Can artificial habitat mitigate impacts of climate change? Quantifying nesting habitat microclimate and use by little penguins (*Eudyptula minor*)

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This thesis is presented for the degree of Doctor of Philosophy
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Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

Erin Clitheroe

"...for the shield may be as important for victory, as the sword or spear."
— Charles Darwin, The Origin of Species

Abstract

Climate change continues to have significant effects on seabird species globally. Extensive work has linked variability in marine climate with changes in phenology, reproductive success and distribution for a wide range of taxa. Despite the reliance of seabirds on island and coastal habitats for breeding, comparatively few studies address the compounding effects terrestrial climate change may have on reproductive success and survival, particularly for populations breeding at the warm edges of a species' range. Edge populations may be key for not only predicting species' responses to expected change in climate but also for maintaining long term adaptive capacity of a species. For edge populations, conservation may rely on the intensive management and restoration of terrestrial habitat to facilitate population resilience and buffer the adverse effects of climate change. Among the critical elements of successful conservation planning for long term species persistence is a comprehensive understanding of habitat use, microhabitat conditions and climate change impacts at range edges.

This thesis investigated the use and microclimate conditions of nesting habitat used by a disjunct rear edge population of little penguins (*Eudyptula minor)*, seeking to identify implications of terrestrial climate change for this species. To achieve this, I characterised little penguin nesting habitat on Penguin Island, Western Australia and quantified relationships between nest attributes, microclimate (temperature and humidity), nest use and reproductive success. I monitored 50 natural nests and 113 existing nest boxes fortnightly for nesting activity and reproductive success over three little penguin breeding cycles (2013 - 2016). Nest characteristic data were collected, and microclimate measurements recorded using temperature and humidity loggers. Subsequently, I implemented a manipulative study testing artificial nest design and shading treatments to determine how to most effectively emulate the microclimate of natural cavities.

Little penguins did not select nest sites randomly, but instead based nest site selection on topographical, vegetation and nest site attributes. Natural nests were preferentially selected at sites with taller vegetation, close to a known landfall site and with a south-westerly facing entrance. In contrast, nest box use was predominately driven by the structure of the box, with longer boxes more likely to be used. Neither landscape nor nest site attributes were found to influence the overall success of either natural or artificial nests.

Nest boxes were ineffective at replicating microclimate conditions of natural nests. Nest boxes experienced consistently higher daily maximum temperature (~2 ˚C) and maintained temperatures above little penguins' upper thermoneutral limits (30 ˚C and 35 ˚C) for around one hour longer than natural nests. After accounting for ambient temperature, relative humidity and wind, fine scale biotic and abiotic nest characteristics also influenced the maximum daily nest temperature and hours of exposure to upper thermoneutral limits (reducing time of exposure by up to two hours in natural nests and three hours in nest boxes). To further investigate the potential impact of climate change on temperatures within nests, I fitted models which simulated a 2 ˚C temperature increase scenario. The number of days annually where natural and artificial nest conditions exceeded thermally stressful conditions (≥30 ˚C) are predicted to increase by approximately 37% and 56% and the number of days exceeding hyperthermic conditions (≥ 35 ˚C) are predicted to increase by approximately 41% and 49% respectively. Such changes will expose penguins to dangerous and potentially fatal thermal conditions, particularly during the late breeding and moulting phases of their annual cycle.

Experimental manipulation of boxes and shading revealed nest design and shading methods were effective at reducing nest temperature. Shaded timber boxes and buried plastic tunnels had thermal profiles either comparable to, or up to 2 ˚C cooler than, natural nests. Compared to exposed boxes, artificial shading and shading vegetation had the greatest

buffering effect, significantly lowering maximum nest temperature by around 4.5 ˚C and reducing the time of exposure to upper thermoneutral limits by approximately one hour.

Results here provide critical insight into how predicted changes in terrestrial climate may compound marine climate change impacts on seabird colonies at latitudinal margins, providing a more complete understanding of the climate limitations and management implications of edge populations. This thesis revealed that current and future thermal environments of little penguin terrestrial habitat on Penguin Island can exceed physiological limits for this species. Intervention to improve artificial nests and better quantify consequences is urgently needed given recent estimates of a declining population could lead to the local extinction of this colony. I outline the potential to use well-designed artificial nests as a method for increasing the resilience of vulnerable populations. Crucially, this thesis reveals that management to ameliorate climate change impacts must be purposive and thoughtful and highlights the potential for poorly designed or positioned artificial nests to become not only ineffective but present an ecological trap, potentially accelerating population decline.

Acknowledgement of country

I would like to acknowledge the Whadjuk people of the Noongar nation as the traditional owners of the land on which fieldwork for this research took place. I wish to acknowledge the strength of their enduring and dynamic culture and offer respects to their Elders, past, present and emerging.

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Statement of Contribution

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Chapter		Contribution (%)	
Chapter 3	Location and vegetation influence use of natural, but not artificial, nests in a rear edge population of little penguins (*Eudyptula minor*)	E Clitheroe	78
		J Fontaine	10
		B Cannell	10
		K Murray	2
Chapter 4	Microclimate of little penguin (*Eudyptula minor*) nests on Penguin Island, Western Australia	E Clitheroe	78
		J Fontaine	10
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		K Murray	2
Chapter 5	Artificial nests as a climate adaptation tool: buffering climate change effects on the little penguin (*Eudyptula minor*)	E Clitheroe	80
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CHAPTER 1

General Introduction and thesis objectives

1.1 Introduction

Climate change is adversely affecting marine and terrestrial systems worldwide (Parmesan and Yohe 2003; Parmesan 2006; Hoegh-Guldberg and Bruno 2010; Chen *et al.* 2011; Doney *et al*. 2012; Bellard *et al.* 2012; Diffenbaugh and Field 2013; IPCC 2018). An increase in sea temperature plus rising ocean acidity are accepted as the key factors driving variability and change in marine systems (Hoegh-Guldberg and Bruno 2010; Pratchett *et al.* 2011; Doney *et al*. 2012; Lough *et al.* 2012). The impacts on biotic systems are expected to intensify, resulting in widespread extinctions and significant shifts in the phenology of breeding and movement patterns of marine taxa around the world (Chambers *et al.* 2005; Hoegh-Guldberg and Bruno 2010; Dawson *et al*. 2011; Young *et al.* 2012; Cahill *et al.* 2013; Diffenbaugh and Field 2013). Given their reliance on both marine (foraging) and terrestrial (breeding) habitats and upper tropic position, seabirds are a group particularly vulnerable to the combined effects of changing climate (Young *et al*. 2012).

Climate change is widely accepted as a major contributing factor threatening many seabird species (Chambers *et al*. 2005; Congdon *et al*. 2007; Grémillet and Boulinier 2009; Chambers *et al*. 2011; Young *et al*. 2012; Dias *et al*. 2019). Existing at the ocean-land ecotone and utilising both marine and terrestrial environments, seabirds are exposed to synergistic marine and terrestrial climate pressures (Sydeman *et al*. 2012). Climate variability is known to influence the abundance, productivity, community structure and behaviour of many seabird populations (Congdon *et al*. 2007; Grémillet and Boulinier 2009; Chambers *et al.* 2011

Chambers *et al*. 2013;). Furthermore, climate change is thought to be producing a poleward shift in distribution of numerous taxa including seabirds, and population contractions at the lower latitudinal edges of species' range are being observed (McChesney and Carter 2008). Populations inhabiting the latitudinal margins of a species distribution are particularly sensitive to climate driven pressures and are becoming increasingly pertinent for predicting species' responses to expected climate change (Hampe and Petit 2005; Grémillet and Boulinier 2009).

Populations at latitudinal margins are more often exposed to climatic extremes relative to those at the range core, are adapted to unique environmental conditions and may have higher adaptive capacity in periods of rapid change (Safriel *et al.* 1994; Fraser 1999; Munwes *et al.* 2010). Recent studies suggest that peripheral populations harbour higher genetic diversity than central populations; indeed, they may be key for providing adaptations to novel environments created through climate change (Hampe and Petit 2005; Eckert *et al.* 2008; Sexton *et al.* 2009). Thus, populations on latitudinal fringes are relevant for not only predicting species' responses to expected climate change but for maintaining the long term adaptive capacity of a species (Lomolino and Channell 1995; Hampe and Petit 2005; Pauls *et al.* 2013).

Previous research predicting future distributions of species frequently focused on species' bioclimate envelopes and assumed a homogeneous landscape, ignoring other factors that may be important for predicting a species distributional range (Pearson and Dawson 2003). However, it is becoming increasingly clear that distributional response for many species will be dependent on their capacity to migrate through dynamic heterogeneous landscapes (Pearson and Dawson 2003). Species that have limited dispersal ability will have to rely on *in situ* adaptation to persist (Davis *et al.* 2005; Vedder *et al.* 2013) or risk extinction (Thomas *et al.* 2004). Seabirds, with their fragmented breeding locations which are frequently on islands, epitomize this issue. All seabirds rely on land (islands, continental margins, ice shelves) for reproduction – a crucial bottleneck in their life cycle. For many species, particularly populations existing at range edges, this will likely mean dealing with challenging thermal conditions.

As marine top predators, reliant mainly on nekton (fish and squid) and zooplankton (copepods and krill), it is not surprising that the bulk of the literature focusing on climate change impacts on seabirds is centred around changes in marine productivity and associated food webs. However, in recent decades, temperatures over land have increased at a rate twice of that observed over oceans (Diffenbaugh and Field 2013) and few studies have examined how changes in the terrestrial environment could be compounding climate change impacts on seabirds. Potential impacts of increased air temperature can include direct physiological effects such as heat stress (Oswald and Arnold 2012; Cook *et al.* 2020) and associated behavioural changes including alteration in incubation behaviour and phenotypic expression in chicks (Hart *et al.* 2016; Cook *et al.* 2020). Furthermore, indirect impacts of climate change include changes in rainfall patterns and vegetation type and cover, affecting the suitability and availability of core nesting or roosting habitat (Chambers *et al.* 2011; Chambers *et al.* 2012; Hart *et al.* 2018).

Gaining a holistic understanding on how both changing terrestrial and oceanographic conditions are impacting seabird population dynamics and what climate change predictions are most likely to affect seabirds is integral to facilitate the effective conservation of seabird species and development of appropriate adaptation strategies (Sydeman *et al.* 2012). While there is potential for some species to cope with climate change through the adjustment of life-history characteristics, many seabird populations have limited scope for shifting poleward thus their persistence will rely on adapting to changing conditions *in situ*. The resilience of species may be enhanced by buffering potential adverse effects of climate change through management-based adaptation strategies (Chambers *et al.* 2013). Managing habitat quantity and quality is one compensatory measure that can be used to buffer seabirds against environmental change (Chambers *et al.* 2011).

The use of artificial nest structures is a strategy commonly used in improving habitat for fauna species. In seabirds they are used in several contexts including the establishment or translocation of seabird colonies (Priddel *et al.* 2006; Miskelly *et al.* 2009; Carlile *et al.* 2012), monitoring/research (Wilson 1986; Podolsky and Kress 1989; Klomp *et al.* 1991; Wilson 1993; Bolton 1996; Perriman and Steen 2000; Johannesen *et al.* 2002), and the provision or restoration of seabird nesting habitat (Priddel and Carlile 1995; Gaston 1996; Houston 1999; Lalas *et al.* 1999; Kemper *et al.* 2007). However, in many cases artificial nests are deployed with limited knowledge on the suitability of the microclimate or the potential consequences of providing suboptimal environments for inhabitants. Artificial nests are often inadequate at replicating conditions of natural nests and ineffective at buffering against increasing ambient temperatures. (Ropert-Coudert *et al.* 2004; Lei *et al.* 2014; Rowland *et al.* 2017). Despite this, warmer and drier terrestrial conditions associated with climate change are likely to reduce both the quality and availability of important nesting vegetation, potentially increasing the reliance on artificial nests as an adaptation strategy. The potential of artificial nests as a tool to maintain optimal microclimate and mitigate negative climate change effects remains largely unexploited.

Penguin Island, situated in the Shoalwater Islands Marine Park, Western Australia, is home to a genetically distinct population (Cannell *et al.* 2012) of little penguins (*Eudyptula minor*). It is the largest of three colonies located at a lower latitude than all other known populations in WA, and as such this population exists at the northern edge of this species' range and at its likely thermal limit (Stahel and Gales 1987). Peripheral populations such as these hold high ecological value due to their adaptive potential (Hampe and Petit 2005; Eckert *et al.* 2008; Sexton *et al.* 2009). However, the conservation value of Penguin Island's penguins is further elevated due to the significant economic and social importance this colony maintains.

Penguin Island's population has been shown to respond negatively to elevated sea surface temperatures causing reduced prey abundance leading to speculation that future temperature increases will further depress already low reproductive success (Cannell *et al.* 2012). In addition to changes in the marine environment, reduced rainfall and increased terrestrial temperatures associated with climate change are likely to alter the terrestrial habitat and vegetation used by the breeding population. Little penguins are burrow nesting seabirds, however, on Penguin Island the sandy substrate is too soft in which to excavate stable burrows and penguins instead nest under dense vegetation, in rocky crevices or in artificial nest boxes (Dunlop *et al.* 1988; Klomp *et al.* 1991; Ropert-Coudert *et al.* 2004). Because of a warming and drying climate (Andrys *et al.* 2017) a reduction in vegetation extent is probable with subsequent negative impacts both on the thermal environment of the nest as well as soil stability (Dann and Chambers 2013).

The vulnerability of this population to effects of ongoing climate change highlights the ecological importance for investigating response of seabirds to climate change on land as well as at range edges. The ability of this population to persist will be partly dependent on its ability to adapt to changes in food resources and availability. However, high air temperature can also reduce population stability through negative effects on survival and breeding productivity (Dann 1991; Chambers *et al.* 2011; Cannell *et al.* 2016). Thus, the resilience of penguins here coping with marine variability could be enhanced if additional pressures, such as increased thermoregulatory demands posed by changing terrestrial climate, are mitigated. It may be possible to buffer effects of rapid oceanographic change, through management of their terrestrial breeding habitat such as providing artificial nests (Figure 1.1). However, this demands a comprehensive understanding of nest habitat preference to ensure the continued efficacy of artificial nests as an effective climate change mitigation strategy for Penguin Island's little penguin population.

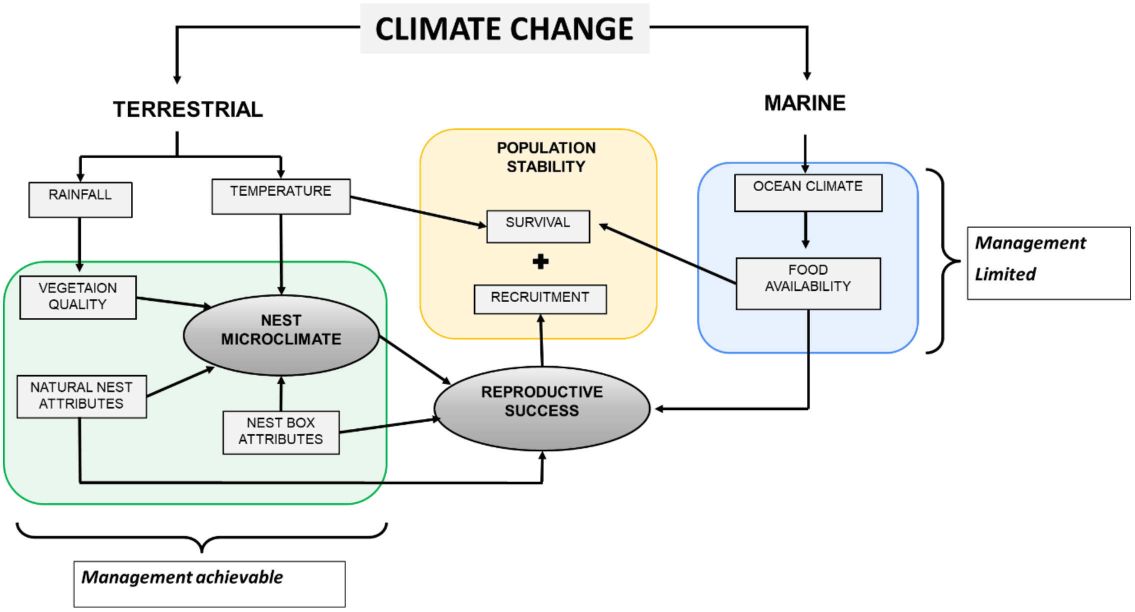

Figure 1.1: The persistence of Penguin Island's little penguin colony will rely on continued adult survival and sufficient recruitment into the colony. Marine climate change and associated changes in availability and abundance of penguin prey will likely affect this stability of this population by reducing both adult survival and reproductive success. However, it may be possible to mitigate effects of rapid oceanographic change through management of their terrestrial breeding habitat.

1.2 Thesis objectives and structure

The broad objectives of this thesis were to describe and quantify use and microclimate of nesting habitat used by a genetically distinct population of little penguins (*Eudyptula minor)* at the northern edge of this species' distribution. It sought to identify implications of terrestrial climate change and evaluate the efficacy of artificial nests as an adaptive management option for this species. To achieve this, I characterised little penguin nesting habitat and quantified relationships between nest attributes, microclimate (temperature and humidity), nest use and reproductive success. I tested two artificial nest designs and shading treatments, assessing their capacity to provide microclimate conditions comparable to natural nest burrows. This thesis set out to answer three main questions:

1. How do nest characteristics influence nest use and breeding success?
2. Do current artificial nests replicate microclimate conditions of natural nest sites and what factors influences nest temperature?
3. Can we improve artificial nests to replicate microclimate conditions of natural nest sites?

This thesis is organised as a series of chapters for publication answering each of the questions above (Chapters 3 – 5). These are preceded by a literature review providing background information (Chapter 2). Chapters 2 to 5 are bounded by an introductory chapter introducing the topic and discussion chapter which synthesises findings and makes recommendations for management and future research. Due to the stand alone structure of the research chapters there is a degree of repetition, particularly in introductory material, descriptions of study site and species and some field techniques. Where possible, I reference sections of relevant chapters.

The next chapter in the thesis (Chapter 2) is a literature review. It reviews the literature relevant to the study highlighting knowledge and research gaps. It details knowledge on the impacts of climate change as it relates to seabirds and the observed and predicted effects on seabird demographics. It examines nest habitat selection studies exploring how data from these studies can aid in conservation of seabird terrestrial breeding habitat, and reviews published studies on the use of artificial nests in seabird conservation to determine the benefits of artificial nest boxes in the conservation of seabirds.

The first data chapter, Chapter 3, investigates use of nesting habitats by little penguins on Penguin Island. I describe and quantify characteristics of both natural and artificial nests and employ generalized linear mixed models to identify what habitat features influence probability of nest use and probability of nest success. The objective of this chapter is to define important features of little penguin nesting habitat to inform management decisions.

Chapter 4 is a detailed quantitative study investigating microclimate of natural and artificial little penguin nesting habitats. It describes microclimate (temperature and relative humidity) of artificial nest boxes *in situ* on Penguin Island and examines how they differ from natural nest burrows. Linear mixed models and generalized linear mixed models are used to investigate the influence of climate and nest attributes (measured in Chapter 3) on nest microclimate. It subsequently uses these models to predict future nest temperatures under a climate scenario of 2 ˚C of warming and the implications for this range edge population. The aim of this chapter is to provide insight into how predicted changes in climate may impact populations living at their thermal limit and seeks to inform management decisions concerning the suitability of artificial and natural nesting habitats under changing climatic conditions.

In Chapter 5, I implement a manipulative study testing artificial nest design and shading treatments to determine how to most effectively emulate the microclimate of natural cavities. I test two nest designs and shading treatments and quantify the microclimate within in relation to box design and shading type. Linear mixed models and generalized linear mixed models are used to investigate the effect of nest type and shading treatment on nest temperature. The aim of this chapter is to investigate one possible option for climate change mitigation and provide insight into appropriate management measures for little penguin persistence and to provisioning of artificial habitats globally, especially seabirds.

Chapter 6 provides an overall synthesis of the findings. It discusses the efficacy of artificial nests as a climate adaptation tool and implications for management. It recommends management actions that could help to conserve and improve both the natural and artificial breeding habitat on Penguin Island, while maintaining the ability to monitor the breeding population. It defines longer term pressures posed by climate change and prioritises other mitigating management responses that can be put in place to increase persistence of little penguins and other range restricted seabirds.

This thesis offers critical insight into how predicted changes in terrestrial climate may compound marine climate change impacts on seabird colonies at latitudinal margins, providing a more complete understanding of the climate limitations and management implications of edge populations. It reveals that current and future thermal environments of little penguin terrestrial habitat on Penguin Island can exceed physiological limits for this species. It outlines the potential to use well-designed artificial nests as a method for mitigating climate impacts on burrow nesting seabirds. Crucially, this thesis reveals that management to ameliorate climate change impacts must be purposive and thoughtful and highlights the potential for poorly designed or positioned artificial nests to become not only ineffective but present an ecological trap, potentially accelerating population decline.

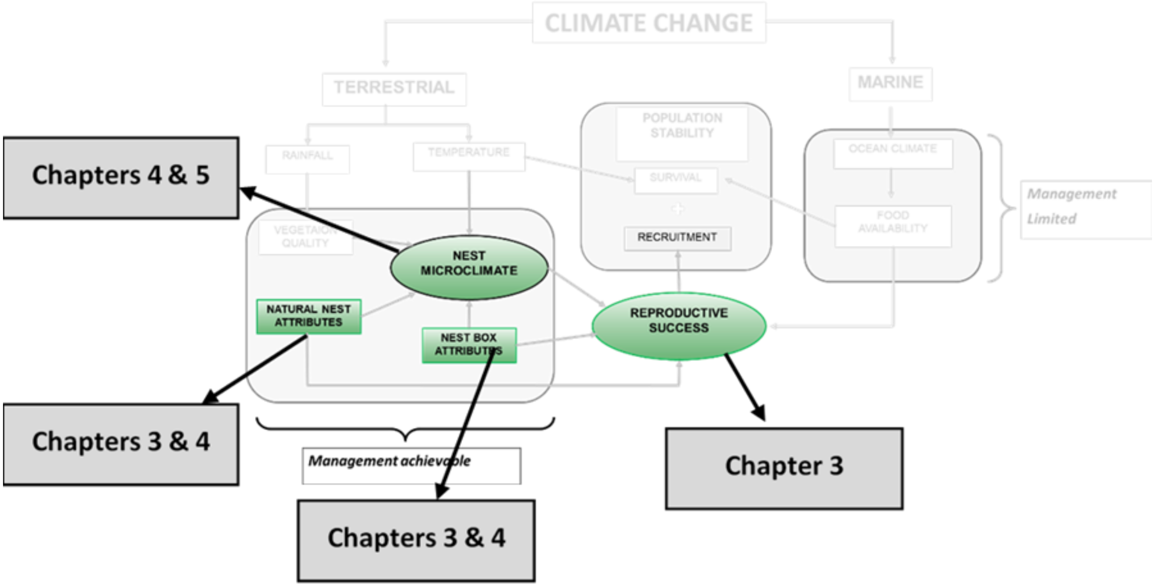

Figure 1.2: Schematic of thesis chapters as they relate to the terrestrial components of population stability.

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CHAPTER 2

Climate change, nest selection and the use of artificial nests for seabirds: literature review.

2.1 Abstract

This chapter synthesises published research relevant to climate change impacts on seabirds. Specifically, it reviews the scientific literature linking climate driven changes in the marine environment with demographic response of seabirds, focusing on species found in temperate climatic zones. It examines nest habitat selection studies in order to explore how data from these studies can aid in conservation of seabird terrestrial breeding habitat and reviews current literature on the use of artificial nests in seabird conservation to determine the benefits of using artificial nest boxes in the conservation of seabirds. Sixty-three studies addressing climate change, 39 habitat selection studies and 26 studies investigating artificial habitat were reviewed. This revealed that climate variation, particularly large-scale oceanographic processes, will have significant negative effects on several seabird demographic parameters. However, studies focusing on low latitude populations or impacts of terrestrial climate change on seabirds are under-represented in the literature. The importance of habitat characteristics in the selection and reproductive output of nests varied greatly between studies indicating that preferred nest characteristics are specific to a species or a population. The most common use of artificial nests was found to be for the purpose of enhancing habitat in declining seabird populations. While demographic responses to artificial nest provision varied, many studies report improved reproductive success or increases in population abundance. The negative consequences of artificial nest use for seabirds are poorly researched and require

further investigation. This review proposes that a greater understanding of nest site preference and microclimate is required to ensure the efficacy of artificial nests as a climate adaptation tool for seabird populations most exposed to climate change.

This literature review was undertaken and written in 2013/2014, thus while some text has been revised to include more recent research, tables and figures have not been updated and reflect the literature reviewed at the time of writing.

