predation and rapid recolonization (Davitt et al., 2018; Beggs et al., 2019a; Beggs et al., 2019b). I found that multiple predator species were widespread across the study areas. Focusing on just one or two predator species may not be effective, as remaining species could pose an equally significant threat to nests. As predator abundance was not negatively related to nest success in our study, and given the dubious long-term effectiveness of culls, further research is required to determine the efficacy of this management practice in supporting regent honeyeater nesting success.

Overall, I have demonstrated a successful method for the landscape-scale surveying of nest predators. My thesis highlights the importance of thoroughly examining the interactions between nest predators and threatened woodland birds. Further research is required to build on my findings, including the study of predators at nest sites in real time, the observation of parental behaviour in response to predator abundance, and experimental predator suppression / exclusion. This research is required to understand the dynamics of regent honeyeater nest predation and its true predictors, in order to inform better management of the species and improve nesting success.

6 Conclusion

This thesis aimed to develop an understanding of the distribution of nest predators in key regent honeyeater breeding areas and to examine the impact of predator abundance / species richness on regent honeyeater nest success. I modelled the distribution of nest predator species across two key breeding areas of the regent honeyeater, finding that habitat features such as canopy cover, shrub cover, ground cover, hollow abundance and water proximity were associated with predator abundance / species richness at a community level. I also found that nest sites and favoured characteristics of regent honeyeater nesting habitat had a positive but non-significant relationship with predator abundance and species richness. I have developed an understanding of the landscape-scale predictors of predator abundance / species richness in key regent honeyeater habitat, which can be used to inform the future management of the regent honeyeater and other threatened woodland birds. Furthermore, I have demonstrated a successful approach to model predator distribution across a large area, which is easily adaptable to future studies.

Many studies have examined the relationship between the abundance of a single predator species and nest success, however the study of a predator community is less common. Contrary to my hypothesis, I found a positive relationship between nest survival and predator abundance / species richness. As regent honeyeater nest failure was not explained by predator abundance / species richness, it is clear that other factors are at play in determining regent honeyeater nest success. My findings highlight a number of areas for future research and provide insights that can be used to inform the management of woodland birds threatened by nest predation. Overall, this thesis fulfils its aims of developing an understanding of the distribution of key nest predators and examining its relationship with regent honeyeater nest success, contributing to the future management, and hopefully the survival, of an iconic Australian species.

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Appendix 1 – Additional site information

Table 9: Study site type

	NRHMP	Crates et al. (2018)*	New sites
Number of sites	126	41	79
Percentage of sites	51%	17%	32%

*Goulburn River region only

Table 10: Sites by region

	Central	North	North-west	West	South	Goulburn River
Number of sites	40	40	41	43	41	41
Percentage of sites	16%	16%	17%	17%	17%	17%

Table 11: Predominant Vegetation Community across study sites

	Other	River-oak	White-box	Yellow-box/ mugga ironbark
Number of sites	38	54	34	120
Percentage of sites	15%	22%	14%	49%

Table 12: Water Proximity of study sites

	On-site	50-200m	>200m
Number of sites	48	53	145
Percentage of sites	20%	22%	59%

Table 13: Nest proximity of study sites

	On-site	50-200m	>200m
Number of sites	34	41	171
Percentage of sites	14%	17%	70%

Table 14: Mistletoe Abundance across study sites

	None	1-10 clumps	>10 clumps
Number of sites	85	95	66
Percentage of sites	35%	39%	27%

Table 15: Hollow Abundance across study sites

	None	1-3 hollows	>3 hollows
Number of sites	32	101	113
Percentage of sites	13%	41%	46%

Table 16: Woody Debris Abundance across study sites

	Low	Medium	High
Number of sites	85	141	20
Percentage of sites	35%	57%	8%

Table 17: Canopy Cover across study sites

	0-15%	15-30%	>30%
Number of sites	11	66	169
Percentage of sites	4%	27%	69%

Table 18: Shrub Cover across study sites

	0-15%	15-30%	>30%
Number of sites	118	63	65
Percentage of sites	48%	26%	26%

Table 19: Ground Cover across study sites

	Short grass	Long grass/low shrub	Bare ground/leaf litter
Number of sites	114	40	92
Percentage of sites	46%	16%	37%