2.2 Introduction

Global climate change is one of the most important threats affecting marine and terrestrial systems (Hoegh-Guldberg and Bruno 2010; Pratchett *et al.* 2011; Doney *et al.* 2012; Lough *et al.* 2012; IPCC 2018). Effects of climate change on biotic systems will be profound. The IPCC (2018) estimate that global temperature is currently increasing at 0.2 ˚C per decade with average global air temperature likely to rise by 1.5 ˚C above pre-industrial levels between 2030 and 2052. The world's oceans absorb most of this thermal energy and as a result the upper 100 m of the ocean will also continue to warm by 0.6°C - 2°C by 2100 (Collins *et al.* 2013). Water temperature is a primary controlling factor for marine ecosystem function, and increasing sea temperature coupled with ocean acidification are accepted as the major processes behind variability and change in marine systems (Guldberg and Bruno 2010; Pratchett *et al.* 2011; Doney *et al.* 2012; Lough *et al.* 2012; Hoegh- IPCC 2018).

Increasing ocean temperatures will have significant direct consequences causing a rise in sea level, increased ocean stratification, reduction in sea-ice, and altered patterns of circulation, precipitation and fresh water input (Doney *et al.* 2012). Effects of rising acidity could lead to direct loss of taxa and altered community dynamics (Hoegh-Guldberg and Bruno 2010; Doney *et al.* 2012). Impacts on biotic systems are expected to intensify, resulting in widespread extinctions and significant shifts in the phenology and movement patterns of taxa around the world (Chambers *et al.* 2005; Hoegh-Guldberg and Bruno 2010; Dawson *et al.* 2011; Young *et al.* 2012; Cahill *et al.* 2013; Diffenbaugh and Field 2013). Given their reliance on both marine (foraging) and terrestrial (breeding) habitats and upper tropic position, seabirds are a group particularly vulnerable to the combined effect of changing climate (Young *et al.* 2012; Jenouvrier 2013; Dias *et al.* 2019).

In marine systems, seabirds are upper trophic level predators (Sydeman *et al.* 2012). They are strongly influenced by oceanographic change. For example, the El Niño-Southern Oscillation (ENSO) and sea surface temperature (SST) have been shown to influence changes in the abundance, distribution, productivity, community structure and behaviour of many species (Congdon *et al.* 2007; Chambers *et al.* 2009; Grémillet and Boulinier 2009; Chambers *et al.* 2011; Chambers *et al.* 2013; Kowalczyk *et al.* 2015; Precheur *et al.* 2016; Champagnon *et al.* 2018; Desprez *et al.* 2018). Populations existing at the warm edge of a species' range are at high risk of local extinction (Thomas *et al.* 2004; Grémillet and Boulinier 2009; Cahill *et al.* 2013). Understanding how changing oceanographic conditions are impacting seabird population dynamics and what climate change predictions are most likely to affect seabirds is integral to facilitate effective conservation of seabird species and development of appropriate adaptation strategies (Sydeman *et al.* 2012).

While there is potential for some species to cope with climate change through the adjustment of life-history characteristics, the resilience of species to environmental change can be enhanced by buffering adverse effects of climate change through management-based adaptation strategies (Chambers *et al.* 2011; Chambers *et al.* 2013). Managing breeding habitat quantity and quality is one compensatory measure that can be used to buffer seabirds against environmental change (Chambers *et al.* 2011; Hobday *et al.* 2015). The use of artificial nest structures is a technique commonly used to provide additional habitat for nesting seabirds (Wilson 1986; Priddel and Carlile 1995; Gaston 1996; Houston 1999; Lalas *et al.* 1999; Kemper *et al.* 2007; Bried *et al.* 2009; Libois *et al.* 2012; Sherley *et al.* 2012a; Sutherland *et al.* 2014;). However, their application and value as a climate adaptation strategy remains largely unexploited. This area of research is becoming increasingly important as changing rainfall and temperature will have implications for the quality of breeding habitat, in particular the microclimate of the nest (Dann and Chambers 2013; Hart *et al.* 2016).

This chapter will identify the physical changes in the marine environment influenced by climate change and the oceanographic processes that could potentially affect seabird populations. It reviews the literature linking climate driven changes in the marine environment with trends in seabird demographics, focusing on those species found in temperate climatic zones. The second part of this review examines nest habitat selection studies exploring how data from these studies can aid in conservation of seabird terrestrial breeding habitat. Finally, this chapter reviews current literature on the use of artificial nests in seabird conservation to determine the benefits of using artificial nest boxes in the conservation of seabirds.

2.3 Observed and predicted impacts of climate change on marine climate

Increases in CO_2 levels in the atmosphere have driven an increase in global air temperatures (IPCC 2018) with profound effects on marine climate and ocean productivity (Grémillet and Boulinier 2009; Doney *et al.* 2012). The key climate change processes likely to alter ocean climate and their potential effects are widely published throughout the peer-reviewed literature and are summarised below (Table 2.1).

Table 2.1: Predicted physical changes to the marine environment through climate change (Grémillet and Boulinier 2009; Chambers *et al.* 2011; Wernberg *et al*. 2011; Doney *et al.* 2012; Poloczanska *et al*. 2012).

Process	Impact
Sea level rise	Temperature increases can cause surface waters to expand and increase glacial melt resulting in sea level rise. This can lead to inundation and flooding of coastal environments as well as shoreline erosion and realignment.
Reduced mixing	Warmer surface water can prevent upwelling of cooler nutrient rich water into the euphotic zone, subsequently reducing primary productivity.

‘Freshening’ of polar oceans	Warmer air temperatures are inducing melting of Arctic and Antarctic inland and coastal ice causing a ‘freshening’ (increases in freshwater inflow) of polar oceans, further strengthening vertical stratification in the water-column, altering mixing and affecting productivity of surface waters during summer months.
Changed precipitation patterns	Warmer atmosphere and sea surface temperature is altering rainfall patterns. In low rainfall areas, rainfall will be reduced further resulting in decreased sediment and nutrient runoff. The opposite will occur in areas of high annual rainfall. Changes in nutrient and sediment inputs will have both positive and negative effects on marine organisms affecting productivity.
Reduced oxygen levels	Reduced oxygen levels in the upper layers of the ocean are likely to be observed as a consequence of increasing stratification and warming SST Lower oxygen levels generally observed in warmer surface waters will place physical stress on many marine organisms potentially leading to mass mortality.
Altered wind patterns and storms	Rising air temperatures and warmer SST’s influence regional wind patterns affecting ocean circulation and affect the strength and frequency of storms and hurricanes potentially impacting vulnerable coastal habitats. Large pressure differentials generated by warmer air temperatures are thought to intensify and change seasonality of upwelling wind enhancing primary productivity.
Ocean acidification	Increased oceanic CO_2 uptake is a major driver of ocean acidification. Increased acidity combined with increased ocean temperature will affect phytoplankton and zooplankton species (both negatively for some and positively for others) altering the composition of plankton communities. Altered ocean chemistry will also affect coral calcification resulting in erosion of reef structure.
Change in ocean currents	Uneven heating of the ocean will likely alter behaviour of ocean currents having major implications for regional climates.
Change in natural modes of climate variability (e.g. ENSO)	Increases in the amplitude and frequency of natural modes of climate variability including the El Nino-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NOA) when interacting with warm SSTs. There is no clear indication on how or if these will change. Despite this it is wise to adopt a precautionary approach and assume that ENSO events will continue as a source of inter-annual climate variability affecting marine environments.

Described changes in physical and chemical conditions of the ocean climate (Table 2.1) are likely to have a negative impact on marine ecosystem functions primarily by reducing primary productivity thereby affecting food webs and top predators such as seabirds (Grémillet and Boulinier 2009; Young *et al.* 2012). Existing at the ocean-land ecotone utilising both marine and terrestrial environments, seabirds are particularly sensitive to change and are exposed to multiple climate stressors from both marine and terrestrial environments (Sydeman *et al.* 2012).

2.4 Climate change and seabirds

The impact of climate change on seabirds will be evident via both direct and indirect mechanisms (Grémillet and Boulinier 2009; Croxall *et al.* 2012; Young *et al.* 2012). For example, changes in adult survival or breeding success will be impacted by increased storm intensity via mass seabird mortality and/or destruction of breeding colonies (Chambers *et al.* 2011; Hass *et al.* 2012; Newell *et al.* 2015). On land, overheating of adults, eggs, or chicks will negatively impact the same demographic components of adult survival and recruitment (Stokes and Boersma 1998; Gaston *et al.* 2002; Kemper *et al.* 2007; Chambers *et al.* 2011; Pichegru 2012). However, the indirect effects of climate change will play a significant role in determining the future persistence of seabird populations and distribution. Changes in physical ocean conditions (Table 2.1) are very likely to amplify up through marine food webs to change abundance and distribution of key seabird prey items (Grémillet and Boulinier 2009; Sydeman *et al.* 2012). Responses of seabirds will differ for many reasons. These may include their life history characteristics, foraging guilds, and specialisation to local environments (Chambers *et al.* 2011). For example, species that exhibit considerable breeding site philopatry such as the little penguin (*Eudyptula minor*) (Stahel and Gales 1987) or those with highly restricted geographical range such as the Galápagos penguin (*Spheniscus mendiculus)* (Vargas *et al.* 2007) are probably at the most immediate risk of extinction given their limited dispersal capacity (Thomas *et al.* 2004; Grémillet and Boulinier 2009).

2.4.1 Observed climate change impacts on temperate seabirds

A growing body of literature exists investigating the link between climate variability, to past and ongoing changes in reproductive output, survival, and population abundance of seabird species. A systematic search of electronic database Web of Science using combinations of the search terms 'seabird' 'sea bird' 'climate change' 'climate variability' 'climate' 'warming' 'impact' and 'effect' and a subsequent search of citations within resulting articles found 63 studies addressing this topic. Each of the 63 reviewed studies explored climate change impacts on 52 different species of seabird from 11 families, representing only 15% of the world's seabird species. While research on climate change impacts has been carried out in various locations around the world, most studies (46%) were carried out in polar or sub-polar climatic zones. Studies focusing on seabirds in temperate zones made up 38%, while only 17% of papers examined tropical seabird species. Species existing at lower latitudes are under-represented in the literature. This likely reflects the latitudinal gradient in species richness observed in the distribution of seabirds, decreasing towards low latitudes, and increasing towards high ones with the greatest diversity observed between 37 and 59 ˚S (see Chown et al. 1998).

From the reviewed literature (Table 2.2), six response variables were measured including reproduction (e.g. breeding success), abundance, survival, behaviour (e.g. change in foraging behaviour), distribution and phenology (timing of breeding or migration in relation to climate variables). The most common response variable considered was reproduction, found in 35% of papers followed by phenology (29%) behaviour (12%) abundance (12%) and survival (9%) (Figure 2.1a). Notably distribution, which is suggested as a likely response to climate change (Murawski 1993; Hampe and Petit 2005; Perry *et al.* 2005; Cheung *et al.* 2009; Doney *et al.* 2012), received the least attention making up only 3% of studies although this is likely due to difficulties associated with collecting long-term at sea observational data from which to confidently establish trends (Barbraud *et al.* 2012). Of the climate processes investigated, SST and ENSO or NAO (North Atlantic oscillation) dominated most previous seabird-climate research. Large-scale oceanographic variation and SST accounted for 58% of all climate-seabird research studies (Figure 2.1b).

ENSO related changes in food availability and its influence on important demographic parameters of seabird species has been observed off the Western Australian coast, at the Houtman Abrolhos islands, where significantly poorer breeding was observed in breeding colonies of lesser noddy (*Anous tenuirostris),* brown noddy (*A. stolidus*), sooty tern (*Sterna fuscata*), and wedge-tailed shearwater (*Puffinus pacificus)* (Surman and Nicholson 2009). The authors suggest a link between the reduced breeding productivity and ENSO-related changes in offshore food webs during the breeding season. In New Zealand, success, effort and timing of breeding in the red-billed gull (*Larus novaehollandiae scopulinus*) were strongly correlated with ENSO-driven reduction in prey availability (Mills *et al.* 2008). Some studies have directly linked SST and ENSO events to changes in abundance of seabird populations. For example, a strong El Nino event in 1982-1983 was linked to a 65%-72% population decrease in Humboldt penguin (*Spheniscus humboldti*) colony size in Peru (Hays 1986).

While most (75%) of the studies reviewed predicted changes in the marine environment will have negative effects on seabirds, there is evidence that some species may in fact benefit, at least in the short term, from fluctuating ocean thermal regimes. Changes in the spatial distributions and migratory patterns of seabird prey are not uniform, decreasing productivity in some areas while increasing productivity and thus food availability in others (Grémillet and Boulinier 2009). This may initially lead to increased productivity in some species. For example, northern gannets (*Sula bassana*) in Newfoundland have demonstrated a gradual increase in population size that has been linked to increase of local prey abundance due to warming of surface water temperature (Montevecchi and Myers 1997). Species with the ability to extend their distributional range may also benefit (Dunlop 2009). Whereas those with limited geographic plasticity, like the Galápagos penguin (Vargas *et al.* 2007) are most at risk.

Table 2.2: Studies investigating seabird-climate associations for temperate species and key details and findings of each study.

Author/s	**Location**	**Species**	**Environmental parameter**	**Seabird parameter**	**Observed trend**
Montevecchi and Myers (1997)	North America (Newfoundland)	Northern gannet *(*Sula *bassana)*	SST	Abundance	Increased abundance observed with warmer sea surface temperature
Peacock *et al.* (2000)	New Zealand	Yellow-eyed penguin *(Megadyptes antipodes)*	Air temp, precipitation, ENSO	Reproductive success	Decline in breeding success due to warmer drier climate
Perriman *et al.* (2000)	New Zealand	Little penguin *(Eudyptula minor)*	El Nino/ La Nina	Reproductive success and phenology	La Nina was associated with later breeding and reduced egg lay. Chick survival was reduced.
Numata *et al.* (2000)	New Zealand	Little penguin *(Eudyptula minor)*	ENSO	Behavioural/reproductive phenology	Increased foraging trips, poorer body condition and later breeding observed in ENSO years
(Culik *et al.* 2000)	Chile	Humboldt penguin *(Spheniscus humboldti)*	SST	Behaviour	Further foraging range associated with warmer SST.
(Oedekoven *et al.* 2001)	California	Common murre *(Uria aalge)*, sooty shearwater *(Puffinus griseus)*, Cassin's auklet *(Ptychoramphus aleuticus)*	SST, ENSO	Abundance and distribution	Species population declined following El Nino years.
Frederiksen *et al.* (2004)	Scotland	Black-legged kittiwake *(Rissa tridactyla)*, common murre *(Uria aalge)*, European shag *(Phalacrocorax aristotelis).*	SST, NAO	Reproductive phenology	High NOA indices associated with earlier breeding in kittiwakes and guillemots and high SST associated with earlier breeding in shags.

Author/s	Location	Species	Environmental parameter	Seabird parameter	Observed trend
Chambers (2004)	South Eastern (SE) Australia	Little penguin *(Eudyptula minor)*	SST, ENSO	Reproductive success and phenology	Warm SST linked to earlier onset of breeding and increased breeding success in short term.
Crawford *et al.* (2008)	South Africa	Leach's storm petrel *(Oceanodroma leucorhoa)*, crowned cormorant *(Microcarbo coronatus)*, Hartlaub's gull *(Chroicocephalus hartlaubii)*, kelp Gull *(Larus dominicanus)*, African penguin *(Spheniscus demersus)*, cape gannet *(Morus capensis)* cape cormorant *(Phalacrocorax capensis)*, bank cormorant *(Phalacrocorax neglectus)*, swift tern *(Sterna bergii)*	Local climate change	Abundance/distribution	Changes in both distribution and population
Frederiksen *et al.* (2008)	Europe	European Shag *(Phalacrocorax aristotelis)*	Extreme weather events	Survival	Reduced survival during extreme weather events
Mills *et al.* (2008)	New Zealand	Red-billed gull (Larus *novaehollandiae scopulinus)*	ENSO/ Wind	Reproductive phenology and effort	Proportion of non-breeders and laying date was negatively correlated with SOI and frequency of NE wind
Watanuki *et al.* (2009)	Asia - Japan	Rhinoceros auklet *(Cerorhinca monocerata)*	Air temperature, ice cover	Reproductive phenology	Mismatch between breeding season and food availability
Surman and Nicholson (2009)	South Western (SW) Australia	Lesser noddy *(Anous tenuirostris)*, brown noddy *(Anous stolidus)*, sooty tern *(Onychoprion fuscatus)*, wedge-tailed shearwater *(Puffinus pacificus)*	ENSO	Reproductive success	Reproductive output was significantly reduced for all species during ENSO events

Author/s	Location	Species	Environmental parameter	Seabird parameter	Observed trend
Wanless *et al.* (2009)	UK	Arctic tern *(Sterna paradisaea)*, common tern *(Sterna hirundo)*, sandwich tern *(Thalasseus sandvicensis)*, common murre *(Uria aalge)*, razorbill *(Alca torda)*, Atlantic puffin *(Fratercula arctica)*, black-legged kittiwake *(Rissa tridactyla)*, European shag *(Phalacrocorax aristotelis)*, Northern Fulmar *(Fulmaris glacialis)*, common eider *(Somateria mollissima).*	SST, NAO	Reproductive phenology	Earlier breeding observed in tern species, but opposite trend seen black-legged kittiwake, common murre, razorbill and Atlantic puffin
Wolf *et al.* (2009)	California	Cassin's Auklet *(Ptychoramphus aleuticus)*	Sea level	Reproductive success and phenology	Changes in timing and success of breeding in association with higher sea level
Cullen *et al.* (2009)	SE Australia	Little penguin *(Eudyptula minor)*	SST	Reproductive phenology and success	Earlier laying and increased breeding success with increased SST
Ropert-Coudert *et al.* (2009)	SE Australia	Little penguin *(Eudyptula minor)*	Storm activity and extreme weather	Behaviour/reproductive success	Reduced foraging and breeding success observed after periods of extreme storm activity
Wolf *et al.* (2010)	California	Cassin's auklet *(Ptychoramphus aleuticus)*	SST and upwelling intensity	Abundance	Decrease in population likely with projected increases in SST
Sherley *et al.* (2012b)	South Africa	Bank Cormorant *(Phalacrocorax neglectus)*	Extreme weather events and air temp	Reproductive success	Reduced reproductive success with increased wave height and increases in air temperature.

Author/s	**Location**	**Species**	**Environmental parameter**	**Seabird parameter**	**Observed trend**
Cannell *et al.* (2012)	SW Australia	Little penguin *(Eudyptula minor)*	SST	Reproductive phenology and success	Reduced breeding success and later onset of laying observed with higher SST
Surman *et al.* (2012)	SW Australia	Lesser noddy *(Anous tenuirostris)*, brown noddy *(Anous stolidus)*, sooty tern *(Onychoprion fuscatus)*, wedge-tailed shearwater *(Puffinus pacificus)*	SST and ENSO	Reproductive success	Poorer breeding success observed during ENSO as well as outside of ENSO years due to warm SST and strong Leeuwin current
da Silva *et al.* (2012)	Brazil	Magellanic penguin *(Spheniscus magellanicus)*	SST and La Nina	Behaviour	Distribution expansion to lower latitudes associated with low SST
Genovart *et al.* (2013)	Spain	Cory's shearwater *(*Calonectris *diomedea)*	ENSO	Survival/ reproductive success	SOI associated with reduced survival probability due to potential storm activity and impacts on food availability
Dehnhard *et al.* (2013)	South America	Rockhopper penguin *(*Eudyptes *chrysocome)*	SST	Survival	Increased survival with low SST

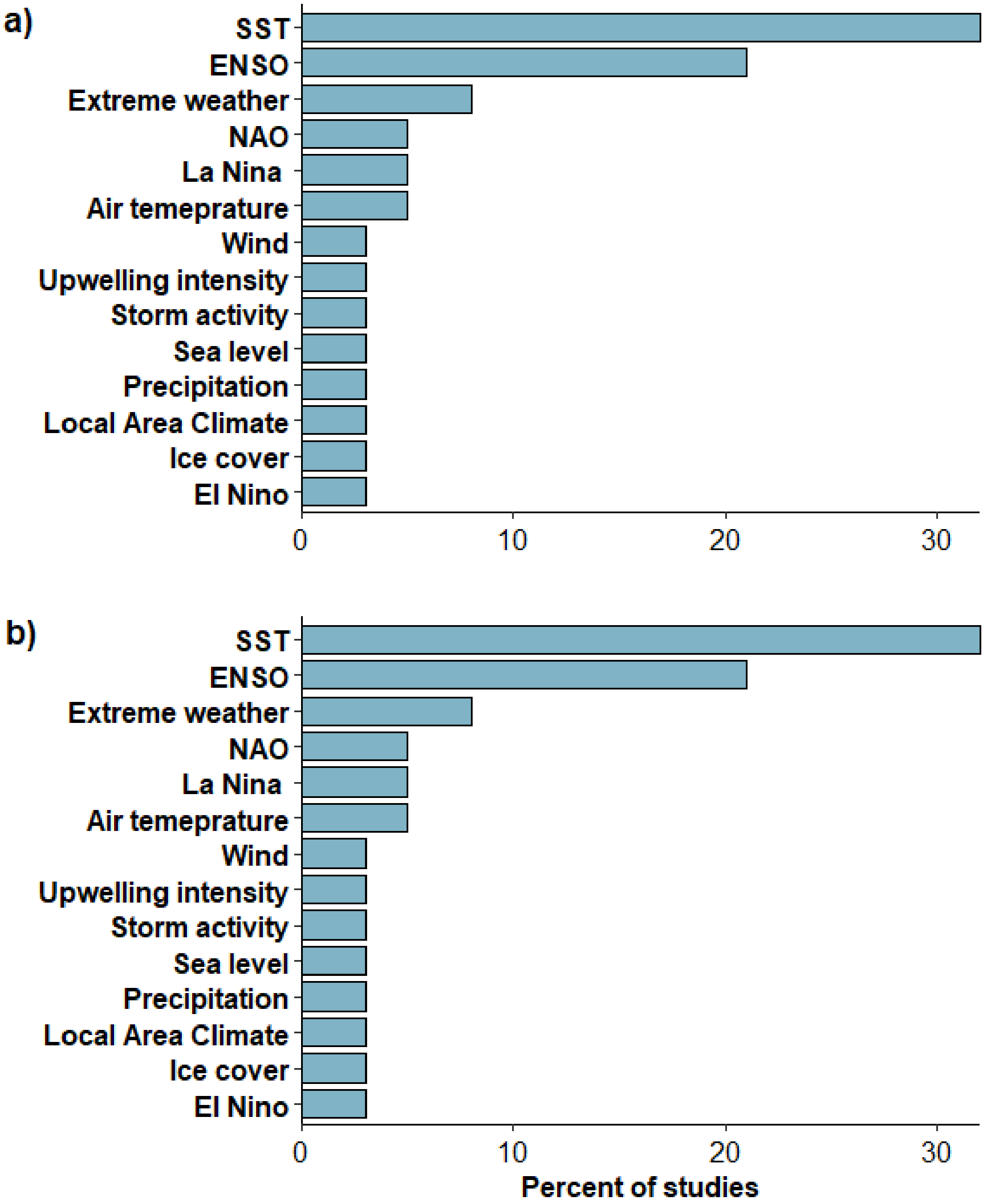

Figure 2.1: Percentage of reviewed studies categorised by (a) measured demographic response, and (b) measured climate parameters.

Evidence supporting the connection between ENSO and SST and changes in temperate seabird populations is widely published. However, at regional scales, data is still limited for many species, locations and climate processes. Other marine climate-driven processes found to influence temperate seabird populations include increases in sea level, extreme weather events and changing wind patterns (Mills *et al.* 2008; Ropert-Coudert *et al.* 2009; Wolf *et al.* 2009; Sherley *et al.* 2012b). However, research is limited, and fewer data are available in which to confidently establish trends and potential impacts (Congdon *et al.* 2007).

As marine top predators, seabirds are reliant mainly on nekton (fish and squid) and zooplankton (copepods and krill), it is not surprising therefore that the bulk of the literature focusing on climate change impacts on seabirds is centered around changes in the marine environment, prey availability and food webs. However, warming over land will likely exceed ocean warming by a factor in the range 1.4 – 1.7 (Collins *et al.* 2013), and few studies (3 of 63 reviewed) address how changes in the terrestrial habitat could be compounding climate change impacts on some species. Potential impacts of increased air temperature include direct negative physiological effects such as heat stress as well as indirect effects through alteration of terrestrial habitats and vegetation (Chambers *et al.* 2011; Chambers *et al.* 2012). For example, Sherley *et al.* (2012b) linked nest failure in a South African bank cormorant (*Phalacrocorax neglectus*) population to extended periods of high maximum temperatures during the breeding season.

High latitude taxa such as Alcids (*Alcidae*) and Penguins (*Spheniscidae*) are particularly at risk from impacts of increasing land temperatures as physiological adaptations to life in cold water consequently increase the risk of hyperthermia during breeding and feather moult whilst on land (Simeone *et al.* 2004; Cannell *et al*. 2011; Chambers *et al.* 2013; Cannell *et al.* 2016). In temperate and tropical climates, penguins can be exposed to temperatures exceeding their upper thermal threshold as they have little opportunity to escape solar insolation during breeding or moult (Chambers *et al.* 2011; Oswald and Arnold 2012).