Table 20: Blossom Abundance across study sites

	None	Mild	Heavy
Number of sites	38	153	55
Percentage of sites	15%	62%	22%

Appendix 2 – Analysis of common brushtail possum detection methods

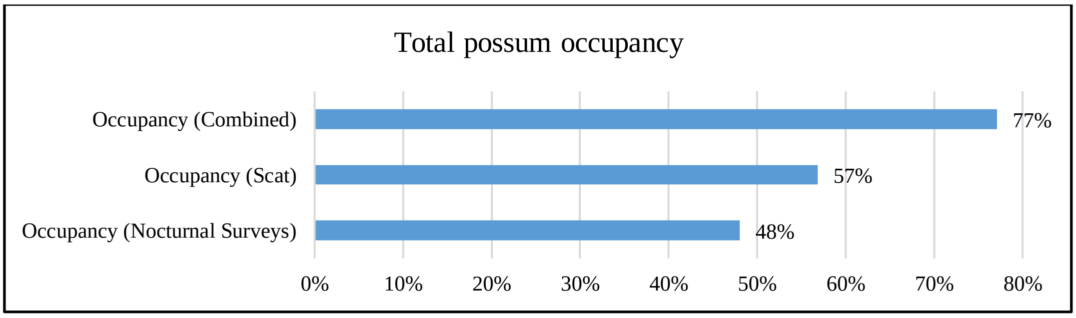

Figure 14: Percentage of sites where common brushtail possums were detected, separated by detection method.

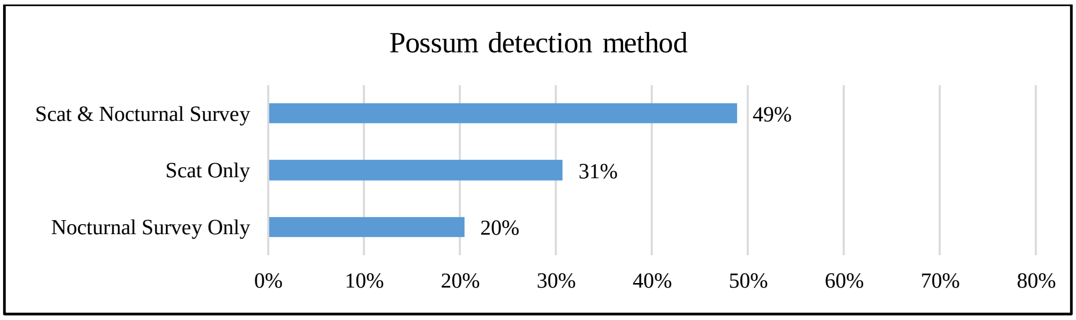

Figure 15: Percentage of sites at which possums were detected through only nocturnal surveys, only scat surveys or both scat and nocturnal surveys.

Common brushtail possums were more likely to be detected through scat surveys (57% of sites) than nocturnal surveys (48% of sites) (Figure 14). At most sites (51%) where possums were detected only one survey method was able to detect their presence (Figure 15).

Appendix 3 – Occupancy Modelling results

Table 21: Most parsimonious occupancy models for each predator species. Five models are included unless fewer than four had a lower AICc than the null model. ΔAICc shows the difference between the AICc of the model and the AICc of the most parsimonious model. The Akaike weight (w_i) indicates the percentage (proportion) of variation explained by the model. Ψ precedes the occupancy covariates, while p precedes the detectability covariates.

Species	Occupancy Model	ΔAICc	w_i
Australian magpie	Ψ(shrub).p(wind)	0.00	0.44
	Ψ(canopy + shrub).p(wind)	0.52	0.34
	Ψ(canopy + ground + shrub).p(wind)	3.03	0.10
	Ψ(ground + shrub).p(wind)	3.59	0.07
	Ψ(hollows + shrub).p(wind)	4.14	0.06
Australian raven	Ψ(wood).p(visit)	0.00	0.62
	Ψ(1).p(visit)	2.40	0.19
	Ψ(wood).p(1)	2.92	0.14
	Ψ(1).p(1)	5.33	0.04
Common brushtail possum	Ψ(hollows + blossom + wood).p(1)	0.00	0.36
	Ψ(hollows + blossom).p(1)	1.16	0.20
	Ψ(hollows + blossom + wood).p(spotlighter)	1.22	0.19
	Ψ(ground + hollows + blossom + wood).p(1)	1.97	0.13
	Ψ(hollows + blossom).p(spotlighter)	2.18	0.12
Glider spp.	Ψ(blossom).p(wind)	0.00	0.30
	Ψ(blossom + mistletoe).p(wind)	0.16	0.28
	Ψ(blossom).p(1)	0.75	0.21
	Ψ(blossom + mistletoe).p(1)	1.07	0.18
	Ψ(mistletoe).p(wind)	3.84	0.04
Grey butcherbird	Ψ(hollows).p(temp + visit)	0.00	0.28
	Ψ(hollows).p(visit + wind)	0.41	0.22
	Ψ(hollows).p(visit)	0.63	0.20
	Ψ(hollows).p(temp + visit + wind)	1.08	0.16
	Ψ(1).p(temp + visit)	1.35	0.14
Grey shrike-thrush	Ψ(1).p(time + visit + wind)	0.00	0.25
	Ψ(water).p(time + visit + wind)	0.22	0.22
	Ψ(hollows).p(time + visit + wind)	0.25	0.22
	Ψ(hollows).p(time + wind)	0.89	0.16
	Ψ(1).p(time + wind)	0.93	0.16
Laughing kookaburra	Ψ(ground).p(1)	0.00	0.52
	Ψ(1).p(1)	0.12	0.48
Noisy miner	Ψ(blossom + shrub).p(temp)	0.00	0.43
	Ψ(blossom + shrub + water).p(temp)	1.76	0.18
	Ψ(blossom + shrub).p(1)	2.04	0.16
	Ψ(hollows + blossom + shrub).p(temp)	2.06	0.15
	Ψ(blossom + shrub + hollows + water).p(temp)	3.39	0.08
Pied butcherbird	Ψ(shrub).p(time + wind)	0.00	0.25
	Ψ(1).p(time + wind)	0.22	0.22
	Ψ(1).p(time)	0.48	0.19
	Ψ(shrub).p(time)	0.75	0.17
	Ψ(shrub).p(wind)	0.75	0.17

Species	Occupancy Model	ΔAICc	w_i
Pied currawong	Ψ(veg).p(visit)	0.00	0.48
	Ψ(hollows + veg).p(visit)	0.39	0.40
	Ψ(veg).p(1)	4.53	0.05
	Ψ(hollows + veg).p(1)	4.86	0.04
	Ψ(hollows).p(visit)	5.67	0.03
White-winged chough	Ψ(shrub + veg + wood).p(wind)	0.00	0.29
	Ψ(shrub + wood).p(wind)	0.09	0.28
	Ψ(hollows + shrub + wood).p(wind)	0.46	0.23
	Ψ(shrub + water + wood).p(wind)	2.05	0.10
	Ψ(hollows + shrub + veg + wood).p(wind)	2.16	0.10

Table 22: Summaries of the most parsimonious occupancy model for each species showing the relationship between species level occupancy and occupancy / detectability covariates. Beta (β) indicates the effect of the covariate level on the response variable. Standard Error (SE) indicates the statistical accuracy of an estimate. Significant effects ($p < 0.05$) are shown in bold.