The effect of extreme temperature stress was observed in a colony of African penguins (*Spheniscus demersus*) after temperatures reached 37 °C on Halifax Island, Namibia (latitude 22°00'S). Within a two hour period, 34 (19%) surface nests containing eggs and 53 (38%) surface nests containing chicks were lost with a total chick mortality of 37% (Kemper *et al.* 2007). Indirect effects of increased temperature on African penguins have also been observed in South Africa. On Robben Island (latitude 33°47'S), heat stressed penguins heading to sea to cool down left the nest contents unattended and vulnerable to predation from gulls (Sherley *et al.* 2012a). In contrast to the observations of Kemper *et al.* (2007) in South Africa, Yorio and Boersma (1994) examined nest desertion of Magellanic penguins (*Spheniscus magellanicus)* in South America and concluded that despite high temperatures experienced at the colony site during the study, heat stress was unlikely to cause nest abandonment (nest desertion more likely due to poor body condition in incubating birds); (but see Boersma and Rebstock 2014). The differences among these studies likely stem from differences in nest position; Magellanic penguin nests studied in South America were sheltered whereas the African penguin nests were exposed to direct sunlight on open surfaces and thus higher thermal maxima. While these studies provide insight into the potential effect of increased thermal conditions at seabird nesting colonies, further research examining direct and indirect impacts of climate at seabird colonies is required to identify broader response patterns and consequences for species.

2.4.2 Climate change impacts on little penguins

As with other seabird species, most studies investigating climate change impacts on the little penguin focus on variability in local and large scale marine climate. Ocean SST and

ENSO are documented to influence the breeding success, breeding phenology and survival of little penguins (Wienecke *et al.* 1995; Numata *et al.* 2000; Perriman *et al.* 2000; Chambers 2004; Cullen *et al.* 2009; Dann and Chambers 2009; Cannell *et al.* 2012). Changes in ocean temperature have been found to influence several aspects of breeding behaviour in little penguins. In New Zealand, Numata *et al.* (2000) found that in the 1998/1999 breeding season, one colony of little penguins in Oamaru on the South Island made longer foraging trips and were in poorer breeding condition with an increased occurrence of egg desertion. The authors attributed this to the 1998/1999 La Nina event which drove a change in the surface temperature of the ocean and consequently decreased fish abundance. Breeding was delayed by up to 4 months in a second colony approximately 500 km north of the Oamaru colony during the same season (Numata *et al.* 2000).

Within Australia, Chambers (2004) reported that ENSO influenced hatching success in little penguins on Phillip Island (SE Australia), but found it had little influence on laying date, survival and health of the chicks or over all breeding success of the colony. Increases in local sea surface temperatures, however, were found to positively influence the breeding performance of little penguins including timing of breeding, the number of chicks raised per pair and chick weight at fledging (Cullen *et al.* 2009). In Western Australia, SST and the warm water western boundary (Leeuwin) current off Australia have been found to negatively affect breeding performance of little penguins breeding on Penguin Island (Cannell *et al.* 2012). High SST in the pre-breeding period was linked to lower fledgling success, fewer chicks produced per pair, and lower fledging weights (Cannell *et al.* 2012). The Leeuwin current was also related to an extended laying period in little penguins (Cannell *et al.* 2012; Wooller 1991). The potential shift in breeding phenology could have detrimental effects on this population as little penguins laying later in the breeding season will be exposed to higher land temperatures and thermally stressful or hyperthermic conditions (Cannell *et al.* 2012). In contrast, little penguins in Victoria are likely to be positively influenced, at least in the short term, by warmer local sea surface temperature (Chambers *et al.* 2013). Although responses differ between populations, both are owing to temperature-related fluxes in prey availability and foraging success (Cullen *et al.* 2009; Cannell *et al.* 2012; Chambers *et al.* 2013; Carroll *et al.* 2016).

The ability to adapt to rapid environmental change either through changes in foraging ecology, geographic distribution or a combination of both will determine whether seabirds will survive environmental change or go extinct (Grémillet and Boulinier 2009). Perhaps at the highest risk of extirpation are seabird populations existing at the warm edges of a species' range. Population extinctions of this kind have been termed 'warm edge contractions' (Grémillet and Boulinier 2009; Cahill *et al.* 2013). For example, this process may be occurring in the tufted puffin (*Fratercula cirrhata*) where populations at the species' most southern colonies (California, Washington and Oregon in North America) are undergoing marked declines with the southernmost populations in California believed to be extirpated in the late 1990s (Gjerdrum *et al.* 2003; McChesney and Carter 2008; Hart *et al.* 2018). Populations inhabiting the latitudinal margins of a species distribution are particularly vulnerable to climate driven pressures and are becoming increasing important for predicting species' responses to expected climate change (Hampe and Petit 2005; Grémillet and Boulinier 2009). While there is potential for some species to cope with climate change through the adjustment of life-history characteristics and distribution, the persistence of some populations can be enhanced by buffering potential adverse effects of climate change through habitat management. To manage habitat effectively it is essential to first identify what habitat features are important to species (Jones 2001).

2.5 Habitat selection and implications for management

In birds, the choice of nest site is an example of habitat selection at the finest spatial scale (Cody 1981). The nest site provides a location where adult birds, eggs and chicks are be protected from predators and sheltered from environmental extremes as well as facilitating courtship and pairing (Cody 1981; Stokes and Boersma 1998; Hansell 2000; Mainwaring *et al.* 2014; Deeming and Reynolds 2015). This is a considerably sensitive portion of a bird's life cycle as the nest site is a location at which the parent, egg and chick are exposed for a relatively long period of time (Deeming and Reynolds 2015). There are several important factors that may influence the choice of a nest site including the proximity to feeding areas, shelter, concealment from predators and microclimate. This set of preferred features is of high importance as it can influence both breeding and survival of nesting birds (Burger 1987; Burger and Gochfeld 1988; Gloutney and Clark 1997; Stokes and Boersma 1998).

Climate change is predicted to alter coastal environments and consequently, the suitability of breeding habitat will likely become limited for some species (Chambers *et al.* 2011; Schumann *et al.* 2013). Habitat preferences may also change in response to shifts in the environment (Burger and Gochfeld 1988). Species may respond to changing climate in two ways. Those that have greater geographic plasticity may alter their breeding range, minimising physiological costs but potentially incurring additional biotic costs such as increased predation and interspecific competition (Martin 2001). Species that have a limited geographic distribution, may be forced to remain in habitat types to which they will become poorly suited. Either outcome will have deleterious consequences for long term population trends (Martin 2001). This emphasises the importance of gaining a better understanding of seabird nest habitat preferences as well as how habitat requirements will vary according to climate, to ensure effective habitat management and mitigation of negative climate change impacts (Chambers *et al.* 2011).

2.5.1 Nest habitat selection in seabirds

A search of electronic database Web of Science for literature investigating nest habitat selection in seabirds, using various combinations of the search terms ‘sea bird’ ‘seabird’ ‘nest’ ‘nesting’ ‘breeding’ ‘habitat’ ‘selection’ ‘preference’ and ‘choice’ and a subsequent search of citations within resulting articles yielded a total of 39 studies covering 38 seabird species from eight avian families. Studies covered a broad geographical range across all climatic zones, although there was a slight bias towards studies carried out in temperate zones. Across the 39 studies, there was a great deal of variation in the number (ranging between one and 13), and type (biotic and abiotic) of habitat variables measured, as well as the spatial scale at which the study was carried out (Figure 2.2). Twenty-one studies (54%) focused on selection at the scale of general breeding habitat while 15 studies (38%) investigated selection at the nest site or burrow. Only two studies investigated selection across multiple spatial scales.

There was a marked difference in the approach used to test for selection (Table 2.3). For most studies (67%) authors used either nest densities, or the frequency of physical characteristics around nests, as a surrogate for habitat preference. The remaining studies accounted for preference by comparing used and unused or available habitat. In these studies, habitat is defined as habitat that is currently occupied, unused habitat is that habitat not occupied and available habitat covers only habitat types accessible to the study species (Jones 2001). Of the 39 studies addressing nest site preference, 17 also investigated breeding performance and its association with nest habitat characteristics.

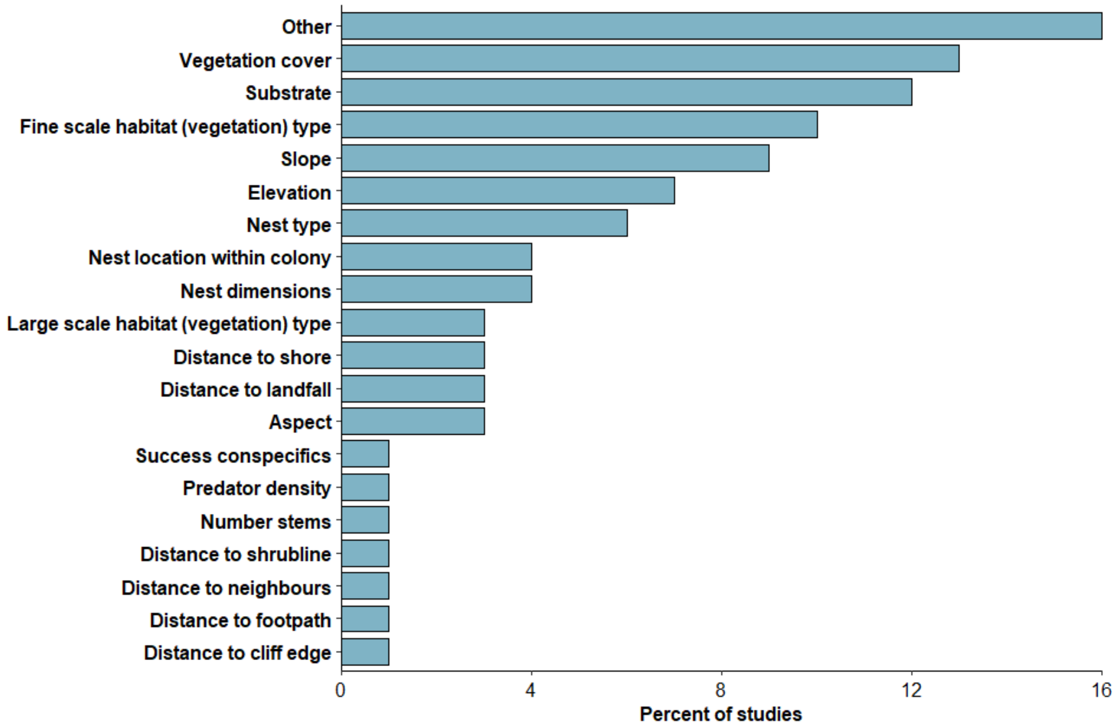

Figure 2.2: Habitat features found to be important in habitat selection studies of seabirds.

Table 2.3: Number of studies using separate methods to determine 'preference' and associated breeding parameters.

Method	Breeding parameters also measured	Breeding parameters not measured	Total
Used vs. Unused/available	4	9	13
Usage patterns	12	14	26
Total	16	23	39

Habitat features found to influence the choice of nesting site varied between studies (Figure 2.2), suggesting that preferred nest characteristics are specific to a species or population however similarities in nesting habitat features were observed for species with similar nesting behaviour (i.e. cavity vs surface nesting). For surface nesting species, biotic characteristics such as vegetation density or cover were commonly identified as important factors determining nest choice, often attributed to predator avoidance or protection from exposure (Clark *et al.*1983; Saliva and Burger 1989; Seddon and Davis 1989). For burrow nesting species, abiotic and topographical features that influence burrow stability, drainage or environment such as slope and substrate were more influential (Nettleship 1972; Stokes and Boersma 1991; Catry *et al.* 2003).

To assess the adaptive nature of habitat selection, studies must also demonstrate increased fitness in preferred habitats (Jones 2001; Chalfoun and Schmidt 2012). Without information on breeding outcomes it is difficult to determine if detected differences in habitat have any bearing on nesting choice of individuals (Jones 2001). Therefore, studies should be able to demonstrate congruence between habitat preferences and relevant fitness components such as breeding success (Chalfoun and Schmidt 2012). Less than half of the studies reviewed examined both nest attributes and breeding success and few sought to establish a relationship between the two. Regardless, the few studies that examined this often reported an association between selected nest attributes and breeding success (Nettleship 1972; Carter 1997; Velando and Freire 2003; García-Borboroglu and Yorio 2004; Bourgeois and Vidal 2007).

The reproductive performance of many seabird colonies is frequently related to features of the breeding habitat. Breeding success can be influenced by characteristics such as the degree of cover (Ramos *et al.* 1997; Stokes and Boersma 1998; Velando and Freire 2003; García-Borboroglu and Yorio 2004), nest cavity dimensions (Bourgeois and Vidal 2007), substrate (Stokes and Boersma 1991) and angle of slope (Nettleship 1972). For example, breeding success in four Procellariformes [Cory's shearwater (*Calonectris diomedea*); little shearwater (*Puffinus assimilis*); Bulwer's petrel (*Bulweria bulwerii*) and band-rumped storm petrel (*Oceanodroma castro*)] was much higher for those individuals nesting in cavities with a high degree of vegetative shelter (Ramos *et al.* 1997). A similar observation was made for nesting European shags (*Phalocrocrax aristotelis),* where nests with a greater percentage of both lateral and overhead cover were more successful (Velando and Freire 2003). In contrast, some authors have found habitat characteristics to be less important for influencing reproductive output and success and more likely to be influenced by other factors such as parental condition or experience (Best and Stauffer 1980; Pugesek and Diem 1983). For example, in California gulls (*Larus californicus*), parental age is the major contributing factor associated with successful breeding and while nest site variables contributed, they did so through co-variation with parental age (Pugesek and Diem 1983).

The importance of habitat characteristics in the selection and reproductive output of nests varies between species and populations. However, when comparing studies on nest selection in seabirds some patterns became apparent. The two most common characteristics influencing the use and breeding success of nesting seabirds included the degree of vegetative cover (either directly over or adjacent to the nest) and substrate composition. The preference for greater vegetation cover has been reported across a number of bird taxa and likely is a response to minimising predation risk (Goodenough *et al.* 2009) and/or exposure (Stokes and Boersma 1998). Substrate composition can influence vegetation structure and growth (Borboroglu *et al.* 2002) as well as play an important role in maintaining stability and microclimate of nest burrows (Stokes and Boersma 1991). Shifts in thermal and precipitation regimes are likely to modify the vegetative cover and substrate in seabird nesting habitats and subsequently, breeding outcomes of seabirds may also be affected (Chambers *et al.* 2011).

Published research suggests that habitat characteristics, such as substrate composition and vegetation structure, influence several seabird demographic parameters. However few studies consider the association of substrate or vegetation characteristics with microclimate and their influence on nest choice or reproductive output. Studies of nest selection in other avian taxa suggest that habitat use is sensitive to variation in thermal environment and is influenced by the physiological tolerance of a species as well as the need to secure a nest site with a microclimate that promotes successful reproduction (Martin 2001; Hovick *et al.* 2014;; Frey *et al.* 2016). Exposure to thermal extremes can often lead to reduced reproductive success or survival, ultimately affecting population stability (Reyna and Burggren 2012; Carroll *et al.* 2015; Tanner *et al.* 2017). With the forecasted alterations to temperature and rainfall associated with climate change, understanding how the microclimate of a nest will change is vital in predicting the impact of these shifts on seabird populations. Some species may be able to adapt by expanding their breeding range (Martin 2001), but for others it may mean nesting in sub-optimal nest sites and subsequently, reduced breeding success.

A potential strategy aimed at mitigating climate pressures in the nesting environment is the use of artificial nest boxes (Chambers *et al.* 2012; Sutherland *et al.* 2014). Nest boxes are becoming an increasingly valuable tool as they not only provide opportunities to study the influence of microclimate on nest choice and breeding success but they can potentially enhance colony recruitment and survival (Dann and Chambers 2013). Knowledge gained from habitat selection studies is commonly used to guide the management of seabird nesting habitat but is seldom applied in the design and application of artificial nests. As climate change will significantly alter seabird breeding habitat, adaptive management of artificial nests is essential for ensuring that the optimal microclimate required for successful breeding is maintained (Chambers *et al.* 2011).

2.6 Artificial nests and seabird habitat management

For burrow/cavity nesting seabirds, a commonly documented technique for enhancing habitat and increasing nest site availability is the installation of artificial nests. Not only are they a popular conservation tool for enhancing bird nesting habitat, they can often be utilised within a monitoring program given the ease with which nest boxes may be repeatedly checked throughout a breeding season (Priddel and Carlile 1995). Artificial nest boxes are reported to have increased breeding effort, breeding success and population size in several seabird species (de León and Mínguez 2003; Bolton *et al.* 2004; Libois *et al.* 2012; Sutherland *et al.* 2014).

A search of the electronic databases for studies where artificial nest boxes were utilised in the research or management of seabird species revealed a large volume of literature, however for the purpose of this review only those that made reference to measures of usage or reproductive performance (i.e. breeding success, hatching success, fledging success, chick health) were included. These studies (n=26) are summarised in Table 2.4. Common uses of artificial nests could be grouped into 3 categories; translocation purposes, where nest boxes were used in the establishment or translocation of seabird colonies; monitoring/research, where nest boxes were utilised to obtain data on seabird life history traits; and habitat restoration/ provision, where nest boxes were used in the provision or restoration of seabird nesting habitat. Of the three, the most common use for artificial nest structures, making up 50% of articles, was for the purpose of enhancing habitat and providing additional nest sites where suitable habitat is limited.

Table 2.4: Studies detailing use and reproductive rates of seabirds nesting in artificial nests and key details and findings of each study.

Author	**Species**	**Climatic region**	**Location**	**Purpose of artificial nest**	**Measured response variable/s**	**Species response**	**Hypothesised mechanisms responsible for response**
Wilson (1986)	Rhinoceros auklet (*Cerorhinca monocerata)*	Temperate	USA	Monitoring/ research	Usage and reproductive parameters	Chick growth in boxes comparable to those in natural. Birds readily used boxes with usage up to 89 % vs. 53% in natural nests.	Artificial burrows more stable than natural and therefore used more frequently.
Podolsky and Kress (1989)	Leach's storm petrel *(Oceanodroma leucorhoa)*	Temperate	USA	Monitoring/ research	Usage and reproductive parameters	6 -10 of 264 artificial burrows were used for breeding. 2 fledged successfully.	Manipulated with sound stimulation.
Klomp *et al.* (1991)	Little penguin (*Eudyptula minor)*	Temperate	SW Australia	Monitoring/ research	Usage and reproductive parameters	Usage of boxes ranged from 64% - 75%. Reproductive success was not different between natural and artificial nests.	Not discussed.
Wilson (1993)	Rhinoceros auklet (*Cerorhinca monocerata*)	Temperate	USA	Monitoring/ research	Reproductive parameters	Auklets used an average of 91% of burrows provided. 64% of those produced chicks.	Not discussed.
Priddel and Carlile (1995)	Gould's petrel *(Pterodroma leucoptera)*	Temperate	SE Australia	Habitat provision	Usage and reproductive parameters	Breeding success was comparable to or higher in boxes than natural burrows.	Secure from predators and protected from adverse weather and free from protrusions likely to cause loss or breakage of egg.

Author	Species	Climatic region	Location	Purpose of artificial nest	Measured response variable/s	Species response	Hypothesised mechanisms responsible for response
Bolton (1996)	Storm petrel *(Hydrobates pelagicus)*	Sub-arctic	UK	Monitoring/ research	Usage and reproductive parameters	Hatching and fledging success not significantly different to natural.	Not discussed.
Gaston (1996)	Ancient murrelet *(Synthliboramphus antiquus)*	Sub-arctic	Canada	Habitat provision	Usage	3 years after installation most boxes had been visited and occupation rates were the same as natural burrows.	Replicate natural burrow habitat.
Houston (1999)	Little penguin (*Eudyptula minor)*	Temperate	New Zealand	Habitat provision	Reproductive parameters	Breeding success was as high as 70% and some penguins moved from natural burrows to boxes.	Not discussed.
Lalas *et al.* (1999)	Yellow-eyed penguin *(Megadyptes antipodes)*	Temperate	New Zealand	Habitat restoration	Usage	Nest boxes preferred over natural nests and occupied throughout the year.	Replicate natural nest attributes.
Kemper *et al*. (2007)	African penguin *(Spheniscus demersus)*	Temperate	South Africa	Habitat provision	Reproductive parameters	Breeding success greater in plastic burrows than other nest types (bush/surface/building).	Protection from heat and predators.
Perriman and Steen (2000)	Little penguin (Eudyptula minor)	Temperate	New Zealand	Monitoring/ research	Reproductive parameters	Reproductive success was higher for penguins nesting in boxes over natural. Number of breeding pairs increased after introduction of nest boxes.	Protection from predation from dogs.

Author	Species	Climatic region	Location	Purpose of artificial nest	Measured response variable/s	Species response	Hypothesised mechanisms responsible for response
Johannesen *et al.* (2002)	Little penguin (Eudyptula minor)	Temperate	New Zealand	Monitoring/research	Usage and reproductive parameters	Higher breeding success in nest boxes than natural and 46% of birds initially breeding in natural nests moved into a box.	Potentially due to higher fidelity to boxes than burrows.
de León and Mínguez (2003)	European storm petrel *(Hydrobates pelagicus)*	Temperate	Spain	Habitat provision/ restoration	Usage and reproductive parameters	Occupancy rates increased yearly. Nesting success was higher for pairs nesting in boxes over natural.	Protection from weather and predators.
Bolton *et al.* (2004)	Maderian storm petrel *(Oceanodroma castro)*	Temperate	Azores archipelago	Habitat provision/ restoration	Reproductive parameters and population abundance	12% increase of breeding population in the first year and 28% increase in second year. Breeding success in boxes was almost 3 times greater than birds in natural sites.	Stones that cause egg damage are absent from artificial burrows.
Miskelly and Taylor (2004)	Common diving petrels *(Pelecanoides urinatrix)*	Temperate	New Zealand	Establish new colony/ translocation	Fledging success	Approximately half of translocated chicks fledged from artificial boxes, however most breeding attempts in the new location were in natural burrows.	Provision of habitat.
Priddel *et al*. (2006)	Gould's petrel *(Pterodroma leucoptera)*	Temperate	SE Australia	Colony establishment/ translocation	Usage and reproductive parameters	Fledging success from boxes 95-100%. breeding success was comparable or higher in artificial burrows. Usage also increased.	Provision of habitat.

Author	**Species**	**Climatic region**	**Location**	**Purpose of artificial nest**	**Measured response variable/s**	**Species response**	**Hypothesised mechanisms responsible for response**
Kemper *et al*. (2007)	African penguin (*Spheniscus demersus)*	temperate	South Africa	Habitat provision/ restoration	Reproductive parameters	Artificial burrows were significantly more successful than surface nests.	Parents less likely to flee during disturbance and leave chicks exposed during guard stage.
Bried *et al.* (2009)	Common tern *(Sterna hirundo,* roseate tern *(Sterna dougallii),* maderian storm petrel *(Oceanodroma castro)*	Temperate	Azores archipelago	Habitat provision/ restoration	Reproductive parameters	Maderian storm petrels in boxes experienced higher breeding success than natural.	Protection from weather.
Miskelly *et al*. (2009)	Common diving petrel *(Pelecanoides urinatrix,* fairy prion *(Pachyptila turtur),* grey-faced petrel *(Pterodroma macroptera,* pycrofts petrel *(Pterodroma pycrofti),* Chatham petrel *(Pterodroma axillaris)*, Magenta petrel *(Pterodroma magentae),* fluttering shearwater *(Puffinus gavia),* Hutton's shearwater *(Puffinus huttoni)*	Temperate	New Zealand	Colony establishment/ translocation	Reproductive parameters and return rate	93 - 100% translocated chicks fledged, of 1546 fledged birds, 6 have returned to translocation sites.	Not discussed.
Allen *et al.* (2011)	White-flippered penguin *(Eudyptula minor albosignata)*	Temperate	New Zealand	Research/monitoring	reproductive parameters	63% breeding success, 75% hatching success, 85% fledging success.	Not discussed.

Author	Species	Climatic region	Location	Purpose of artificial nest	Measured response variable/s	Species response	Hypothesised mechanisms responsible for response
Carlile *et al.* (2012)	Bermuda petrel *(Pterodroma cahow)*	Temperate	Bermuda	Establishment new colony/ translocation	fledging success	Almost all translocated birds fledged (101/104) and all returning birds have opted to use artificial burrows.	Provision of habitat.
Sherley *et al*. (2012a)	African penguin *(Spheniscus demersus*)	Temperate	South Africa	Habitat provision/ restoration	Reproductive success	Penguins nesting in artificial structures had increased reproductive success than birds nesting under vegetation.	Shelter from the weather and protection from predators. Reduced risk of collapse associated with natural burrows.
Pichegru (2012)	African penguin *(Spheniscus demersus)*	Temperate	South Africa	Habitat provision/ restoration	Reproductive parameters	Lower hatching success in fibreglass than cement or surface. Chick survival higher in both artificial than surface. Cement Pipe nest had best overall breeding success.	Artificial nests provided shelter from weather and predators. Reduced success in fibreglass design due to elevated temperatures.
Libois *et al.* (2012)	Mediterranean storm petrel *(Hydrobates pelagicus melitensis)*	Temperate	Spain	Habitat provision/ restoration	Reproductive parameters/ survival	Greater survival and breeding success found for those birds nesting in artificial structures than natural. Breeding numbers have increased since installation of boxes.	Protection from predators.
Adams *et al.* (2014)	Cassin's auklet *(Ptychoramphus aleuticus)*	Temperate	USA	Improve old boxes (microclimate). habitat provision	Usage and reproductive parameters	Occupancy was 100% after replacement.	Not discussed.

Author	Species	Climatic region	Location	Purpose of artificial nest	Measured response variable/s	Species response	Hypothesised mechanisms responsible for response
Sutherland *et al.* (2014)	Little penguin (*Eudyptula minor)*	Temperate	SE Australia	Habitat provision/ restoration	Usage and reproductive parameters	Penguins readily occupied boxes. In poor breeding years, breeding productivity was greater in nest boxes. Survival and mass of fledgling was greater in boxes.	Protection from predators, improved microclimate and reduced abandonment.

Studies have shown that seabirds can benefit significantly from the provision of artificial nest boxes with positive population growth observed for a number of species (Bolton *et al.* 2004; Libois *et al.* 2012). For example, a Mediterranean storm-petrel (*Hydrobates pelagicus melitensis*) colony in Spain increased their breeding population from 64 pairs to 108 pairs over 13 years after the installation of nest boxes. Similarly, a breeding population of Madeiran storm-petrels (*Oceanodroma castro*) increased by 28% two years after the installation of nest boxes in a colony in the Azores Archipelago (Bolton *et al.* 2004). Population increases observed here are likely a consequence of an overall improvement in breeding productivity. In both cases, the authors reported greater breeding success for birds using boxes when compared with those nesting in natural nest sites (Bolton *et al.* 2004; Libois *et al.* 2012).

Higher breeding success observed in nest boxes is frequently reported and is often attributed to added protection from predators (Kemper *et al.* 2007; Libois *et al.* 2012; Sherley *et al.* 2012a), reduced damage to eggs (Bolton *et al.* 2004) and reduced exposure (Kemper *et al.* 2007; Sherley *et al.* 2012a). In Africa, two separate studies investigating breeding success at two different islands off the coast of Africa (Halifax Island, Namibia and Robben Island, South Africa) found that breeding productivity was higher in artificial nests than for natural nests (Kemper *et al.* 2007; Sherley *et al.* 2012a). At both colonies, success was attributed to higher survival of chicks during the guard stage; penguins nesting in artificial structures were less likely to be disturbed from their nest by the presence of people or predators, and chicks remained protected from predators and exposure (Kemper *et al.* 2007; Sherley *et al.* 2012a).

In addition to improved breeding success, studies have shown that often, birds can show a preference for nesting in artificial nests over natural sites. After the installation of nest boxes at yellow-eyed penguins nesting sites, penguins showed a preference for the artificial nests over natural nests in open habitat, likely due to protection from solar insolation provided by greater overhead cover (Lalas *et al.* 1999). Similarly, a breeding colony of little penguins at the Otago peninsula, New Zealand, showed both increased breeding success and a preference for artificial nests over natural nests (Perriman and Steen 2000). Fidelity to nest sites was also found to be greater in little penguins breeding in nest boxes compared to natural nest sites in Otago (Johannesen *et al.* 2002). On Penguin Island, Western Australia, nest boxes are also being utilised to facilitate monitoring and increase nesting habitat for little penguins (Klomp *et al.* 1991). However contrary to other studies, while rapid occupation of the nests suggest the nest boxes were suitable as nest habitat, there was no difference in the breeding success between the penguins breeding in boxes and those breeding in natural nests (Klomp *et al.* 1991) Furthermore, use of artificial nests for breeding on Penguin Island is found to be relatively low and penguins nesting in boxes exhibit lower nest site fidelity than those nesting in natural nest sites (Ropert-Coudert *et al.* 2004; Tavecchia *et al.* 2016).

Collectively, these studies provide strong evidence to suggest that artificial nests can improve breeding in some seabird populations by providing a nest site that provides greater protection from predators and extreme weather (Kemper *et al.* 2007; Libois *et al.* 2012). However, potential negative consequences of the use of nest boxes for seabirds are poorly researched and require further investigation. Disadvantages of artificial nest box use include the potential for parasite build up (Møller 1989; Stamp *et al.* 2002); allowing supra-optimal breeding density or increased attractiveness to predators (Mänd *et al.* 2005) and increased temperature in poorly designed structures (Ropert-Coudert *et al.* 2004; Pichegru 2012; Adams *et al.* 2014). Negative impacts of nest boxes have been well documented for other bird taxa and there is good evidence to suggest that in some cases, artificial nest structures can act as an ecological trap whereby artificial nests are preferentially used but fitness is reduced (Severns 2011; Hale *et al.* 2015). For example, barn owls (*Tyto alba*) readily use boxes for nesting however owls fledging from nest boxes had a lower survival rate than those fledging from natural nest locations (Klein *et al.* 2007). In this case, the boxes failed to provide owl fledglings with a safe platform to practice flight, increasing the chance of mortality during the fledging stage (Klein *et al.* 2007). In North American wood ducks (*Aix sponsa*), a reduction in reproduction and population observed following the installation of grouped and highly visible nest boxes was attributed to increased frequency of conspecific brood parasitism leading to inefficient incubation and reduced hatching success (Eadie *et al.* 1998; Semel and Sherman; 2001). In some cases, negative impacts are not immediately apparent. For example, in a lesser kestrel (*Falco naumanni*) population, installation of nest boxes initially lead to a population increase however an extreme temperature event resulted in greater mortality in artificial boxes due to elevated thermal conditions (Catry *et al.* 2011). In these cases, negative outcomes have been a result of uninformed design or placement highlighting the importance of researching optimal nesting requirements prior to design and installation of artificial nests along with continued reassessment to ensure any negative consequences are identified and mitigated (Stamp *et al.* 2002; Klein *et al.* 2007).

Artificial nests are becoming increasingly relevant in buffering climate change impacts on seabirds. A trend in warming temperatures, decreasing rainfall and increasing intensity of extreme weather events, necessitate reassessment and modification of artificial nest structures to maintain safe optimal microclimate for successful breeding. Documented cases where microclimates within artificial nests are shifting away from species' optimum are emerging. Success of artificial nests for African penguins (*Spheniscus demersus*) was found to be design-dependent, with poor hatching success in fibreglass burrows due elevated temperature inside that nest type (Pichegru 2012). Similarly, Lei *et al.* (2014) found that artificial nests for African penguins were hotter and maintained high temperature for longer periods of time than natural nests. Increasing temperatures inside Cassin's auklet (*Ptychoramphus aleuticus*) nest boxes have prompted modifications to reduce temperature (Adams *et al.* 2014). Appropriately designed artificial nests are paramount in the management of seabird nesting habitat but even more so for thermally sensitive species with high nest site fidelity (such as the little penguin) given the possibility they may continue to use a nest even after internal conditions have become sub-optimal.

2.7 Implications for Penguin Island's little penguin colony

Climate change will have a wide range of effects on the productivity, survival and population abundance of many seabird populations. Particularly vulnerable are those populations existing at the warm edges of a species' range. The little penguin population on Penguin Island, Western Australia is one such group and one of three colonies existing at a lower latitude than all other known populations in Western Australia. This population is living close to its likely thermal limit (Stahel and Nicol 1982; Horne 2010). Little penguins here can experience changes in breeding phenology and reductions in breeding performance as a result of reduced prey abundance and distribution caused by a warmer ocean climate (Cannell *et al.* 2012). In addition to changes in the marine environment, there will be significant change in their terrestrial habitat due to predictions of reduced rainfall and increased terrestrial temperatures in this temperate zone (Bates *et al.* 2008; Andrys *et al.* 2017). Changes in this population's terrestrial habitat could have deleterious consequences as little penguins on Penguin Island rely on dense vegetation under which to nest. This highlights the urgency and significance of investigating and implementing effective climate adaptation strategies to conserve this genetically distinct population of little penguins. While the ability of this population to survive will be largely dependent on its own ability to adapt to changes in food resources and availability, it may be possible to increase the resilience of the population through management of their terrestrial habitat and the application of artificial nest structures. This thesis proposes that a greater understanding of nest site preference and microclimate is required to ensure the efficacy of artificial nests as a climate adaptation tool for Penguin Islands little penguin population.

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CHAPTER 3

Location and vegetation influence use of natural, but not artificial, nests in a rear edge population of little penguins (*Eudyptula minor*)

3.1 Abstract

Climate change will likely cause a ‘poleward’ shift in the distribution of multiple taxa, characterised by population extinctions at the lower latitudinal edges of a species’ range. Island breeding seabirds have few options to shift breeding poleward, instead facing the challenge of adapting *in situ* or face local extirpation. Nowhere is this more true than for rear edge populations where conservation will rely heavily on intensive management and restoration of habitat. To allow for targeted conservation and management of edge populations it is essential to gain a comprehensive understanding of the relationship between a population and their habitat requirements. In this study I quantified the characteristics of both natural and artificial little penguin nests and evaluated the influence of nest characteristics on probability of use for nesting. Little penguins did not select nest sites randomly, but instead based nest site selection on topographical, vegetation and nest site attributes. Natural nests were preferentially selected at sites with taller vegetation, close to a known landfall site and with a south-westerly facing entrance. In contrast, nest box use was predominately driven by the structure of the box, with longer boxes more likely to be used. Neither landscape nor nest site attributes were found to influence the overall success of either natural or artificial nests. These results provide the initial steps towards understanding nest habitat preference and use for this population, demonstrating the heterogeneity of nesting habitats used by little penguins across their range and emphasises

the need for population specific information to guide management decisions and implementation of adaptation strategies for seabird conservation.

3.2 Introduction

It is now widely accepted that global climate change is altering the geographical distribution of species worldwide (Parmesan and Yohe 2003; Hampe and Petit 2005; IPCC 2014). The geographical range of many species is expected to undergo a 'poleward' shift, characterised by population expansions at the higher latitudinal margins (leading edge) and population extinctions at the lower latitudinal edges (rear edge) of a species' range (Parmesan and Yohe 2003). Range shifts have already been documented for a number of taxa and are estimated to be occurring at a rate averaging 19 km per year for marine and 0.61 km per year for terrestrial species (Sorte *et al.* 2010; Smale and Wernberg 2013). In order to persist through changing climate, species must respond either by shifting their range in accordance with suitable climatic space or, adapt to changing conditions *in situ* (Hampe and Petit 2005; Rehm *et al.* 2015). Due to the rate at which change is occurring, it is thought the former is more probable, where movement is not otherwise impeded (Bridle and Vines 2007; Rehm *et al.* 2015). Species that have limited dispersal capacity or a narrow habitat niche are likely to experience range contractions rather than shifts, consequently, *in situ* adaptation of populations at the edges of their distribution will be key to avoid climate driven extinction (Opdam and Wascher 2004; Thomas *et al.* 2004; Rehm *et al.* 2015).

The ecological importance of rear edge populations has recently been the subject of much debate (Bunnell *et al.* 2004; Hampe and Petit 2005; Rehm *et al.* 2015; Pironon *et al.* 2017). It has traditionally been thought that populations existing at the latitudinal margins of their range are genetically depauperate, inherently prone to extinctions and thus are of little conservation value (Thomas *et al.* 1994; Channell and Lomolino 2000; Eckert *et al.* 2008; Pearson *et al.* 2009). However recent reviews have challenged this idea, suggesting that edge populations harbour higher genetic diversity that central populations; indeed, they may be key for providing adaptations to novel environments created through climate change (Hampe and

Petit 2005; Eckert *et al.* 2008; Sexton *et al.* 2009). Populations at latitudinal margins are exposed to higher climatic variability relative to those at the range core, adapted to unique environmental conditions and may have higher adaptive capacity in periods of rapid change (Safriel *et al.* 1994; Fraser 1999; Munwes *et al.* 2010). Thus, populations on latitudinal fringes are becoming increasingly important for not only predicting species' responses to expected climate change but for maintaining long term adaptive capacity of a species (Lomolino and Channell 1995; Hampe and Petit 2005; Pauls *et al.* 2013), yet the ecological characteristics of rear edge populations remain relatively understudied (Blanco-Fontao *et al.* 2010).

In light of this knowledge deficit regarding rear edge populations, increasing attention is being given to the conservation of peripheral populations, in particular, those that occur in seemingly less suitable habitat or that are disjunct from central populations (Bunnell *et al.* 2004). A number of possible climate change adaptation strategies have been proposed in order to facilitate the adjustment of species and ecosystems to changing climate regimes (Hannah *et al.* 2002; Opdam and Wascher 2004; Ficetola and Bernardi 2005; Hampe and Petit 2005; Lawler 2009; Mawdsley *et al.* 2009). For edge populations where typical climate adaptation management strategies are not practicable, conservation may rely on the intensive management and restoration of existing habitat to facilitate population resilience and buffer the adverse effects of climate change. In order to manage habitat effectively it is essential to first identify what habitat features are important to a species (Jones 2001). Perhaps more importantly, it is essential to gather population specific habitat selection information as conservation measures based on data gathered from a species' central populations may be inappropriate and, in some cases, counterproductive for peripheral populations (Hampe and Petit 2005).

For seabirds, the choice of a breeding site that provides optimum conditions for successful reproduction plays a crucial role in the survival of an individual, population or species (Buckley and Buckley 1980). Reproductive performance has been linked to several components of seabird breeding habitat including the degree of cover (Ramos *et al.*1997; Stokes and Boersma 1998; Velando and Freire 2003; Garcia-Borboroglu and Yorio 2004), nest cavity dimensions (Bourgeois and Vidal 2007), substrate (Stokes and Boersma 1991) and topographical attributes (Nettleship 1972). Climate change is predicted to significantly alter coastal environments worldwide and consequently, the availability and suitability of breeding habitat will likely become limited for some species (Chambers *et al.* 2011, Schumann *et al.* 2012). The demographic characteristics of many seabirds, such as generally low fecundity and limited number and range of breeding sites, makes them particularly vulnerable to climate driven extinctions (Bolton *et al.* 2004; Croxall *et al.* 2012).

Little penguins reach their northern- and western-most range limit at three coastal islands off Perth, Western Australia. The three islands, isolated from the next nearest population by approximately 550 km, represent a disjunct rear-edge meta-population of little penguins. Most existing knowledge of little penguin ecology comes from south-eastern Australia and New Zealand however life history traits and adaptive capacity relating to varying selection pressures are likely to differ throughout a species' range (Purves *et al.* 2007). Little penguins nesting off Perth display a unique breeding chronology (breeding peaks during the austral winter rather than spring), likely resulting from pressures related to environmental conditions and prey availability and quality (Wienecke 1993). Contrasts in the habitats of peripheral and core populations could provide insight into future changes in species distributions and adaptation under climate change (Valladares *et al.* 2014).

Current management of terrestrial habitat for populations throughout this species' range focus on the eradication of introduced predators and the conservation of nesting habitat and provision of artificial nests (Dann 2013). However fine scale studies quantifying the habitat characteristics associated with nesting sites of this colony are scant and while some studies have investigated certain attributes of artificial nests (Klomp *et al.* 1991; Wienecke 1993;

Ropert-Coudert *et al.* 2004) there are none to date describing the characteristics associated with the selection of artificial nest boxes or whether these attributes influence the use or occupation of the nests. Additionally, while studies have shown artificial nests to be an effective conservation tool for little penguins in other parts of their range (Sutherland *et al.* 2014) there is limited knowledge on how climate variability might influence habitat availability and nesting requirements and whether artificial nests will remain an effective conservation strategy in a changing climate. In order to predict impacts associated with changes to nest habitat and to allow for targeted conservation and management of the little penguin colony on Penguin Island, it is essential to gain a comprehensive understanding of the relationship between this population and their nesting requirements (Weerheim *et al.* 2003). The aims of this investigation therefore were to (1) quantify the characteristics of both natural and artificial nests, and (2) investigate the influence of nest characteristics on (a) probability of nest use and (b) probability of nest success, for nesting sites (natural and artificial) used by little penguins on Penguin Island, Western Australia.

3.3 Methods

3.3.1 Study area

The site for this study was Penguin Island (32.30°S, 115.69°E), a 12.5 ha island located 700 m off the coast of Rockingham, 42 km south of Perth, Western Australia (Figure 3.1). It is the largest of a chain of limestone rocks and small islands located within the Shoalwater Islands Marine Park. The region is characterised by a Mediterranean climate with mild, wet winters and summer drought often extending from December through until the end of March. February is the hottest month, with mean maximum temperature of 31.6 ˚C. Summer temperatures on occasion exceed 40 ˚C. Average temperatures in July range from 7.8 – 18.4 ˚C (Garden Island climate station no. 009256 1994 -2017, Australian Bureau of Meteorology, 2017). Annual rainfall averages approximately 600 mm, mostly during the winter months (June, July and August). Typical wind patterns along the Perth coastline are characterised by offshore (north-easterly to easterly) winds in the morning switching abruptly to slant onshore (south to south-westerly) winds in the afternoon (Masselink and Pattiaratchi 2001). The region has undergone significant climatic changes with annual temperature increasing by 1.1 ˚C between 1901 and 2013 and mean winter rainfall declining by 19% since the mid-1970s (Bates *et al.* 2008; Hope *et al.* 2015; The Bureau of Meterology and CSIRO 2016). Sea surface temperature (SST) along the southwest coast has also increased by approximately 0.6 ˚C over the past 5 decades (Pearce and Feng 2007). Future climate predictions indicate continued increases in SST and air temperature and decreased winter rainfall for this region and the frequency and intensity of extreme climatic events are increasing (Bates *et al.* 2008; Hope *et al.* 2015; Andrys *et al.* 2017; Ruthrof *et al.* 2018).

Figure 3.1: Location of Penguin Island in Western Australia and in relation to Perth, Fremantle and Rockingham.

Penguin Island is currently managed by the Western Australian Department of Biodiversity Conservation and Attractions as a Class A nature reserve. Class A reserves are areas considered of high conservation or community value and receive the highest level of protection, generally requiring parliamentary approval in order to change the reserve's area or purpose (Land Administration Act 1997 (WA) ss 41-45). It is a popular tourist destination (approximately 35% increase in visitation since 2010 to 127,000 visits in 2017 - 2018; (Smith 2014; Smith 2019) as well as important nesting habitat for several seabird species (Orr and Pobar 1992; Hughes and Saunders 2005). Over 40 species of birds use Penguin Island, 14 of which utilise the island's habitat for breeding (Dunlop *et al.* 1988). The island is characterised by a mix of exposed limestone at high points with steep slopes, ridges and flatter areas near beaches densely vegetated by low shrublands (composed mostly of the spreading woody shrubs *Rhagodia baccata* and *Nitraria billardieri* and the low decumbent shrub, *Tetragonia decumbens*) with some patches of the taller *Acacia rostellifera* (Klomp *et al.* 1991) . These four species make up 75% of the island vegetation cover (Klomp *et al.* 1991) (Figure 3.2).

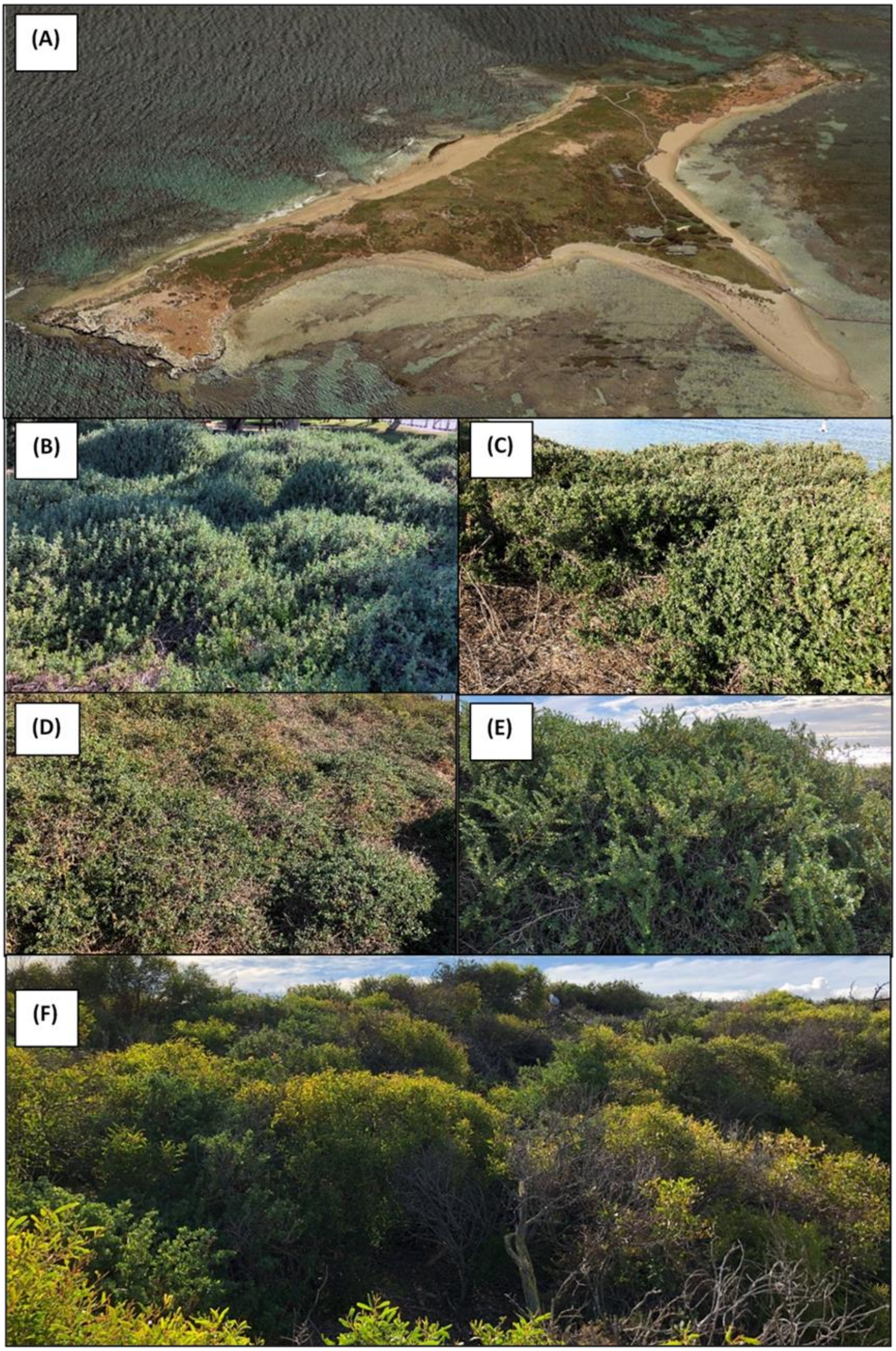


Figure 3.2: Penguin Island and the island's major vegetation types. **(A)** Penguin Island. (**B)** *Tetragonia decumbens* **(C)** *Rhagodia baccata*, **(D)** *T. decumbens-R. baccata* mix, **(E)** *Nitraria billardieri* **(F)** *Acacia sp.*

3.3.2 Study Species

3.3.2.1 *Species description*

Little penguins are the smallest of all penguin species standing approximately 33 cm tall and weighing 1100 – 1400 g (Wienecke 1993). It is the only species known to breed in Australia and is found across the southern coastline of mainland Australia, Tasmania and New Zealand (Marchant and Higgins 1990; Dann 2013). In Australian waters, little penguins are distributed somewhat irregularly, occurring from south of Perth in the Shoalwater islands group (including Carnac, Garden and Penguin islands) in the west (32.12°S), across the southern coast (including Tasmania) and up the eastern coastline to South Solitary Island, New South Wales (30.2052°S, 153.2671°E) (Figure 3.3; Stahel and Gales 1987; Peucker *et al.* 2009). In New Zealand, the breeding distribution encompasses the coast of both the North and South Island as well as Stewart and the Chatham islands (Figure 3.3; Stahel and Gales 1987; Dann 2013).

Figure 3.3: Distribution of little penguins (*Eudyptula minor*) in Australia and New Zealand.

Historically little penguins were split into six subspecies, partitioned geographically and based on considerable variation in breeding phenology, nesting habitat and morphology (Peucker *et al*. 2009; Dann 2013) but more recently, and with molecular evidence, the species is now thought to consist of two clades, one occurring across the south-eastern part of New Zealand's south island and southern Australia and the other restricted to New Zealand spanning from northern portions of the south island and around the entirety of the north island (Dann 2013). The Perth population of little penguins have been considered genetically distinct from other populations in Australia including other south-western colonies (Cannell *et al.* 2012).

Western Australia's largest breeding colony of little penguins inhabits Penguin Island, part of a meta-population representing the northern- and western-most limit of the species range and isolated from the nearest populations by 550 km (Wienecke 1993). Here, little penguins are 15 – 20% heavier than their eastern and southern conspecifics (Wienecke 1993).