Species	Covariate	Relative to	β	SE	z	p
Australian magpie	Shrub Cover (15 - 30%)	Shrub Cover (0 - 15%)	-1.22	0.53	-2.31	**0.021**
	Shrub Cover (>30%)		-3.19	0.68	-4.69	**<0.001**
	Wind Speed (Light)	Wind Speed (None)	-0.81	0.29	-2.80	**0.005**
	Wind Speed (Moderate)		-0.20	0.34	-0.58	0.561
Australian raven	Woody Debris Abundance (Medium)	Woody Debris Abundance (Low)	-0.47	0.43	-1.09	0.276
	Woody Debris Abundance (High)		-10.31	83.09	-0.12	0.901
	Visit (2)	Visit (1)	-0.48	0.44	-1.08	0.282
	Visit (3)		-1.31	0.52	-2.51	**0.012**
Common brushtail possum	Hollow Abundance (1 - 3)	Hollow Abundance (None)	0.70	0.57	1.23	0.220
	Hollow Abundance (>3)		1.75	0.62	2.83	**0.005**
	Blossom Abundance (Mild)	Blossom Abundance (None)	-0.77	0.62	-1.25	0.211
	Blossom Abundance (Heavy)		0.94	0.85	1.10	0.270
	Woody Debris Abundance (Medium)	Woody Debris Abundance (Low)	0.73	0.43	1.70	0.089
	Woody Debris Abundance (High)		-0.71	0.75	-0.95	0.342
Glider spp.	Blossom Abundance (Mild)	Blossom Abundance (None)	1.54	0.91	1.69	0.091
	Blossom Abundance (Heavy)		3.01	1.76	1.71	0.088
	Wind Speed (Light)	Wind Speed (None)	-0.47	0.45	-1.04	0.296
	Wind Speed (Moderate)		-1.76	1.06	-1.65	0.099
Grey butcherbird	Hollow Abundance (1 - 3)	Hollows (None)	2.00	1.09	1.83	0.067
	Hollow Abundance (>3)		1.40	1.09	1.28	0.200
	Temperature (10 - 20°C)	Temperature (<10°C)	-0.96	0.58	-1.66	0.098
	Temperature (>20°C)		-1.48	0.71	-2.08	**0.038**
	Visit (2)	Visit (1)	-0.89	0.46	-1.96	0.050
	Visit (3)		-1.23	0.52	-2.38	**0.017**
Grey shrike-thrush	Time of day (Midday)	Time of day (Morning)	-0.37	0.26	-1.40	0.162
	Time of day (Afternoon)		-10.19	72.10	-0.14	0.888
	Visit (2)	Visit (1)	-0.68	0.30	-2.23	**0.026**
	Visit (3)		-0.27	0.28	-0.96	0.340
	Wind Speed (Light)	Wind Speed (None)	0.77	0.34	2.26	**0.024**
	Wind Speed (Moderate)		0.18	0.44	0.40	0.688
Laughing kookaburra	Ground Cover (Long grass / low shrub)	Ground Cover (Short grass)	-1.19	1.08	-1.10	0.270
	Ground Cover (Bare / leaf litter)		-1.37	0.97	-1.42	0.155