3.3.2.2 Breeding phenology

The breeding chronology of little penguins varies widely across its range with the commencement and duration of egg laying differing depending on geographical location (Reilly and Cullen 1981; Dann 2013). In southern Australia, the best studied population on Phillip Island (38.4899°S, 145.2038°E), Victoria, have a breeding chronology more consistent with most of the species range; breeding normally extends from late August to February, however onset of egg laying is highly variable with eggs recorded as early as May (Reilly and Cullen 1981; Dann 1992; Dann 2013). In contrast, breeding on Penguin Island on Penguin Island peaks during the austral winter with nesting activity observed from April to December (Wooller *et al.* 1991), thus spanning portions of all four seasons and exposing them to a range of climatic conditions (Klomp *et al.* 1988; Klomp *et al.* 1991; Wienecke 1993). The unusual breeding chronology seen in Penguin Island's colony (Figure 3.4) is likely a response to the high temperatures and low humidity experienced in this region (Klomp *et al.* 1991; Wienecke 1993), as well as the inter-annual variation in the timing and duration of prey species (Cannell *et al.* 2012).

Egg laying ranges from late April to early December (Figure 3.4; Cannell *et al.* 2012). Often a bimodal breeding pattern, in which two distinct laying peaks can be identified, is observed (Wienecke 1993). In most cases, two eggs are laid two days apart and double brooding (a second clutch of eggs are laid after successfully raising the first) occurs regularly (Wienecke 1993). The eggs are incubated on average 35 days, and chicks fledge at seven to nine weeks (Chiaradia and Kerry 1999; Kemp and Dann 2001; Dann 2013). Both parents participate in the incubation of eggs and rearing of the chicks and are guarded alternately by the parents for the first two to three weeks, after which both parents go to sea for one to two day stints, returning to provision chicks (Chiaradia and Kerry 1999; Dann 2013).

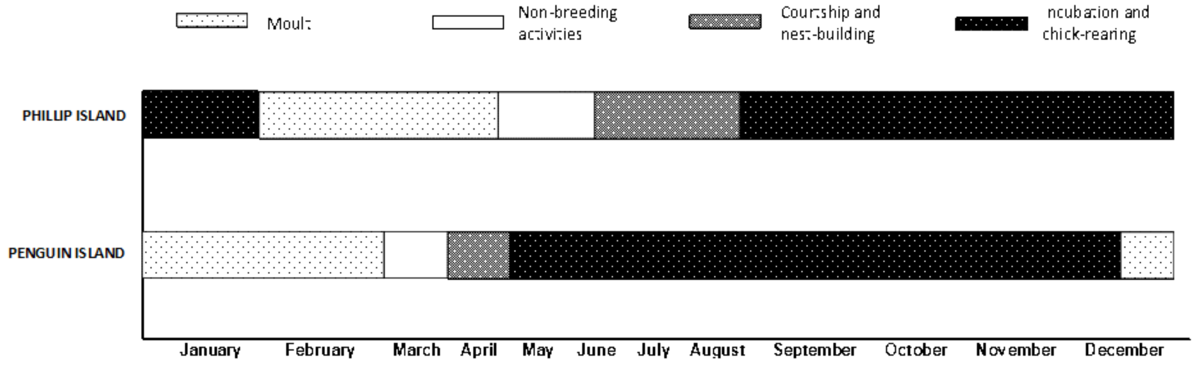


Figure 3.4: Comparison of annual lifecycle and timing of breeding between little penguins from Phillip Island, Victoria; 38.4899° S (Reilly and Cullen 1981; Reilly and Cullen 1983; Dann 1992; Chiaradia and Kerry 1999) and Penguin Island, Western Australia; 32.3057° S (Wienecke 1993).

3.3.2.3 Terrestrial habitat and diet

Habitat. In Australia, little penguins mostly inhabit offshore islands, breeding in loose colonies adjacent to the sea in a variety of vegetation types ranging from sparsely vegetated rocky caves, grasslands, woodlands and forests (Stahel and Gales 1987; Marchant and Higgins 1990; Dann 2013). On Penguin Island, nesting habitat consists of low (<1.5 m) shrubland and limestone caves (Klomp *et al.* 1991). Unlike other colonies, soil burrows are uncommon due to the friability of the island's sandy substrate (Wienecke *et al.* 1995). Rather, penguins on Penguin Island rely on dense vegetation, under which they dig a shallow nest bowl (Wienecke 1993) as well as artificial nest boxes for breeding (Klomp *et al.* 1991). Nest boxes on Penguin Island were first installed in 1986 and are similar to those used in other little penguin colonies around Australia and New Zealand (Klomp *et al.* 1991).

Diet. Little penguins from Penguin Island forage both north and south of Penguin Island usually within 10 km of the coastline (Cannell *et al*. 2020). Five species of fish make up the majority of the diet of and include sandy sprat (*Hyperlophus vittatus*), blue sprat (*Spratelloides robustus*), garfish (*Hyporhamphus melanochir*), pilchard (*Sardinops sagax*) and anchovy (*Engraulis australis*) (Klomp and Wooller 1988; Wienecke 1989; Murray *et al.* 2011).

3.3.2.4 Population size on Penguin Island

Population size was estimated seven times spanning the 30-year period 1987-2017. However, while study methodologies and analyses have been similar over the period (monitoring of four key landing sites and using mark-recapture analyses), important differences remain because the 20th century estimates do not include the whole of island. The most recent population estimates (2007 onwards) have revealed a declining trend (Table 3.1).

Table 3.1: Population estimates (±SE) of little penguins on Penguin Island, Western Australia

Year	Population	Reference
2007	1695 ± 116	(Cannell 2012)
2008	1413 ± 99	(Cannell 2012)
2010	690 ± 56	(Cannell 2012)
2011	964 ± 90	(Cannell 2012)
2017	517 ± 231	(Cannell 2018)

3.3.3 Study design

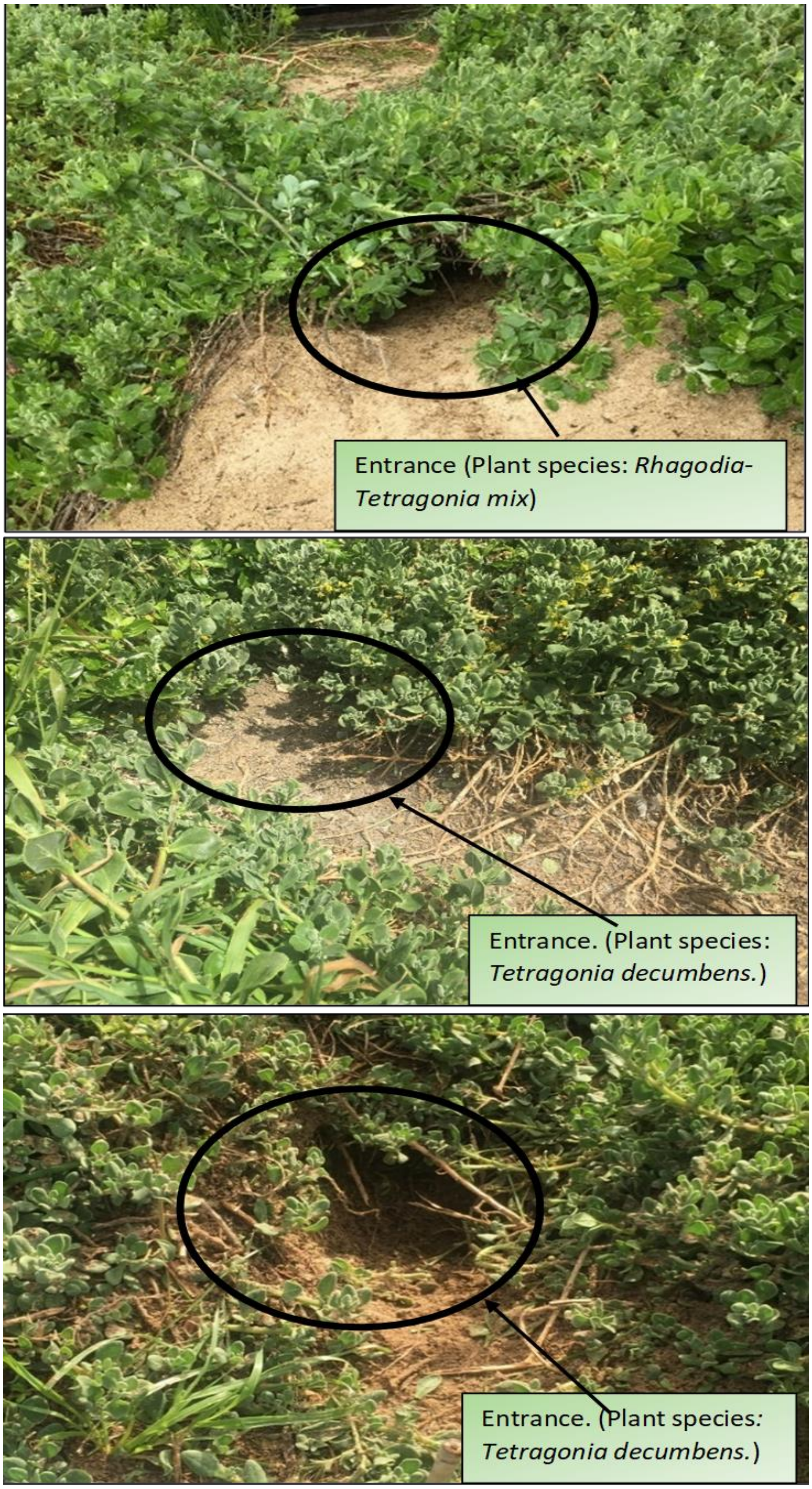
To evaluate factors influencing nest occupancy and success in little penguins on Penguin Island, nesting habitat was monitored over three breeding cycles (January 2014 – January 2017). During this period nest habitat attributes, nest use, and breeding productivity were quantified. I identified three general nest habitat types available to little penguins, (1) artificial nest boxes with removable lids (n=113), (2) natural nests used by little penguins over the study period (n=50), and (3) unused sites within existing penguin habitat that remained unused across the study period (hereafter random nest site; n=27).

3.3.3.1 Nest identification and monitoring

Natural nests were identified using several signs of occupancy including recent excavation, fresh faeces, obvious entrance, presence of nest material, presence of adult or presence of chicks/eggs (Figure 3.5). Once identified as having nesting activity, the sites were marked with a GPS. In 2013, 20 natural nests were located through a thorough search of the available vegetated nesting area during July and August. An additional 33 nests were identified and monitored in 2014, 2015 and 2016 through a thorough search of the available vegetated nesting area during the prospecting and early breeding months (April – June). Most penguin nesting occurs on the leeward (eastern) side of Penguin Island (Dunlop *et al.* 1988; Klomp and

Wooller 1991), consequently, the majority (60%) of the natural nest sites sampled were located within this area. To contrast attributes of used and unused natural nests, an additional 27 random nest sites were identified and marked in 2015 and monitored. Random nest sites were defined as sites that appeared suitable for nesting (sufficient shrub cover for burrowing in areas accessible to penguins) but where no nesting activity occurred across the study period. These sites were randomly selected by generating random points using the software Quantum-GIS (QGIS Development Team 2014). From the designated point, the nearest unoccupied bush or patch of vegetation was used as a random nest point.

Artificial nests boxes were installed on Penguin Island between 1986 and 2006 (55 in 1986, dimensions: 0.9m x 0.4m x 0.4m [lhw]; 25 in 2001, dimensions: 0.74m x 0.3m x 0.35m [lwh]; and 46 in 2006, dimensions: 0.47m x 0.4 x 0.3m [lwh]). The boxes vary in both shape and construction material, depending on installation year (Figure 3.6). Boxes installed in 1986 were placed in the main breeding area (groups of 17, 13, 13 and 12 in areas differing in levels of human activity) with the entrance oriented towards a known little penguin access route (Klomp *et al.* 1991). There is limited information available for how boxes installed in subsequent years were placed, however it is likely they were positioned following similar methods (Cannell pers. comm.). All nest boxes in functional condition were included in the sample. All nest sites included in the study (i.e. artificial, natural and random nest sites) were marked, labelled and their position recorded using a Getac differential global positioning system (dGPS) which ensured a horizontal accuracy of <1 m (at best 0.1 m). Points representing each nest (Figure 3.7) were entered into a geographic information system (GIS) database. Both natural and artificial nests were monitored fortnightly through the year. To ensure the random nest sites were unused throughout the study period they were also monitored fortnightly throughout the majority of the pre-breeding and breeding cycle but the frequency reduced to monthly in the typical late breeding to moult stage, between November and February.



Entrance (Plant species: *Rhagodia-Tetragonia mix*)

Entrance. (Plant species: *Tetragonia decumbens.*)

Entrance. (Plant species*: Tetragonia decumbens.*)

Figure 3.5: Examples of Natural penguin nests on Penguin Island, Western Australia

Figure 3.6: Three nest box types available on Penguin Island. **Top**: Box type installed in 1986. **Middle**: Box type installed in 2001. **Bottom**: Box type installed in 2006.

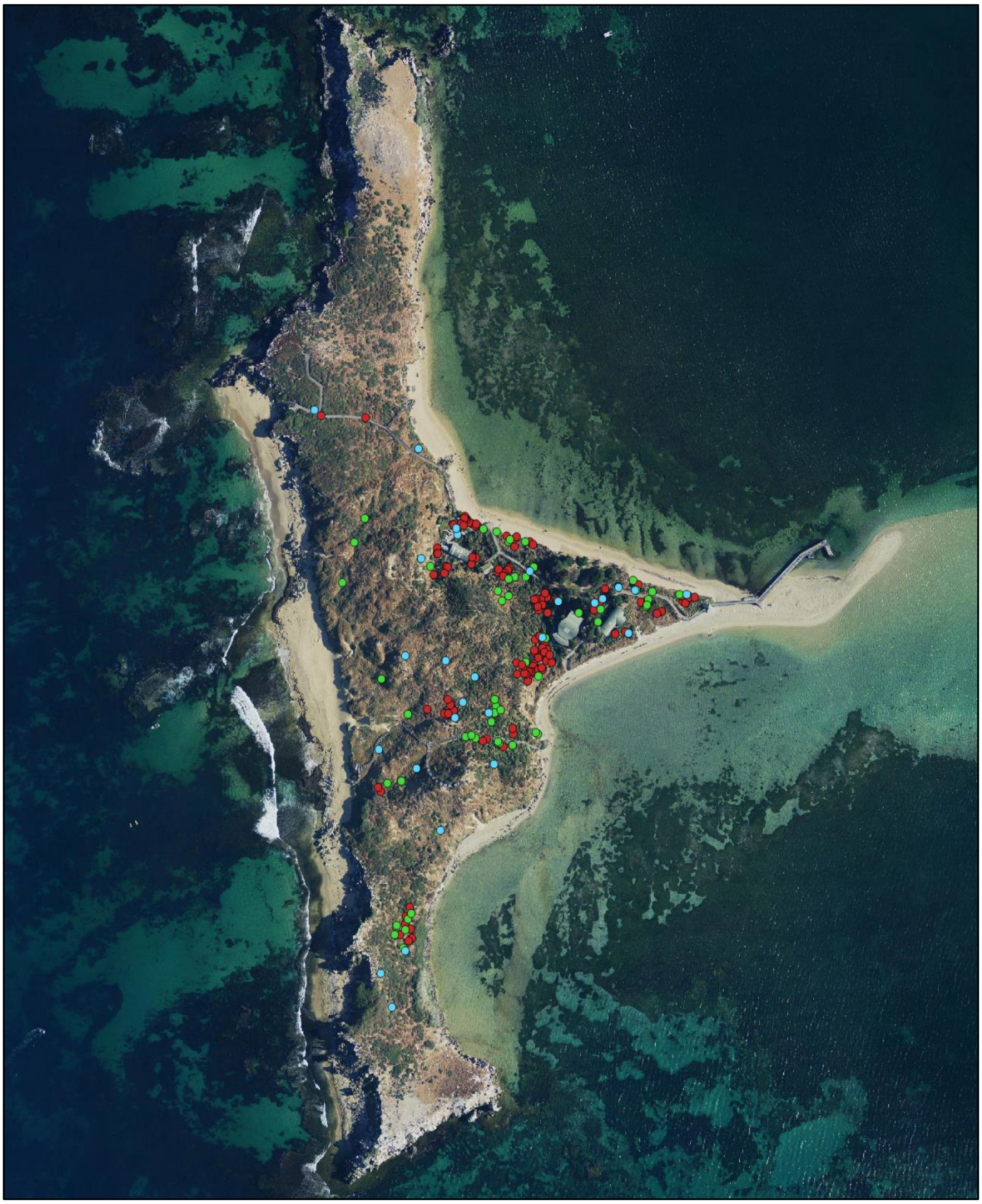


Figure 3.7: Aerial imagery of Penguin Island showing location of sample nest sites. Natural nests **(green),** artificial nests **(red)** and random nest sites **(blue).**

3.3.3.2 *Nest characteristics and nest use*

For each sample nest, a suite of nest habitat variables was recorded. These were stratified to represent (1) characteristics describing the position of the nest within the landscape (hereafter landscape position) and (2) characteristics directly associated with the nest (hereafter nest site). Landscape position measurements thought to influence nest use were taken both in the field and from a GIS database of Penguin Island. These included topographical measurements (slope, aspect and elevation), proximity to landscape features and proximity to anthropogenic disturbance (represented by distance from visitor boardwalks). Nest site measurements covered a range of characteristics thought to potentially influence nest selection of surface and cavity nesting seabirds and included, (1) proximity to neighbours (other nesting penguins), (2) physical dimensions of the nest and (3) vegetation characteristics (vegetation cover and species). As this study covered multiple years and seasons, vegetation characteristics were measured accordingly. Vegetation cover was defined at two spatial scales, (1) within one m of the nest, and (2) in the broader surrounding habitat (within approximately four meters of nest). These measurements included a combination of both visual cover estimates (categorised into the following categories: 1 = <5% cover, 2 = 5- 24% cover, 3 = 25 – 49% cover, 4 = 50 – 74% cover and 5 = 75 – 100% cover) and automated estimation from digital images. The latter allows for more precision than those data collected through visual estimation (Macfarlane 2011). To calculate a foliage cover percentage, photos were analysed using routines coded in MATLAB (2010) as outlined in Macfarlane (2011) and Macfarlane and Ogden (2012). See Table 3.2 for descriptions of all measurements recorded for natural, random and artificial nests.

Nests were considered occupied at the scale of individual years (annual use) and the overall study (used in any of the three years of monitoring). Used nests were defined as those where nesting activity was observed; unused nests were those where no nesting activity was recorded. Both natural nest and artificial nest boxes were classified in the same manner. Natural burrows were checked for occupancy and breeding activity by looking directly into the nests through the entrance with the aid of an LED torch and infrared burrow scope (Faunatech-Ausbat, Victoria) for contents of more elaborate nests with impaired visibility. The contents of each nest were noted at each visit, including evidence of use or nesting activity. Occupancy and breeding activity could be detected with high certainty for both boxes (where the entire nest and its contents are visible) and natural nests (generally shallow and contents easily visible either with the naked eye or through use of burrow scope). Established protocols were used to measure several reproductive variables (Table 3.3). Successful nests were defined for both natural and artificial nests where at least one chick was raised to fledging (i.e. five weeks). A nest was considered unsuccessful if breeding was attempted, but no fledglings were produced.

Table 3.2: Nest attributes measured, description of attribute and frequency of measurement for natural nests, nest boxes and random nest sites on Penguin Island, Western Australia 2014-2016.

Nest Attribute	**Description**	**Frequency of measurement**	**Artificial nest (box)**	**Natural nest**	**Random nest**
Landscape position					
Slope[†]	Slope of the ground on which the nest is located (degrees)	Once only	✓	✓	✓
Elevation[†]	Elevation of the of the position where the nest is located (m)	Once only	✓	✓	✓
Aspect[†]	Aspect of the hill face on which the nest is located (degrees)	Once only	✓	✓	✓
Distance to Boardwalk	Distance from nest site centre to nearest public boardwalk/ path (m)	Once only	✓	✓	✓
Distance to shore	Distance from the centre of nest site to edge of vegetation above shoreline (m)	Once only	✓	✓	✓
Distance to Landfall	Distance from the centre of the nest site to the nearest known landfall site (m)	Once only	✓	✓	✓
Nest site					
Vegetation attributes					
Discrete bush	Natural nest is either a discrete bush or part of a larger vegetation patch	Annual measurement during winter	NA	✓	✓
Vegetation wall	Thickness of vegetation measured from the nest cavity 'ceiling' to the outside edge of the vegetation (mm)	Annual measurement during winter	NA	✓	✓

Nest Attribute	Description	Frequency of measurement	Artificial nest (box)	Natural nest	Random nest
Species	Species of plant that dominated the vegetation surrounding or covering the nest.	Annual measurement during winter	✓	✓	✓
Nest bush height	Maximum height of the vegetation directly over the nest (mm)	Annual measurement during winter	NA	✓	✓
Nest bush length	Length of nest shrub from the edge containing the entrance to the opposite edge of bush (mm). For unused natural nest and random sites this was recorded as width 1.	Annual measurement during winter		✓	✓
Nest bush width	Width of nest shrub (mm). For unused natural nest and random sites this was recorded as width 2.	Annual measurement during winter	NA	✓	✓
Cavity cover	Percentage vegetation over directly over the nest cavity measured using a Gopro HERO4 camera positioned in the centre of the nest bowl facing upwards.	Bi-annual measurement in summer and winter	NA	✓	✓
Box cover	Percentage of vegetation cover covering the nest box lid, categorised into 5 cover classes.	Seasonally (winter, spring, summer, autumn)	✓	NA	NA
Quadrat cover	Percentage of vegetation cover within a circular plot (1 m diameter) centred over the nest, categorised into cover classes.	Seasonally (winter, spring, summer, autumn)	✓	✓	✓
Canopy cover	Vegetation cover falling within a 1x1 m quadrat at a height of 50 cm or above measured using a GoPro HERO4 camera centred on top of the nest facing upward.	Bi-annual measurement in summer and winter	✓	✓	✓

Nest Attribute	**Description**	**Frequency of measurement**	**Artificial nest (box)**	**Natural nest**	**Random nest**
Surrounding ground Cover	Percentage of green vegetation within a rectangular quadrat centred over the nest site. This was achieved using a pole-camera fashioned by attaching a Cannon G12 digital camera to the end of a 4-metre aluminium pole. The camera was positioned directly over the centre of the nest and a photo was remotely taken. The area captured by the photos was approximately 14.5 m^2. The position where the pole contacted the ground was recorded using a differential GPS to ensure accurate repeatability. The compass bearing from which the photo was taken was also recorded to ensure data were comparable across years.	Annually at the beginning of Autumn (before annual weed growth) for all old boxes in 2013, 2014, 2015, and 2016. Natural burrows were included in 2015 and 2016.	✓	✓	X
Nest/ box attributes					
Entrance height	Height of the entrance opening (mm)	Once only for boxes and annually in winter for natural nests	✓	✓	NA
Entrance width	Width of the entrance opening (mm)	Once only for boxes and annually in winter for natural nests	✓	✓	NA
Entrance length	Length from the external opening to the start of the nest bowl (mm)	Once only for boxes and annually in winter for natural nests	✓	✓	NA

Nest Attribute	**Description**	**Frequency of measurement**	**Artificial nest (box)**	**Natural nest**	**Random nest**
Entrance bearing	The bearing recorded using a compass. (degrees)	Once only for boxes and annually in winter for natural nests	✓	✓	✓
Cavity height	Maximum height of the nest cavity from the base of the nest bowl to the cavity ‘ceiling’ (mm)	Annually	NA	✓	NA
Cavity width	Maximum width of the nest cavity (mm)	Annually	NA	✓	NA
Cavity length	Maximum length of the nest cavity from the start of the nest bowl to the back of the nest cavity (mm)	Annually	NA	✓	NA
Tunnel	Presence or absence of an entry tunnel	Once only	✓	NA	NA
Box height	The height of the box (mm)	Once only	✓	NA	NA
Box Width	Width of the box (mm)	Once only	✓	NA	NA
Box Length	Length of the box (mm)	Once only	✓	NA	NA
Box wall	Thickness of a box side walls (mm)	Once only	✓	NA	NA
Box lid	Thickness of a box lid (mm)	Once only	✓	NA	NA
Box Shape	Geometric shape of a nest box (square, rectangle)	Once only	✓	NA	NA
Vents	Presence or absence of ventilation holes	Once only	✓	NA	NA
Distance to neighbour	Distance from the centre of nest to the centre of nearest active nest, (m). Distances were measured up to 10 m after which the measurement was recorded as >10 m.	Annually	✓	✓	✓

[†] elevation, slope and aspect data retrieved from Department transport (2009) Composite Surfaces - Multibeam LIDAR Laser (DOT-022) dataset https://services.slip.wa.gov.au/public/rest/services/SLIP_Public_Services/Imagery_and_Maps/MapServer/19 under active and use licence creative commons attribution 4.0 https://creativecommons.org/licenses/by/4.0/legalcode. The horizonal accuracy for the source data was +/- 4m or better and vertical +/- 0.45m both at a 95% confidence interval.

Table 3.3: Definition of reproductive variables measured for each breeding year.

Reproductive measure	**Description**
Clutch	Number of clutches laid per nest.
Eggs laid	Total number of eggs laid per nest combining all clutches. Observed through fortnightly nest checks
Chicks hatched	Total number of chicks hatched per nest. Eggs were recorded as hatched if chicks were observed (dead or alive). If eggs were recorded and no adults were present or observed on the nest at a later date, the eggs were recorded as abandoned and unhatched. If eggs were observed in a nest at a previous monitoring session and the nest and either one or both eggs were missing at the following session the eggs were recorded as abandoned and unhatched.
Chicks dead	Total number of chicks dead per nest. Chick mortality was recorded if dead chick/s were observed in or nearby the nest, or, if a chick was missing from the nest before reaching 35 days. Chicks 35 days or older missing from the nest that did not fall within a normal weight range (Wienecke *et al.* 2000) at the last encounter were also recorded as dead.
Chicks fledged	Number of chicks reaching fledging age per nest. Chicks were considered to have fledged if they reached a minimum of 35 days age. Chicks missing from the nest but had been previously observed within a normal weight range at 35 days old (Wienecke *et al.* 2000) were recorded to have fledged as chicks are known to wander from the nest from this age (Reilly and Cullen 1981; Stahel and Gales 1987).
Hatching success	Proportion of eggs hatched from eggs laid (Cannell *et al.* 2012; Reilly and Cullen 1981).
Fledging success	Proportion of chicks fledged from hatched eggs
Breeding success	Number of chicks fledged from number of eggs laid (Cannell *et al.* 2012).
Fledging weight†	Maximum mass recorded of fledging after 6 weeks (Cannell *et al.* 2012; Chiaradia and Kerry 1999; Stahel and Gales 1987).
Lay date	Egg lay in little penguins is rarely observed (Pers. Obs) so lay date was estimated by back calculating 35 days from the estimated hatch date which was estimated from the approximate age of chicks when they were first observed. For nests which failed before hatching the lay date was taken as the date the eggs were first observed (Cannell *et al.* 2012).
Nest success	Total number of fledglings produced per nest

† Fledgling weight of chicks being reared in natural burrows was measured only if they were accessible without risking damage to the nest

3.3.4 Data Analysis

The overarching objectives of this investigation were to (1) quantify the characteristics of both natural and artificial nests and (2) investigate the influence of nest characteristics on, (a) probability of nest use and (b) nest success, for nesting sites (natural and artificial) used by little penguins on Penguin Island, Western Australia. Data for natural nests and artificial nests were analysed separately applying univariate and multivariate statistical modelling. All analyses were performed within the statistical software program R version 3.6.1 (R Core Team 2018) and using R Studio version 1.2.1335 (RStudio Team 2018).

3.3.4.1 Characteristics of natural and artificial nests

Descriptive statistics of landscape position and nest site characteristics are reported as frequencies or means ± standard error (SE) for tables; figures represent frequencies or means ± 95% confidence intervals. Lack of overlap of the mean with adjacent confidence intervals was considered evidence of an effect.

3.3.4.2 Nest use models

Prior to any statistical analysis, data exploration was carried out following Zuur *et al.* (2010). Cleveland dotplots were used to identify outliers and multi-panel pair-plots were used to screen for collinearity of variables, assessed using Pearson's correlation coefficient. If the Pearson's correlation coefficient was >0.6 then one variable from the pair was eliminated (Booth *et al.* 1993). A significant correlation was found between distance to landfall and distance to shoreline (r=0.8), and bush wall and bush height (r=0.7). Subsequently, distance to shoreline and bush wall were removed from further analyses.

During data analysis, I applied an information-theoretic approach (Burnham and Anderson 2003) whereby support for predictors given the data was examined. To determine landscape position attributes with the greatest influence on overall use of both natural nests and artificial nests, I fit generalized linear models (GLMs) with a logit link function and binomial distribution and included the explanatory variables; distance to boardwalk, distance to landfall, slope, elevation and aspect. To evaluate which nest site and landscape position attributes had the greatest influence on annual use of natural and artificial nests, generalized linear mixed effect models (GLMMs) with a logit link function and binomial distribution were applied. To avoid overfitting the model, explanatory variables were screened and pre-selected through visual exploration and univariate logistic regression analyses for each variable (Hosmer Jr *et al.* 2013). Natural nest models included the explanatory variables, slope, vegetation cover, bush height and species composition. Artificial nest models included the variables, box entrance direction, box length, box width, aspect, slope, distance to boardwalk and species composition. As nests were visited repeatedly across years, nest ID was included as a random effect in both artificial nest models and natural nest models. While not a factor of interest for this study, year could not be included as a random effect as it was limited to two levels (i.e. 2015 and 2016) and therefore was included as a fixed effect.

Due to the exploratory nature of this study, a balanced *all subsets* approach was used whereby all possible combinations of the predictor variables were tested to examine the effect of nest characteristics and landscape position on nest use. This approach ensures all top ranking sub-models are included in the candidate model set and generally performs better than other ad hoc model selection strategies when defining variable importance (Doherty et al 2012; Morin et al 2020). Selected explanatory variables were fitted to a global model that included all predictors (outlined above) and all possible combinations were tested using the 'dredge' function in the MuMIN package (Barton 2016). Model residuals were visually evaluated for issues with fit or assumptions; no violations were detected. Variance explained for GLMs was estimated as Nagelkerke's pseudo R^2 values. For mixed models, variance explained by the fixed effects (marginal pseudo R^2) was estimated using methods described by Nakagawa and Schielzeth (2013) and the function 'r.squaredGLMM' from the package MuMIN (Barton 2016).

Models were evaluated using Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2003; Symonds and Moussalli 2011; Barton 2016). AICc weight (ω_i) was used to select the best of the competing models. Models with a ΔAICc <5 are presented and models with a ΔAICc <2 were considered as having substantial support (Burnham and Anderson 2003; Burnham *et al.* 2011). To account for model uncertainty and enable more robust inferences, model averaging was applied across all models and parameter and error estimates were derived from a weighted average across multiple models (Burnham and Anderson 2003; Johnson and Omland 2004; Symonds and Moussalli 2011). Prior to averaging, model parameters were standardised based on partial standard deviations to remove effects of collinearity among predictors (Cade 2015). I examined two types of model averaged coefficients to assess strength of evidence for an effect: the conditional model average (where estimates are generated from only the models each covariate appears), and the full model average (where covariates not present in the model contribute zero to the calculation) (Symonds and Moussalli 2011). Full model averaged estimates consequently shrink towards zero; the difference between full and conditional model estimates is referred to as *shrinkage* and represents the degree by which covariates are informative (Symonds and Moussalli 2011; Cade 2015). Shrinkage was examined to assess strength of covariates present in top models (Burnham *et al.* 2011; Grueber *et al.* 2011; Symonds and Moussalli 2011). Predictions and graphical representations of full and conditional model averaged coefficients were produced through the packages ggeffects (Lüdecke and Lüdecke 2017) and sjplot (Lüdecke 2018). Variables were considered to have the strongest evidence of effect if the disparity between the full and conditional estimates (shrinkage) was small and 95% confidence intervals of model-averaged coefficients did not include zero (Johnson and Omland 2004; Burnham et al. 2011; Symonds and Moussalli 2011).

3.3.4.3 Characteristics of successful natural and artificial nests

Due to insufficient sample size of breeding attempts, regression analysis resulted in models either failing to converge or being overfit (Burnham and Anderson 2003). Consequently, to evaluate whether landscape and nest site attributes influenced success of a nest used for breeding (natural and artificial), I compared means and 95% confidence intervals (continuous variables) and frequencies (categorical variables). A lack of overlap of confidence intervals and means was interpreted as evidence of an effect between groups.

3.4 Results

Across three breeding seasons (2014-2016), mean nesting occupancy (nests with evidence of nesting activity) was 75% for natural nests (range = 56-86%) and 49% for artificial nest boxes (range = 46 -50%). Breeding occupancy (nests where breeding was attempted) was 49% for natural nests (range = 32 – 68%) and 24% for artificial nest boxes (range = 20-28%) (Table 3.4).

Table 3.4: Nesting occupancy (percentage of all nests where nesting activity was recorded) and breeding occupancy (percentage of all nests with breeding activity was recorded) for natural and artificial nests across the study period (2014 - 2016) on Penguin Island (count of nests and percentages in parentheses).

Year	**Use type**	**Artificial**	**Natural**
2014	*(n)*	*113*	*50*
	Occupied	57 (50%)	43 (86%)
	Breeding	32 (28%)	34 (68%)
2015	*(n)*	*111*	*50*
	Occupied	51 (46%)	42 (84%)
	Breeding	26 (23%)	24 (48%)
2016	*(n)*	*109*	*50*
	Occupied	55 (50%)	28 (56%)
	Breeding	22 (20%)	16 (32%)
Mean 2014-2016	Occupied	54 (49%)	38 (75%)
	Breeding	27 (24%)	25 (49%)

3.4.1 Nest site characteristics of natural nests and artificial boxes

Nests more often occurred on either no aspect or an easterly aspect but did not differ from orientation of unused nests (Table 3.5; Figure 3.8). Available artificial nests followed a similar pattern in distribution and were more frequently positioned on flat ground or an easterly aspect however differed to natural nesting sites by being less likely to occur on south or west facing aspects (Table 3.5). The slope between nest types (natural vs artificial) or between used and unused natural nests was similar. Used artificial nests, however, were located on steeper slopes (Table3.5; Figure 3.9A). Both used and unused natural nests were located at similar elevations (Table 3.5). However, this pattern was not observed for artificial nests and used boxes were located at lower elevations than unused (Table 3.5; Figure 3.9B). Distance to boardwalk was similar between used and unused nests and between nest types (Table 3.5). Used nests were on average closer to major landfall site than unused nests (Table 3.5; Figure 3.9C). However, used natural nests were on average further from landfall sites than used artificial nests.

There were some notable differences in the vegetation attributes between natural and artificial, and between used and unused nests. Natural nests typically had greater surrounding vegetation cover than artificial nests and used natural and artificial nests had greater vegetation cover than their unused counterparts (Table 3.5, Figure 3.10). Nest vegetation cover also differed between the two nest types. Used artificial nests were represented in all five cover categories however most (67%) were recorded having < 50% cover. In comparison, all natural nests were recorded with greater than 50% cover, most (94%) exceeding 75% (Figure 3.11). Plant species associated with the nests differed between natural and artificial nests but not between used and unused nests. *Tetragonia sp.* was the dominant species associated with natural nests and was present at 84% of used nest sites. Artificial nests were more often associated with *Rhagodia baccata* which was present at 50% of used artificial nest sites (Figure 3.12). Used natural nests occurred under taller vegetation than unused nests (Figure 3.13).

The most marked differences between used natural and artificial nests were observed for the nests' cavity and nest entrance characteristics. Entrance orientation of natural nests were mostly (73%) oriented in a south-east to westerly direction (Figure 3.14). This differed to artificial nests where entrance bearing was much more evenly distributed across all directions

(Figure 3.14). Entrance dimensions of natural nests were longer, wider and higher than artificial nests (Figure 3.15a-c). Similarly, cavities of natural nests were also larger in floor area and were both taller, and wider than artificial nests but were on average not as long (Figure 3.15d-f). Used artificial nests were longer than unused ones (Figure 3.15d-f).

Table 3.5: Nest site characteristics (mean ± standard error, range in parentheses; or frequencies [%]) for used and unused little penguin nests on Penguin Island, Western Australia.

	Natural nests		**Artificial nests (Boxes)**	
Attribute	Used	Unused	Used	Unused
Location/topographical attributes	**[n=51]**	**[n=28]**	**[N=89]**	**[N=23]**
Distance to landfall site (m)	32 ± 1.8 (4-57)	45 ± 3.6 (1-77)	27 ± 1.7 (3-67)	29 ± 4.2 (4 - 65)
Distance to boardwalk (m)	25 ± 4.7 (0.2-113)	30 ± 8.0 (0.7-156)	18 ± 2.4 (0 - 108)	24 ± 4.7 (0.5 - 92)
Slope (degrees)	6.7 ± 0.7 (0.6 – 20.9)	6.5 ± 1.2 (0.6 – 30.0)	6.8 ± 0.6 (0.6 – 21.0)	9.8 ± 1.1 (1.3 – 21.2)
Elevation (m)	5.8 ± 0.5 (1.5 –13.2)	6.7 ± 0.8 (2.0 – 13.7)	4.4 ± 0.3 (1.7 – 13.7)	6.2 ± 0.7 (2.0 – 13.8)
Aspect (% of nests)				
NONE	42	49	47	26
North	13	9	12	13
East	26	28	40	57
South	8	4	1	0
West	12	11	0	4

	Natural nests		**Artificial nests (Boxes)**	
Nest site attributes				
Surrounding vegetation cover (% of nests)	52. 5 ± 1.5 (24-78)	48.1 ± 2.1 (30 - 72)	48.8 ± 1.0 (7 -94)	45.1 ± 1.2 (10 -94)
Nest Vegetation cover (% of nests)				
>75% cover	94	80	12	22
50 - 75% cover	6	20	21	12
25 – 50%	0	0	27	19
5- 25%	0	0	35	35
<5%	0	0	5	12
Bush height (mm)	501 ± 15.4 (200 – 1090)	410 ± 25.6 (170 – 800)	NA	
Species (% of nests)				
R. baccata	16	21	23	18
Tetragonia. spp	53	40	14	20
R. baccata-Tetragonia spp	30	39	24	17
R. baccata-Tetragonia spp -Acacia spp.	1	0	3	6
R. baccata -Acacia spp.	0	0	13	9
Tetragonia spp. - Acacia spp	0	0	10	16
Acacia spp.	0	0	14	14

	Natural nests		Artificial nests (Boxes)	
Wall depth	237 ± 10.8 (50 - 630)	193± 16.7 (20 - 450)	NA	
Cavity cover (%)	96 ± 0.3 (89 -100)	93 ± 2.4 (31 -100)	NA	
Cavity dimensions				
Cavity height / box height(mm)	244 ± 5.9 (110-450)	NA	273 ± 2.4 (200-370)	278 ± 2.2 (210-370)
Cavity Length/ box length (mm)	564 ± 12 (300 - 830)	NA	642 ± 10.0 (460-840)	578 ± 10.2 (330-840)
Cavity width/ box width (mm)	530 ± 12 (300 - 820)	NA	369 ± 3.9 (200-460)	388 ± 2.4 (200 - 460)
Cavity volume/ box volume (m3)	0.08 ± 0.004 (0.02 – 0.15)	NA	0.06 ± 0.001 (0.04 -0.1)	0.06 ± 0.001 (0.04 -0.1)
Cavity area/ box area (m2)	0.3 ±0.01 (0.15-0.58)	NA	0.2 ± 0.004 (0.1 – 0.4)	0.2 ± 0.004 (0.1 – 0.4)
Entrance dimensions				
Entrance height (mm)	163 ± 3.4 (100 - 260)	NA	134 ± 2.1 (100-250)	138 ± 2.4 (100-300)
Entrance width (mm)	222 ± 6.0 (140 - 600)	NA	170 ± 1.6 (120-200)	170 ± 1.4 (120-200)
Entrance length (mm)	395 ± 15 (0-800)	NA	28 ± 3.8 (0-200)	41 ± 4.4 (0-200)

	Natural nests		**Artificial nests (Boxes)**	
Entrance Direction (% of nests)				
N-NE	4	NA	11	10
NE-E	3		12	7
E-SE	7		11	13
SE-S	23		13	14
S-SW	25		18	17
SW-W	25		8	18
W-NW	8		13	10
NW-N	5		14	11
Distance to neighbour (% of nests)				
0-2.5m	13	17	20	28
2.5-5m	48	33	47	40
5-7.5m	19	19	21	20
7.5-10m	6	10	9	5
>10m	15	21	3	7

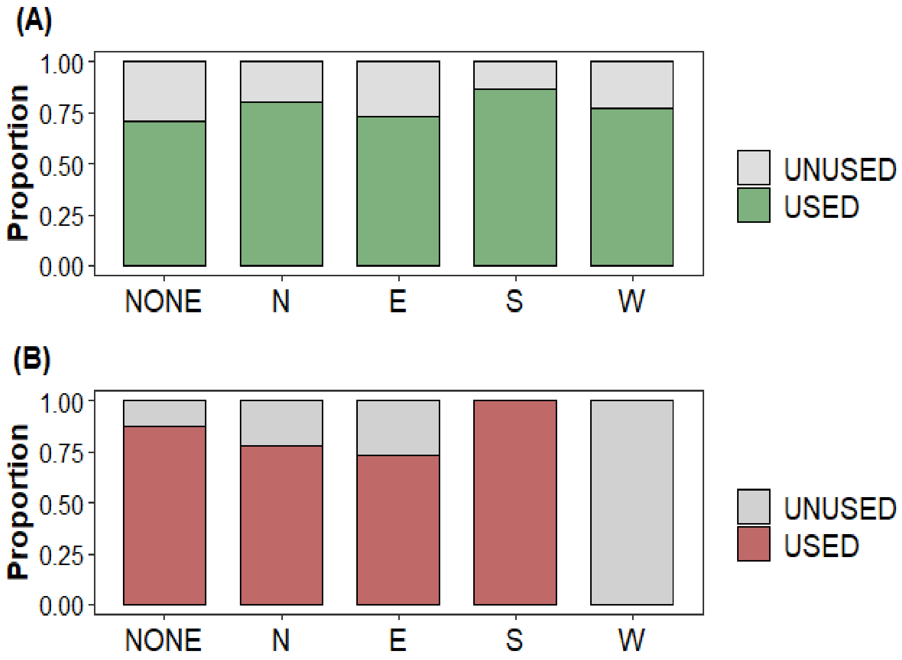


Figure 3.8 Proportion of used and unused **(A)** natural (n=50) and **(B)** artificial (boxes) (n=113) little penguin nests at different aspects, Penguin Island, Western Australia.

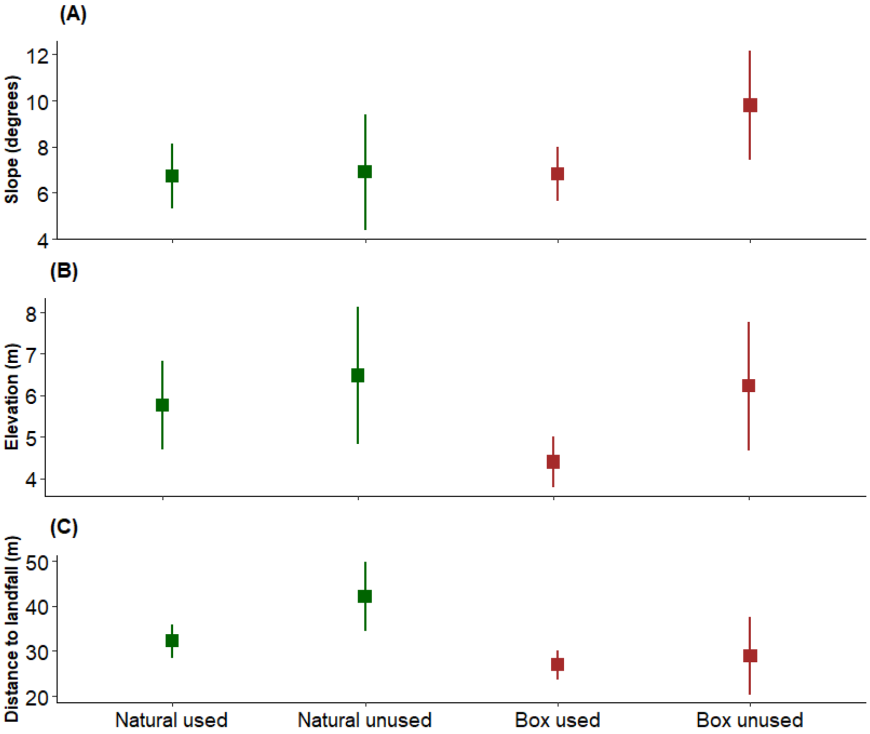


Figure 3.9: Mean and 95% confidence intervals of (A) slope (degrees), (B) elevation (meters above sea level) and, (C) distance to landfall (meters) between natural (used, n = 50 ;unused, n= 26) and artificial (boxes) (used, n = 90 ;unused, n= 22), little penguin nests, Penguin Island, Western Australia.

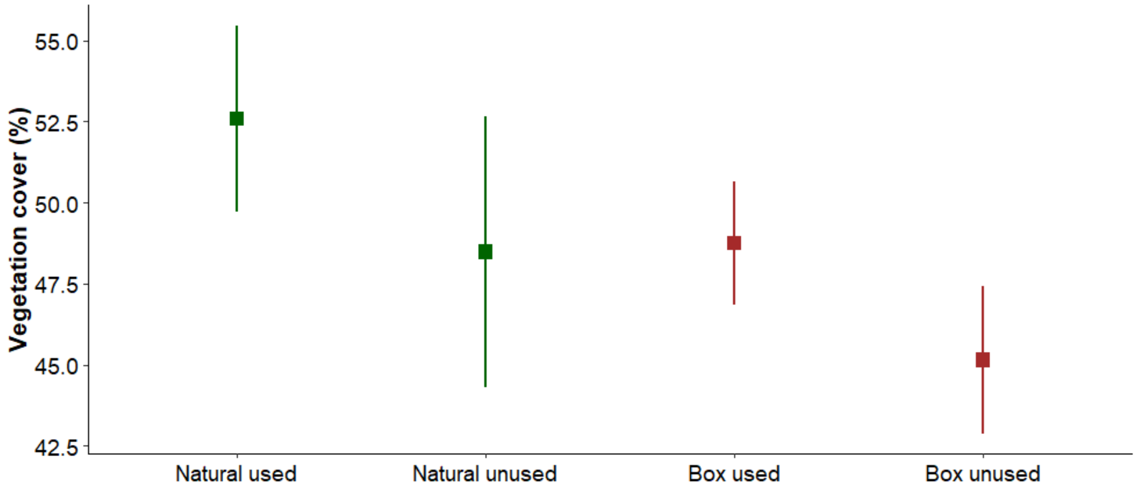


Figure 3.10: Mean surrounding vegetation cover (%) and 95% CI of natural (used, n = 51; unused, n= 30) and artificial (boxes) (used, n =90; unused, n= 88) little penguin nests, Penguin Island, Western Australia.

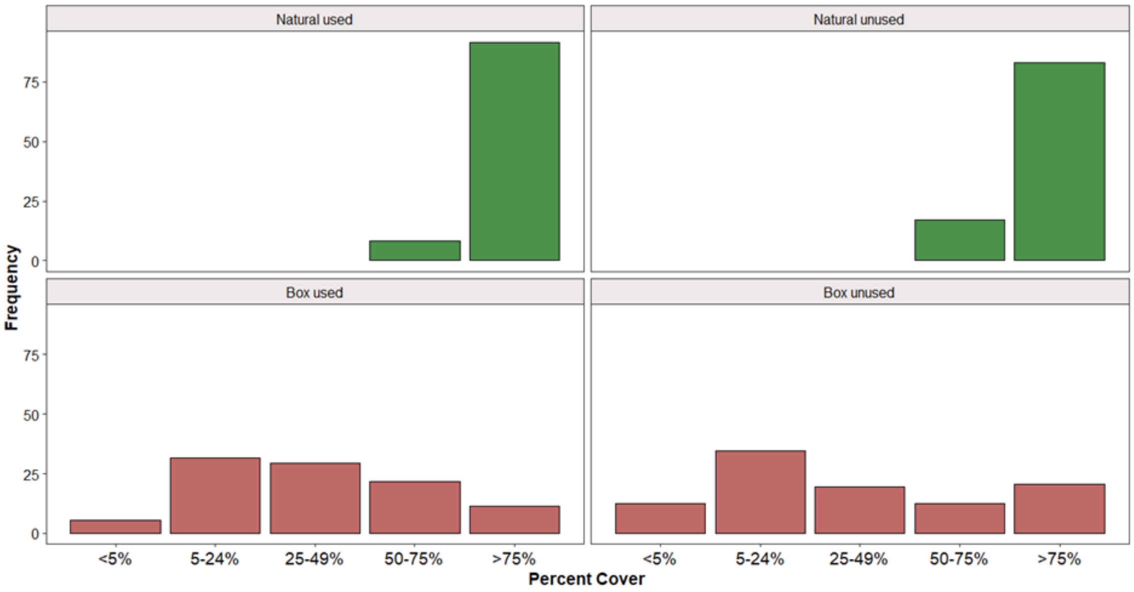


Figure 3.11: Percent vegetation cover within a circular quadrat of natural (used, n = 45; unused, n= 25) and artificial (boxes) (used, n = 69; unused, n= 72) little penguin nests, Penguin Island, Western Australia.