Species	Covariate	Relative to	β	SE	z	p
Noisy miner	Blossom Abundance (Mild)	Blossom Abundance (None)	-0.19	0.46	-0.41	0.680
	Blossom Abundance (Heavy)		-1.45	0.63	-2.29	**0.022**
	Shrub Cover (15 - 30%)	Shrub Cover (0 - 15%)	-0.22	0.39	-0.57	0.572
	Shrub Cover (>30%)		-1.57	0.53	-2.97	**0.003**
	Temperature (10 - 20°C)	Temperature (<10°C)	-1.17	0.56	-2.11	**0.034**
	Temperature (>20°C)		-0.45	0.62	-0.72	0.473
Pied butcherbird	Shrub Cover (15 - 30%)	Shrub Cover (0 - 15%)	-0.76	0.72	-1.06	0.289
	Shrub Cover (>30%)		-1.61	0.87	-1.85	0.065
	Time of day (Midday)	Time of day (Morning)	-1.19	0.59	-2.00	**0.045**
	Time of day (Afternoon)		0.50	0.97	0.51	0.610
	Wind Speed (Light)	Wind Speed (None)	0.79	0.57	1.39	0.164
	Wind Speed (Moderate)		-0.98	1.15	-0.85	0.395
Pied currawong	Veg (River-oak)	Veg (Other)	0.76	0.97	0.78	0.433
	Veg (White-box)		0.91	1.18	0.77	0.442
	Veg (Yellow-box / mugga ironbark)		-1.19	0.77	-1.54	0.123
	Visit (2)	Visit (1)	0.66	0.37	1.77	0.077
	Visit (3)		-0.54	0.47	-1.15	0.250
White-winged chough	Shrub Cover (15 - 30%)	Shrub Cover (0 - 15%)	0.23	0.49	0.47	0.640
	Shrub Cover (>30%)		-2.00	0.82	-2.43	**0.015**
	Veg (River-oak)	Veg (Other)	1.13	0.78	1.46	0.145
	Veg (White-box)		-0.67	0.93	-0.72	0.470
	Veg (Yellow-box / mugga ironbark)		0.15	0.70	0.21	0.830
	Woody Debris Abundance (Medium)	Woody Debris Abundance (Low)	-1.36	0.49	-2.77	**0.006**
	Woody Debris Abundance (High)		-1.24	0.95	-1.31	0.191
	Wind Speed (Light)	Wind Speed (None)	-1.46	0.54	-2.73	**0.006**
	Wind Speed (Moderate)		-0.37	0.59	-0.63	0.532

Appendix 4 – Histograms of aggregate predator measures

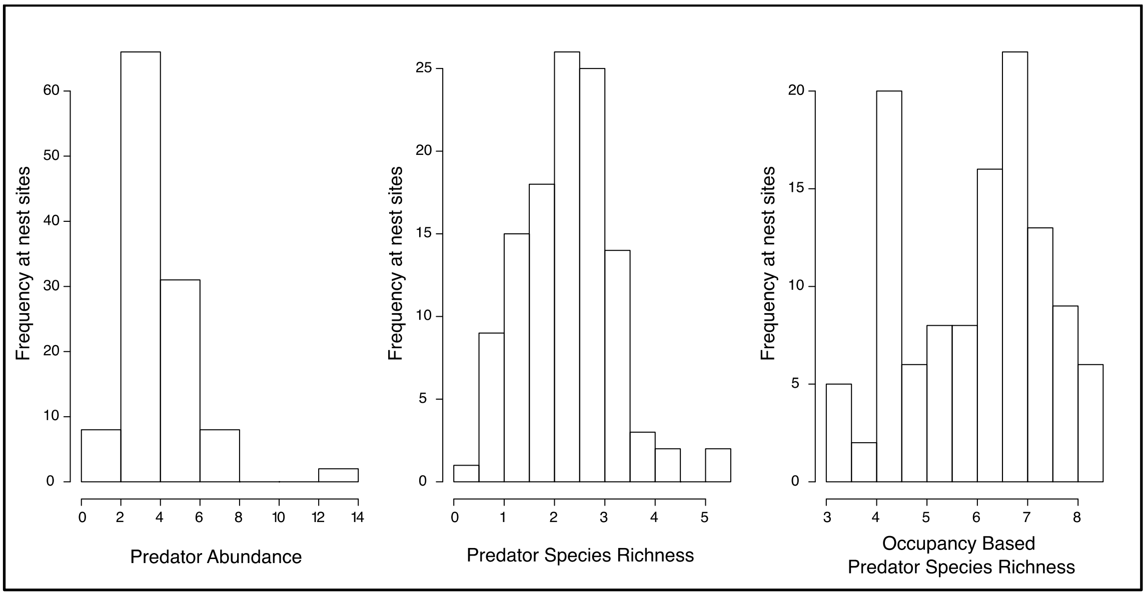

Figure 16: Histograms showing the frequency distributions of aggregate predator measure predictions at regent honeyeater nest sites.