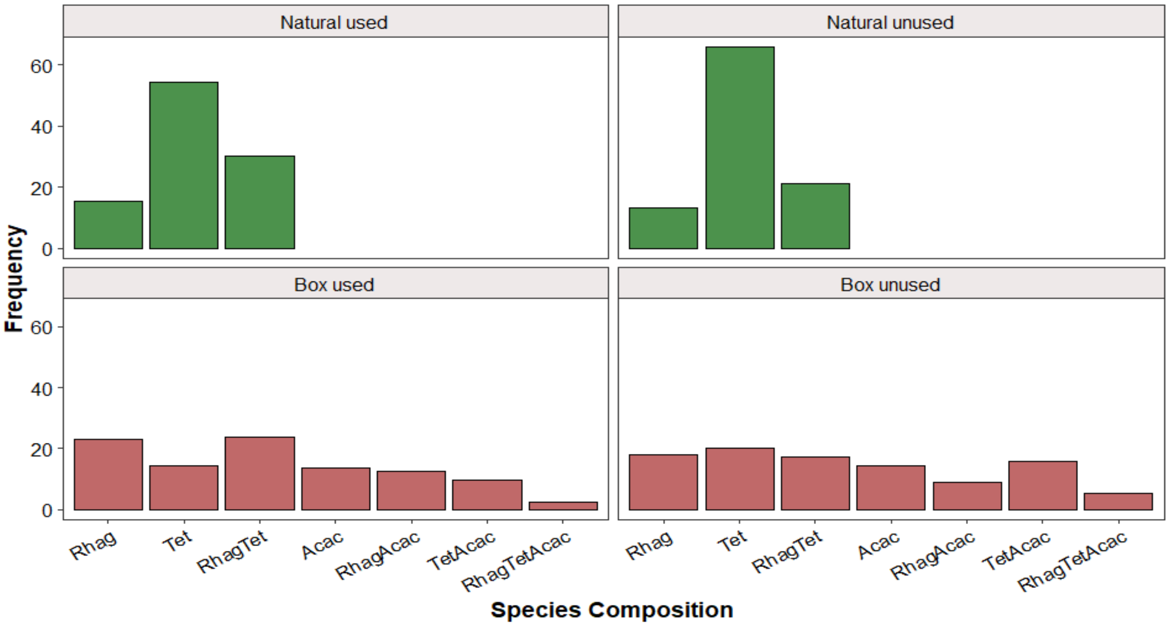


Figure 3.12: Dominant vegetation species (Rhag = *Rhagodia baccata;* Tet =*Tetragonia spp.;* Acac = *Acacia spp.;* RhagTet = *R. baccata – Tetragonia spp. mix;* RhagAcac = *R. baccata – Acacia spp.* mix; TetAcac = *Tetragonia spp. – Acacia spp.* mix; RhagTetAcac = *R. baccata- Tetragonia spp. – Acacia spp.* mix) present within a circular quadrat over natural (used, n = 50 ;unused, n= 29) and artificial (boxes) (used, n = 76 ;unused, n= 76) little penguin nests, Penguin Island, Western Australia.

Figure:3.13 Mean height of the nest bush (mm) and 95% CI of natural little penguin nests (used, n = 49; unused, n= 28), Penguin Island, Western Australia.

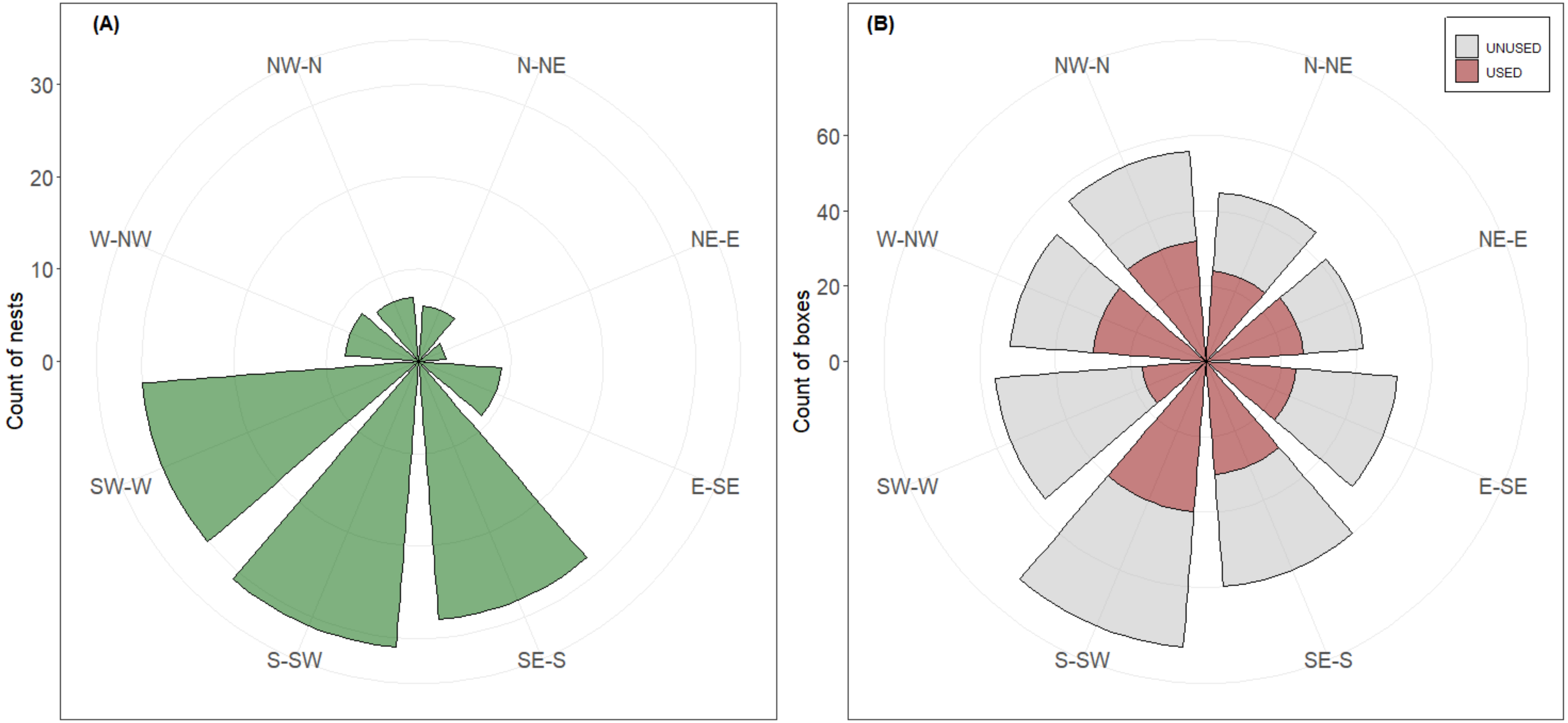


Figure 3.14: Nest entrance orientation of **(A)** natural (n = 47) and **(B)** artificial (boxes) (used, n = 89; unused, n= 87) little penguin nests, Penguin Island, Western Australia. (Length of bars indicate the number of nests found within each octant).

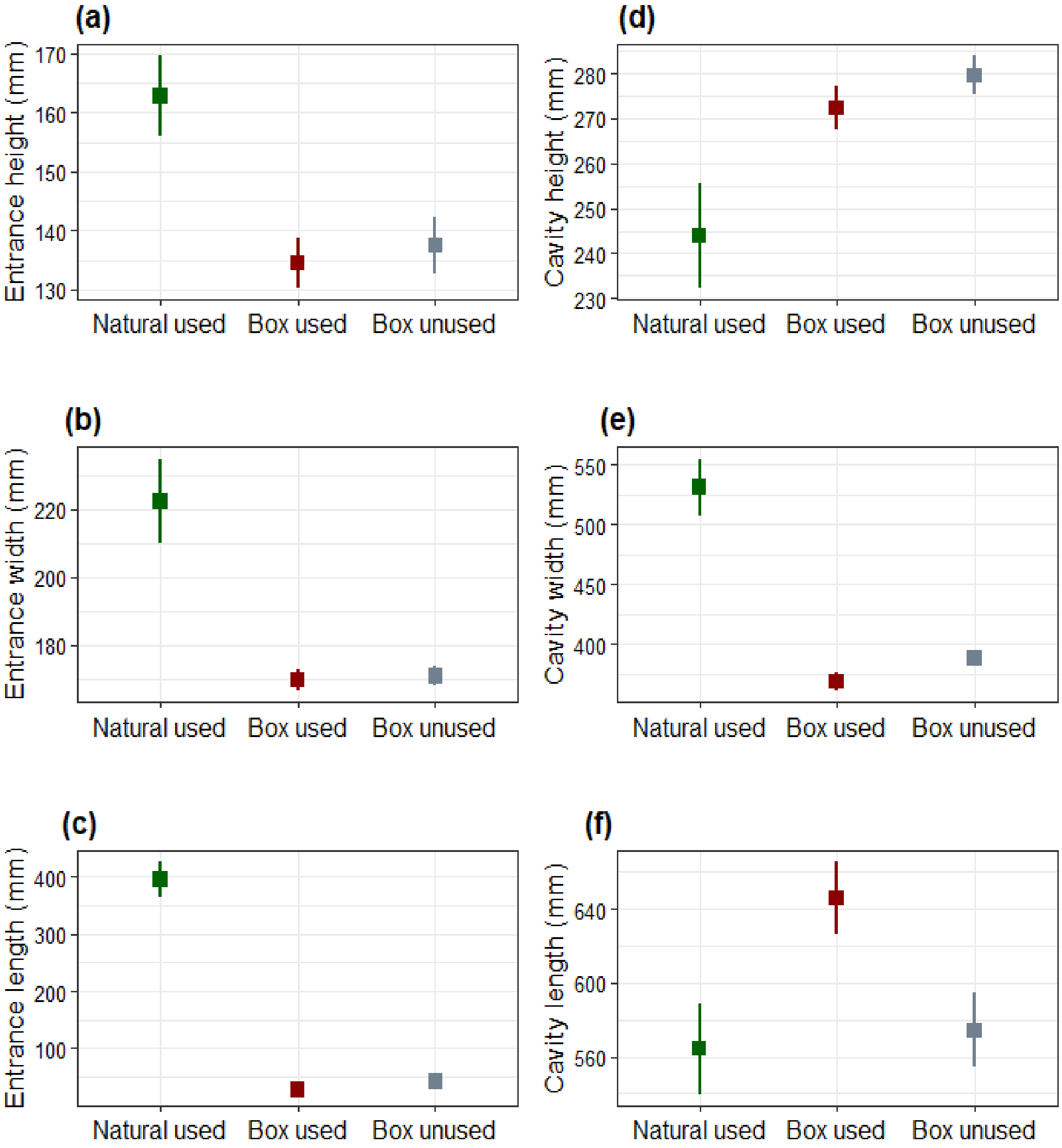


Figure 3.15: Nest dimensions of natural nests and used vs unused artificial nests (boxes). Means and 95% CI **(a)** entrance height (mm); **(b)** entrance width (mm); **(c)** entrance length (mm); **(d)** cavity height (mm); **(e)** cavity width (mm); **(f)** cavity length (mm).

3.4.2 Use of Natural and Artificial Nests

3.4.2.1 Attributes of landscape position that influence the overall use of natural nests

Thirty-two candidate models were evaluated to assess the importance of landscape position variables in predicting overall use of natural nest sites by little penguins. Distance to landfall was supported as a moderate predictor of nest use and was the only predictor present in the top model which had an Akaike weight of 0.35 (Table 3.6). Areas further from landfall sites were less likely to be used for nesting (β = -0.67, CI [-1.2 – -0.1] Table 3.7; Figure 3.16). Two competing models (within 2 AIC_c units of the top model) included the predictors elevation and distance to boardwalk in addition to distance to landfall. Model averaging revealed moderate shrinkage when comparing full and conditional model sets and CI overlapped zero indicating elevation and distance to boardwalk to be uninformative predictors of nest use (Table 3.7).

Table 3.6: Top models (ΔAICc< 5) for all subsets generalised linear model set relating *overall usage* (used vs available) of natural nests by little penguins on Penguin Island to the effects of landscape position variables only. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weights (ω_i), number of parameters (k) and Nagelkerke's pseudo R^2 (R^2).

Model	**AICc**	**ΔAICc**	ω_i	***k***	R^2
Intercept	*104.78*	*4.94*	*0.03*	*2*	*0*
Distance to landfall	99.84	0.00	0.35	3	0.12
Distance to landfall + elevation	101.81	1.97	0.13	4	0.12
Distance to landfall + distance to boardwalk	101.82	1.98	0.13	4	0.12
Distance to landfall + slope	101.99	2.15	0.12	4	0.12

Model	**AICc**	**ΔAICc**	**ω_i**	**k**	**R^2**
Distance to landfall +distance to boardwalk + elevation	103.86	4.02	0.05	5	0.12
Distance to landfall +distance to boardwalk + slope	103.96	4.12	0.04	5	0.12
Distance to landfall + elevation + slope	103.98	4.14	0.04	5	0.12

Table 3.7: Averaged model coefficients representing probability of *overall use* of natural nests by little penguins on Penguin Island based on landscape position variables. ($\hat{\beta}$ = model-averaged coefficient). Model coefficients where 95% CI did not overlap 0 are in bold.

	Full model set				**Conditional model set**			
Predictor	**$\hat{\beta}$**	**Adjusted SE**	***Z value***	**Pr (>|z|)**	**$\hat{\beta}$**	**Adjusted SE**	***Z value***	**Pr (>|z|)**
Distance to landfall	-0.61	0.32	1.90	0.06	**-0.67**	**0.28**	**2.44**	**0.01**
Distance to boardwalk	0.02	0.14	0.18	0.86	0.09	0.25	0.36	0.72
Slope	-0.01	0.13	0.09	0.93	-0.04	0.26	0.18	0.86
Elevation	0.02	0.15	0.15	0.88	0.08	0.27	0.30	0.76
Aspect								
None	*Reference*							
North - East	0.01	0.07	0.12	0.90	0.29	0.29	0.99	0.32
East - South	0.00	0.04	0.03	0.97	-0.05	0.26	0.19	0.85
South - West	0.00	0.05	0.09	0.93	0.16	0.28	0.58	0.56
West - North	0.00	0.04	0.06	0.96	-0.09	0.24	0.35	0.72

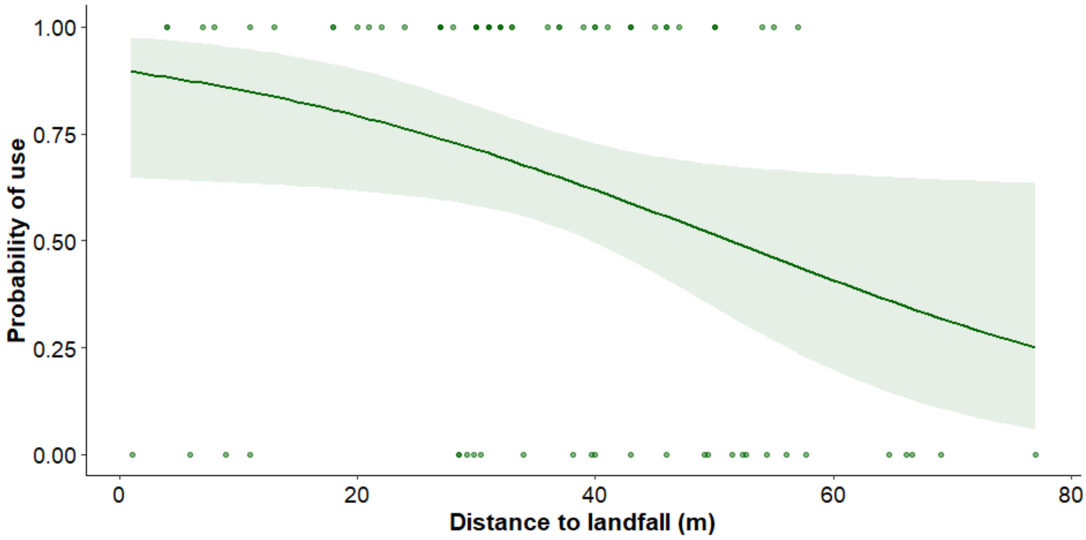


Figure 3.16: Predictions from logistic regression models of the probability of overall use as a function of distance to landfall for natural nests on Penguin Island, Western Australia (Shaded area represent 95% PI).

3.4.2.2 Attributes of landscape and nests that influence the annual use of natural nests

Competitive models resulting from 128 candidate models explaining annual use of natural nests incorporated year as well as four landscape and nest site variables, slope, surrounding vegetation cover, height of the nest bush, and species composition (Table 3.8). Bush height was a strong predictor of nest use with taller bushes having a greater probability of use (β = 1.07, CI [0.34 – 1.80]; Table 3.9; Figure 3.17). Model comparisons revealed substantial support for models including bush height, present in the top 11 models making up >98% of total model weight. While competing models also included vegetation cover, slope and species, examination of model averaged coefficients of these predictor revealed a moderate degree of shrinkage and 95% CI encompassing zero thus were considered uninformative.

Table 3.8: Top models (ΔAICc< 5) for all subsets generalised linear model set relating *annual usage* of natural nests by little penguins on Penguin Island to the effects of nest site and landscape position variables. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ω_i), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	**ω_i**	**k**	**$R^2_{marg.}$**
Intercept	*120.71*	*21.93*	*0.00*	*3*	*0*
Bush height + vegetation cover + slope + year	98.78	0.00	0.29	7	0.36
Bush height + vegetation cover + slope + species + year	98.88	0.10	0.28	9	0.40
Bush height + slope + species + year	100.70	1.92	0.11	8	0.37
Bush height + vegetation cover	100.81	2.03	0.11	8	0.37
Bush height + slope	101.06	2.29	0.09	6	0.31
Slope	102.80	4.02	0.04	7	0.33
Slope + species	103.42	4.64	0.03	6	0.29

Table 3.9: Averaged model coefficients representing probability of *annual use* of natural nests by little penguins on Penguin Island based on nest site and landscape position variables. ($\hat{\beta}$ = model- averaged coefficient). Model coefficients where 95% CI did not overlap 0 are in bold.

	Full model set				Conditional model set			
Predictor	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Slope	-0.50	0.35	1.41	0.16	**-0.62**	**0.28**	**2.18**	**0.03**
Bush height	**1.06**	**0.38**	**2.77**	**<0.01**	**1.07**	**0.37**	**2.88**	**<0.01**
Vegetation cover	0.39	0.33	1.18	0.24	**0.54**	**0.27**	**1.99**	**0.05**
Species								
Rhagodia	*Reference*							
Tetragonia	0.19	0.28	0.68	0.50	0.35	0.30	1.15	0.25
Rhagodia-Tetragonia	0.33	0.37	0.89	0.37	**0.60**	**0.30**	**2.00**	**0.05**
Year								
2015	*Reference*							
2016	**-0.82**	**0.32**	**2.56**	**0.01**	**-0.84**	**0.29**	**2.84**	**<0.01**

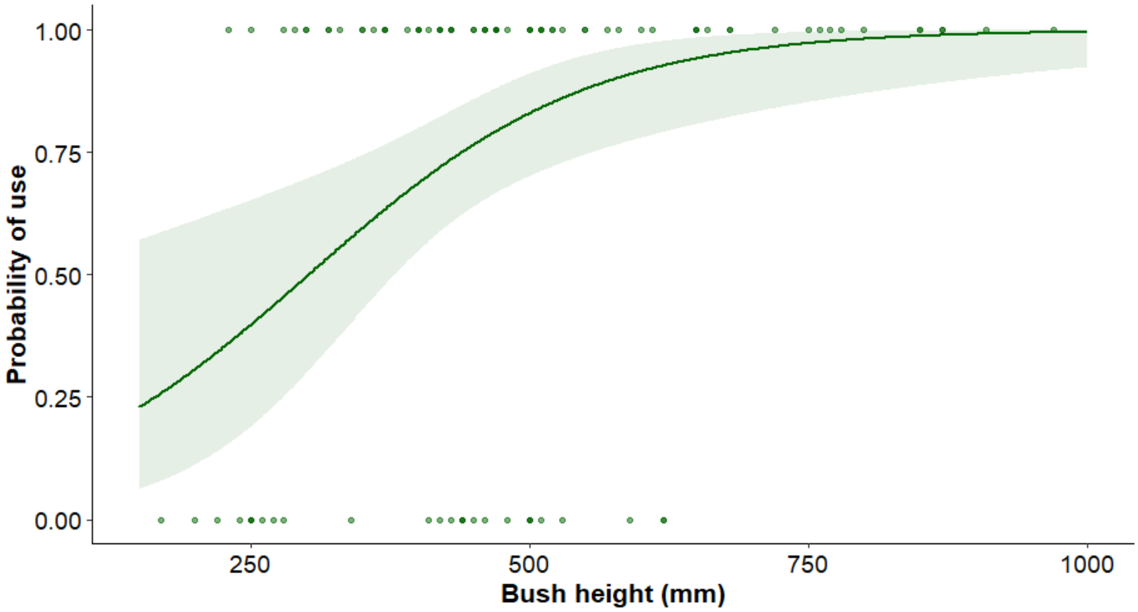


Figure 3.17: Probability of annual use of natural nests by little penguins as a function of the height of the nest bush on Penguin Island, Western Australia

3.4.2.3 Attributes of landscape position that influence the overall use of artificial nests

Models that best explained probability of overall use of artificial nests given landscape position included variables slope, distance to boardwalk and distance to landfall. The top model, which included the variable slope only, had an AICc weight of 0.20 and was 1.5 times more likely than the next competing model, which included distance to boardwalk in addition to slope (AIC weight = 0.13; Table 3.10). Two competing models included a model with distance to boardwalk only and a combination of distance to landfall and slope suggesting these variables may be influencing use of nest boxes. However, there was a moderate to large degree of shrinkage and 95% CI overlapped zero in both full and conditional model sets for slope, distance to landfall and distance to boardwalk indicating all three variables to be weak predictors of use (Table 3.11).

Table 3.10: Top models (ΔAICc <5) for all subsets generalised linear model set relating *overall usage* (used vs available) of artificial nests (boxes) by little penguins on Penguin Island to the effects of landscape position variables only. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ω_i), number of parameters (k) and Nagelkerke's pseudo R^2 (R^2).

Model	**AICc**	**ΔAICc**	ω_i	k	R^2
Intercept	*155.91*	*2.90*	*0.05*	*2*	*0*
Slope	153.01	0.00	0.20	3	0.06
Slope + distance to boardwalk	153.83	0.82	0.13	4	0.07
Distance to boardwalk	154.28	1.27	0.10	3	0.04
Slope + distance to landfall	154.94	1.93	0.07	4	0.06
Slope + elevation	155.05	2.04	0.07	4	0.06
Slope + distance to boardwalk + elevation	155.85	2.84	0.05	5	0.07

Model	**AICc**	**ΔAICc**	**ω_i**	***k***	***R^2***
Slope + distance to boardwalk + distance to landfall	155.98	2.97	0.04	5	0.07
Distance to boardwalk + distance to landfall	156.23	3.22	0.04	4	0.05
Distance to boardwalk + elevation	156.29	3.28	0.04	4	0.04
Slope + elevation + distance to landfall	156.55	3.54	0.03	5	0.07
Elevation	157.35	4.34	0.02	3	0.01
Distance to landfall	157.93	4.92	0.02	3	0.00
Slope + elevation + distance to boardwalk + distance to landfall	157.94	4.93	0.02	6	0.08

Table 3.11: Averaged model coefficients representing probability of *overall use* of artificial nests by little penguins on Penguin Island based on landscape position variables. ($\hat{\beta}$ = model-averaged coefficient). Model coefficients where 95% CI did not overlap 0 are in bold.

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Distance to landfall	-0.01	0.11	0.07	0.95	-0.03	0.21	0.13	0.90
Distance to boardwalk	-0.15	0.23	0.65	0.52	-0.30	0.24	1.27	0.20
Slope	-0.25	0.25	1.00	0.32	-0.38	0.21	1.78	0.07
Elevation	0.01	0.12	0.06	0.95	0.02	0.22	0.11	0.91
Aspect†								
None	*Reference*							
North - East	-0.01	0.08	0.14	0.88	-0.12	0.24	0.52	0.60
East - South	-0.01	0.08	0.07	0.94	-0.06	0.25	0.25	0.81
West - North	-0.02	0.10	0.23	0.82	-0.24	0.23	1.03	0.31

†- Aspect “south – west” no samples

3.4.2.4 Attributes of landscape and nests that influence the annual use of artificial nests

Models that best explained overall use of artificial nests included four predictor variables. The top ranking models contained three variables, entrance direction, box-length, and aspect and had an AICc weight of 0.21 (Table 3.12). The strongest predictor of nest box use was the box length; probability of nest use increased for longer boxes (β = 0.69, CI [0.27 – 1.11]; Table 3.13; Figure 3.18). Box length appeared in all competing models with models including box length making up more than 99% of total model weight. While model comparisons suggested aspect and entrance direction as potential predictors of nest use, model averaging provided weak evidence to support this. Conditional model averaged coefficients suggested nests occurring on W-N or N-E aspects were less likely to be used (β = -0.41 , CI [-0.80 – -0.01] and, β = -0.54 , CI [-1.02 – -0.05], respectively; Table 3.13) however comparison with full model estimates exposed shrinkage and CI's that overlapped zero. Similarly, entrance direction was not well supported when examining model average coefficients thus was unlikely to be an informative predictor of nest box use (Table 3.13).

Table 3.12: Top models (ΔAICc <5) for all subsets generalised linear model set relating *annual usage* of artificial nests by little penguins on Penguin Island to the effects of nest site landscape position variables. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ω_i), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*246.09*	*18.66*	*0.00*	*3*	*0*
Aspect + entrance direction + box length	227.43	0.00	0.16	14	0.27
Aspect + box length + distance to boardwalk	228.65	1.22	0.09	7	0.18
Aspect + entrance direction + box length + year	229.44	2.01	0.06	15	0.28
Aspect + entrance direction + box length + box width	229.75	2.32	0.05	15	0.27
Aspect + entrance direction + box length + distance to boardwalk	229.77	2.34	0.05	15	0.27
Aspect + entrance direction + box length + slope	229.78	2.35	0.05	15	0.27
Entrance direction + box length + slope	230.11	2.68	0.04	12	0.23
Aspect + box length + year	230.54	3.11	0.03	8	0.18
Aspect + box length + box width	230.68	3.25	0.03	8	0.18
Aspect + box length + distance to boardwalk	230.78	3.34	0.03	8	0.18
Aspect + box length + slope	230.79	3.36	0.03	8	0.18
Entrance direction + box length	231.34	3.91	0.02	11	0.22
Aspect + entrance direction + box length + box width + year	231.79	4.36	0.02	16	0.28
Aspect + entrance direction + box length + distance to boardwalk + year	231.81	4.38	0.02	16	0.28

Model	**AICc**	**ΔAICc**	**ω_i**	***k***	**$R^2_{marg.}$**
Aspect + entrance direction + box length + slope + year	231.82	4.39	0.02	16	0.28
Box length + slope	231.91	4.48	0.02	5	0.13
Aspect + entrance direction + box length + box width + distance to boardwalk	232.12	4.69	0.02	16	0.27
Aspect + entrance direction + box length + box width + slope	232.14	4.70	0.01	16	0.27
Aspect + entrance direction + box length + distance to boardwalk + slope	232.15	4.72	0.01	16	0.27
Entrance direction + box length + slope + year	232.21	4.78	0.01	13	0.23
Entrance direction + box length + distance to boardwalk + slope	232.29	4.86	0.01	13	0.23
Entrance direction + box length + box width + slope	232.40	4.97	0.01	13	0.23

Table 3.13: Averaged model coefficients representing probability of *annual use* of artificial nests by little penguins on Penguin Island based on nest and landscape position variables. ($\hat{\beta}$ = model-averaged coefficient). Model coefficients where 95% CI did not overlap 0 are in bold.

	Full model set				Conditional model set			
Predictor	$\hat{\beta}$	**Adjusted SE**	***Z value***	**Pr(>|z|)**	$\hat{\beta}$	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Box length	**0.69**	**0.21**	**3.21**	**<0.01**	**0.69**	**0.21**	**3.27**	**<0.01**
Box width	-0.01	0.11	0.05	0.96	-0.02	0.22	0.10	0.92
Distance to boardwalk	-0.01	0.10	0.06	0.95	-0.02	0.20	0.12	0.90
Aspect†								
None	*Reference*							
East-South	-0.17	0.19	0.89	0.37	-0.22	0.19	1.14	0.25
West-North	-0.42	0.31	1.34	0.18	**-0.54**	**0.25**	**2.18**	**0.03**
North-East	-0.32	0.25	1.29	0.20	**-0.41**	**0.20**	**2.01**	**0.04**
Slope	-0.05	0.17	0.31	0.76	-0.16	0.27	0.59	0.56
Species								
Rhagodia	*Reference*							
Tetragonia	0.00	0.02	0.02	0.98	-0.05	0.21	0.23	0.82
Acacia	0.00	0.02	0.05	0.96	-0.12	0.20	0.62	0.53
Rhagodia-Tetragonia	0.00	0.02	0.04	0.97	0.10	0.20	0.51	0.61
Rhagodia-Acacia	0.00	0.03	0.07	0.94	0.27	0.20	1.36	0.17
Rhagodia-Tetragonia-- Acacia	0.00	0.02	0.01	0.99	-0.03	0.20	0.16	0.87
Entrance Direction								
SW- W	*Reference*							
W - NW	0.37	0.31	1.17	0.24	**0.57**	**0.19**	**2.91**	**<0.01**
NW - N	0.34	0.29	1.15	0.25	**0.52**	**0.19**	**2.72**	**<0.01**
N - NE	0.17	0.19	0.86	0.39	0.26	0.19	1.39	0.16
NE - E	0.33	0.29	1.13	0.26	**0.52**	**0.20**	**2.59**	**<0.01**
E - SE	0.11	0.16	0.66	0.51	0.17	0.18	0.94	0.35
SE - S	0.21	0.21	0.96	0.34	0.32	0.19	1.69	0.09
S - SW	0.26	0.24	1.07	0.29	**0.40**	**0.18**	**2.16**	**0.03**

†- Aspect "south – west" no samples

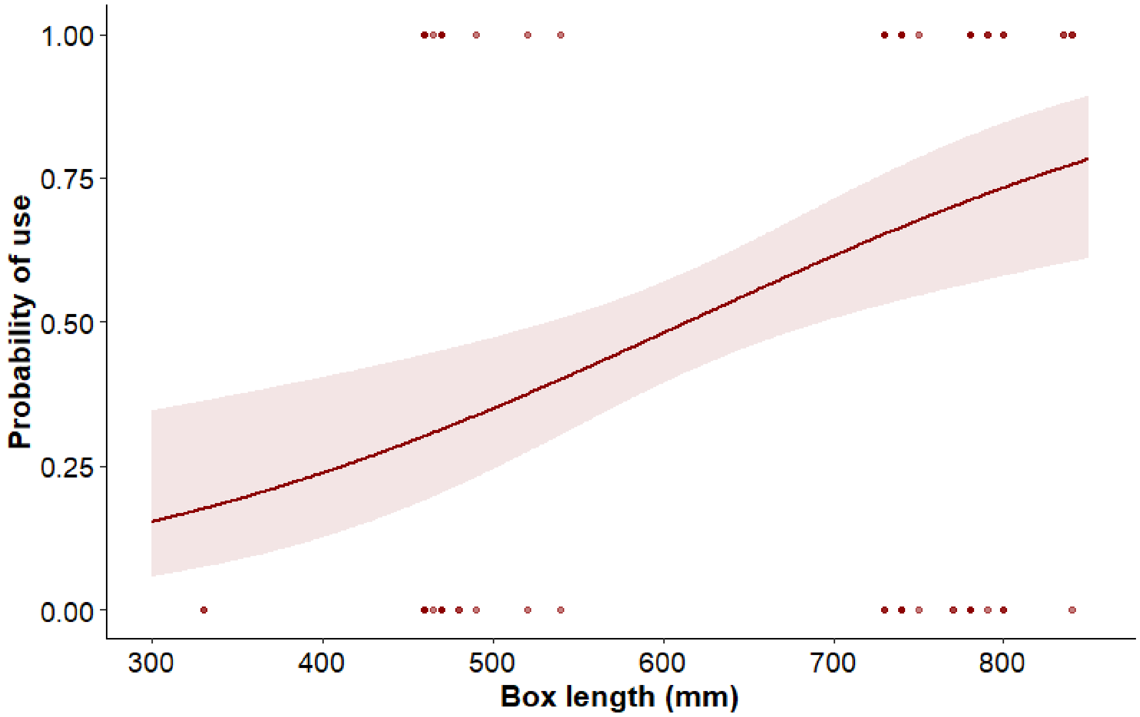


Figure 3.18: Probability of annual use of artificial nests (boxes) as a function of the length of the box on Penguin Island, Western Australia

3.4.3 Breeding success

Of nests where eggs were laid, percent of successful nests (where at least one fledgling was successfully raised from at least one egg) averaged 60% (range 41-82%) for artificial nests and 66% (range 58- 82%) for natural nests across the three year study period (Table 3.14).

For both natural and artificial nests, there was weak evidence of differences between successful vs unsuccessful nests; rather, evidence of difference was reflected in usage (Appendix 3.1; Appendix 3.2). For natural nests, there was a marginal effect of vegetation cover and bush height whereby successful nests (producing at least one fledgling) were found in slightly taller thicker vegetation (Appendix 3.1; Figure A3.1 g-h).

Table 3.14: Number of nests used for breeding that were successful (nests in which at least one fledgling was successfully raised from at least one egg) of natural and artificial nests on Penguin Island

	2014		**2015**		**2016**	
Nest Type	n	Successful (%)	n	% successful	n	% successful
Artificial	32	13 (41%)	26	15 (58%)	22	18 (82%)
Natural	34	20 (59%)	24	14 (58%)	16	13 (82%)

3.5 Discussion

The results from this study highlight the importance of several factors influencing the nesting behaviour of little penguins on Penguin Island. Little penguins did not select nest sites randomly, but instead based nest site selection on topographical, vegetation and nest site attributes. This was evident in both natural and artificial nests. These results provide the initial steps towards understanding nest habitat use, however further investigation using a finer measure of success and incorporating additional environmental factors is needed to define the relationships between habitat characteristics and the breeding outcome of a nest.

3.5.1 Natural nest site selection

At the colony scale, little penguins using natural nests showed a preference for nesting in areas close to a known landfall site. Consistent with previous work, penguins nested closer to landfall locations than random and likely as a means to minimize energy expenditure given their high energetic cost of movement on land (about two times that of similarly sized terrestrial vertebrates; Pinshow *et al.* 1977). Prior work has examined nest placement in New Zealand (Braidwood *et al.* 2011) and south-eastern Australia (Weerheim *et al.* 2003). Distances travelled varied widely due to island topography however in both cases locations nearer to landfall locations had greater likelihood of use.

Slope was another factor influencing nest use probability with nest sites more likely to be found on flat or gently sloping ground, an observation also made in several little penguin colonies on the Tasmanian north-west coast (Marker 2016). Slope has been reported to be important for distribution of nests in other temperate penguin species (e.g. Magellanic penguin (*Spheniscus magellanicus*); Stokes and Boersma 1991). However, while little penguin nests on Penguin Island were more commonly associated with flat or gently sloping ground, Magellanic penguin nests were more numerous on steeper slopes. This difference probably reflects different nesting requirements of the two species. Little penguins on Penguin Island dig shallow nests under dense vegetation. This surface nesting behaviour likely increased the risk of eggs rolling from the nest so nesting on flatter ground may be more desirable. Additionally, due to the unstable nature of Penguin Island's sandy substrate, nesting on steeper slopes increases the risk of sand inundating the nest. In contrast, nesting on steeper ground exhibited by burrow nesting Magellanic penguins may increase drainage and reduce flooding of the nest. The association between used nest sites and gentler slopes could again be in response to reducing energy demands while accessing nest sites on land. In addition, the probability of occupation of an island for nesting by Magellanic penguins was greater where nest site access areas occurred on more gently sloping ground, facilitating penguin access to nesting grounds (Borboroglu *et al.* 2002).

At the nest site scale, little penguins used sites where (1) vegetation was taller, (2) had greater cover in the immediate vicinity of the nest site and in the surrounding area, and (3) where *Tetragonia decumbens* was a dominant species present at the nest. While these vegetation characteristics were influential on nest use, high correlation between vegetation characteristics (for example bush height and bush wall) implies that either factor could be driving nest use by little penguins. Vegetation cover is frequently reported as an important factor for surface nesting seabirds and is proposed to have various functions with the two most common being concealment from predators and protection from solar insolation (Stokes and Boersma 1998; Goodenough *et al.* 2009). Due to the absence of land predators on Penguin Island, the risk of predation is low, thus vegetation cover and bush height are less likely to be providing a selective advantage as a function of nest concealment and potentially associated with protection from warmer temperatures experienced by this population (Klomp *et al.* 1991). A study of nest selection in a South Australian colony of little penguins revealed that the thermodynamic characteristics of a nest were more likely to be influencing nest choice than predation risk (Colombelli-Négrel 2019). For Magellanic penguins breeding in Argentina, higher nest cover is an important characteristic for protecting nesting penguins from the sun (Stokes and Boersma 1998). This is also suggested to be true for yellow-eyed penguins (*Megadyptes antipodes*) in New Zealand (Seddon and Davis 1989). For penguins nesting in temperate and tropical climates, such as those in the genera *Spheniscus* and *Eudyptula* (i.e. *Eudyptula minor, Spheniscus demersus, Spheniscus humboldti, Spheniscus magellanicus and Spheniscus mendiculus*), burrow nesting is an important strategy for reducing heat stress. However, for populations where substrate prohibits successful excavation of burrows, such as the colony on Penguin Island, then vegetation becomes crucial for protecting nests from high temperatures (Stonehouse 1970; Frost *et al.* 1976; Stahel and Nicol 1982; Ropert-Coudert *et al.* 2004).

In addition to cover, plant species appeared to also influence selection of nests. Three species of plant dominate the vegetation on Penguin Island and include *T. decumbens, R. baccata and A. rostellifera*. Little penguins avoided areas dominated by *Acacia sp*. preferring sites where *T. decumbens* was dominant either on its own or co-dominant with *R. baccata*. This supports findings of Klomp *et al.* (1991) who found little penguin nests to occur predominantly in *T. decumbens* bushes. *T. decumbens* is a semi succulent shrub that, on Penguin Island, often develops a thick layer of dead foliage underneath the living portion (E Clitheroe, pers. obs), creating an insulative layer and reducing solar insolation. Alternatively, the strong association between nest site and *T. decumbens* could be due to the high availability of *T. decumbens* on the island.

Results suggested a consistent orientation of the nest entrance with most (74%) falling within a south-east to south-westerly aspect, a pattern also observed by Klomp *et al.* (1991). This could potentially be associated with the prevailing wind and its influence on microclimate. The temperature inside little penguin nest boxes are known to be influenced by wind strength, cooling the air inside and outside of nest boxes (Ropert-Coudert *et al.* 2004). This could indicate that microclimate of a nest may be guiding nest habitat selection. A number of recent studies suggest fine scale microclimate characteristics (temperature and humidity) to be a key component in habitat selection, potentially playing a greater role in nest site selection than topographical or vegetation features (Hovick *et al.* 2009; Rhodes *et al.* 2009; Carroll *et al.* 2015; Frey *et al.* 2016; Anthony *et al.* 2021). Temperature is critical for successful reproduction in birds not only for assisting in successful incubation but also for minimising thermoregulatory costs for parents and chicks (Walsberg 1980; Grant 1982; Webb 1987; Beissinger *et al.* 2005). Therefore, it stands to reason they seek favourable nesting environments (Rhodes *et al.* 2009; Carroll *et al.* 2015).

3.5.2 Artificial nest site selection

In contrast to natural nest use, topographic and vegetation characteristics were not identified as significant predictors of use in nest boxes. The insignificance of position in determining use could be explained by the purposeful, non-random manner in which artificial nests have been placed resulting in most artificial nests being positioned on the eastern side of Penguin Island within 40 m of a known landfall site (Klomp *et al.* 1991).

At the nest site, key predictors of use of artificial nests were primarily structural. Box length was significantly associated with use whereas biotic vegetation variables were less important. These findings indicate that artificial nests could effectively be replicating the high cover and low light "burrow" conditions provided by dense vegetation favoured by little penguins selecting natural nests. Longer boxes are likely to be darker as the nest bowl is further from the entrance. Alternatively, longer boxes may provide additional protection from predators by increasing the distance from the entrance opening to the nest bowl (Mazgajski 2003). The readiness of little penguins to occupy artificial nests is reported frequently in the literature however the occupation of artificial nests on Penguin Island remains low relative to other populations around Australia and New Zealand (Houston 1999; Perriman and Steen 2000; Johannesen *et al.* 2002; Sutherland *et al.* 2014). Furthermore, little penguins nesting in boxes on Penguin Island exhibit lower nest site fidelity than those nesting in natural nest sites (Tavecchia *et al.* 2016). The apparent high occupation rates within other populations might explain why studies investigating the physical characteristics of artificial nests that influence usage are lacking.

3.5.3 Success

Habitat selection theory assumes that habitat preferences influence fitness outcomes and are therefore adaptive, favouring those that provide a fitness advantage (Chalfoun and Schmidt 2012). However, this study found that neither landscape nor nest site attributes influenced the overall success of nests. The lack of congruence between nest use and success observed in this study may be owing to other ecological processes unrelated to habitat (for example, predation rate and food availability), explaining a greater proportion of the variation in the observed nest success. The predation risk on little penguin nests on Penguin Island is relatively low and is therefore unlikely to be significantly affecting the success of a nest however this. There are, however, multiple studies linking ocean climate variability and breeding outcome in little penguin colonies throughout the species' range (Wienecke *et al.* 1995; Numata *et al.* 2000; Perriman *et al.* 2000; Chambers 2004; Chambers *et al.* 2009; Dann and Chambers 2009; Cannell *et al.* 2012). On Penguin Island, local marine climate and its influence of on local food sources is known to affect breeding performance of this colony (Cannell *et al.* 2012). This, combined with the influence of additional factors such as parental quality or the ability of parents to locate a reliable food during breeding, may be overriding or obscuring the effects of nest site attributes on the success of a nest (Zhu *et al.* 2012).

Another possible explanation for the lack of evidence supporting relationships between nest success and nest characteristics is the low population density of Penguin Island's colony. Recent data suggest a significant decline in Penguin Island's breeding population (Cannell 2012, Cannell 2018, Cannell. Unpubl. data DBCA. Unpubl. Data). Populations at low densities are unlikely to follow traditional habitat selection models (Greene and Stamps 2001). In order to detect differences in breeding success based on nest site characteristics, there must be a measurable number of birds nesting in suboptimal habitat (Zhu *et al*. 2012). However, at low population levels, the density of nest sites in poor quality habitat is low and variation in reproductive success is likely to be equal across the occupied habitat (Fretwell and Calver 1969). A third explanation is the possibility that this study failed to include important habitat features in the analyses or measure variables or reproductive measures at scale fine enough to detect differences.

It appears that for Penguin Island's little penguin colony, there is a strong relationship between the selection of a nest site, the decision to breed and the outcome of the nest. Thus, looking at nest use may be an adequate method for determining nest habitat preference particularly when populations or sample sizes are small (Pribil 1998). Regardless, the changing climate is likely to alter the habitat in which little penguins nest, potentially significantly reducing the availability of preferred habitat thus driving more little penguins into suboptimal nest sites. It is important to continue investigation in order to determine the mechanisms driving habitat selection and the adaptive significance of such decisions under a rapidly changing climate (Davis 2005).

3.5.4 Management implications

Past and current management of penguin habitat has been limited to the provision of nest boxes, revegetation using native island species, removal of alien plant species and the provision of visitor walkways (Orr and Pobar 1992). Specific guidelines on current management strategies are absent. Management programs will greatly benefit from studies such as this one that help to understand the nesting requirements of little penguins which can then be applied to on ground management actions. Management programs interested in preserving and enhancing little penguin nesting habitat should be targeted at (1) retaining and expanding areas of high vegetation cover near to known landfall sites on flat or gently sloping ground, (2) planting and retaining established bushes of preferred plant species, (3) concentrating management of nest habitat on the leeward side of Penguin Island, (4) considering design and location when placing artificial nests in the field, and (5) considering nesting habitat preferences when planning infrastructure work.

This study has also identified potential conflict between management objectives that address both the ecological and social values of Penguin Island. Landscape features selected by little penguins for nesting (flat or gently sloping ground near to landfall sites on the leeward side of the island) are also the ideal sites for the placement of visitor and management infrastructure such as buildings, walkways and visitor use areas. A review of current management strategies may be necessary to ensure consideration of penguin nesting habitat when planning for future infrastructure. Additionally, management programs that include provision of artificial nests should consider box design and placement strategies that reflect penguin use patterns identified in this study. Artificial nests are an important management tool and appropriately designed artificial nests may be critical if quality natural habitat become limited due to climate or anthropogenic driven change.

The peripheral position of Penguin Island's little penguin colony combined with its isolation from other colonies makes it an important colony for not only indicating early response of this species to climate change, but also for preserving the genetic diversity and adaptation potential of the species (Gibson *et al.* 2009). To boost the resilience of this colony to climate change effects and to guide management it is essential to gain a colony-specific understanding of the habitat requirements of this species. This study provides an important step towards gaining that knowledge however conservation efforts would benefit greatly from continued investigation of habitat use and selection in other colonies that would identify potential inter- and intra-population variation. Furthermore, research focussing on the link between habitat use and fitness would help provide insight into the implications of climate driven change on habitat availability.

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CHAPTER 4

Microclimate of little penguin (*Eudyptula minor*) nesting habitats on Penguin Island, Western Australia

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4.1 Abstract

The persistence of edge populations will require the implementation of adaptation strategies based on a comprehensive understanding of how climate change is altering microhabitat conditions and thus habitat suitability at range edges. Using three years of data, I quantified and compared microclimate of artificial nest boxes and natural nest burrows of an edge population of little penguins existing at the north-western limit of their range. I used mixed models to investigate how local climate conditions and nest characteristics (location and vegetation cover) influence nest temperature. Nest boxes were ineffective at replicating microclimate conditions of natural nests. Nest boxes experienced consistently higher daily maximum temperature (~2 ˚C) and maintained temperatures above little penguins' upper thermoneutral limits (30 ˚C) for one hour longer than natural nests. After accounting for ambient temperature, relative humidity and wind, fine scale biotic and abiotic nest characteristics also influenced the maximum daily nest temperature and hours of exposure to upper thermoneutral limits (reducing hours of exposure by up to two hours in natural nests and three hours in nest boxes). To further investigate the potential impact of climate change on temperatures within nests, I fitted models which simulated a 2 ˚C temperature increase scenario. The number of days annually where natural and artificial nest conditions exceeded thermally stressful conditions (≥30 ˚C) are predicted to increase by approximately 37% and 56% and the

number of days exceeding hyperthermic conditions (≥35 ˚C) are predicted to increase by approximately 41% and 49% respectively. Such changes will expose penguins to dangerous and potentially fatal thermal conditions, particularly during the late breeding and moulting phases of their annual cycle. Results here provide critical insight into how predicted changes in terrestrial climate may compound marine climate change impacts on seabird colonies at latitudinal margins, providing a more complete understanding of the climate limitations and management implications of edge populations. This study revealed that current and future thermal environments of little penguin terrestrial habitat on Penguin Island can exceed physiological limits for this species. Intervention to improve artificial nests and better quantify consequences is urgently needed given recent estimates of a declining population could lead to the local extinction of this colony.

4.2 Introduction

Climate change continues to profoundly affect marine and terrestrial systems worldwide (Parmesan and Yohe 2003; Parmesan 2006; Hoegh-Guldberg and Bruno 2010; Chen *et al.* 2011; Bellard *et al.* 2012; Doney *et al.* 2012; Diffenbaugh and Field 2013; IPCC 2018). The impacts of rising global temperatures on biotic systems include large scale modification of the distribution of species globally, with species predicted to move poleward and upward in elevation as they respond to spatial shifts in climate (Chambers *et al.* 2005; Hoegh-Guldberg and Bruno 2010; Jiguet *et al.* 2010; Dawson *et al.* 2011; Young *et al.* 2012; Cahill *et al.* 2013; Diffenbaugh and Field 2013; Vilà-Cabrera *et al.* 2019). Populations existing at the lower latitudinal margins of a species' distribution (the rear edge) are considered most at risk of local extinction (Guisan and Thuiller 2005; Jiguet *et al.* 2010; Vilà-Cabrera *et al.* 2019). In cases where distributional limits are set by physical factors (i.e. temperature), persistence of marginal populations will rely heavily on developing novel adaptive strategies to cope with climate change stressors (Hampe and Petit 2005; Monteiro *et al.* 2019).

In recent years, the significance of rear edge populations has gained considerable attention (Bunnell *et al.* 2004; Hampe and Petit 2005; Rehm *et al.* 2015; Pironon *et al.* 2017). These populations may be key for not only predicting species' responses to expected change in climate but for maintaining long term adaptive capacity of a species (Lomolino and Channell 1995; Hampe and Petit 2005; Pauls *et al.* 2013). The longevity of rear edge populations will likely be dependent on climate change velocity; however, careful management could prolong population persistence and maintain genetic diversity until long term or ex-situ conservations strategies are achieved (Hannah *et al.* 2014). Among the critical elements for successful conservation planning for long term species persistence is comprehensive understanding of microhabitat conditions and climate change impacts at range edges (Hannah *et al.* 2002; Mawdsley *et al.* 2009; Hannah *et al.* 2014; Varner and Dearing 2014). It would seem reasonable to extend this understanding to include artificial habitats. However, the effect that climate change may have on the suitability of artificial habitats have received little attention, despite their wide use in the management of a variety of taxa around the world (Bolton *et al.* 2004; Harley 2006; Priddel *et al.* 2006; Corrigan *et al.* 2011; Libois *et al.* 2012; Goldingay *et al.* 2015).

In seabirds, artificial nests are used in a number of contexts including the establishment or translocation of seabird colonies (Priddel *et al.* 2006; Miskelly *et al.* 2009; Carlile *et al.* 2012), monitoring/research (Wilson 1986; Podolsky and Kress 1989; Klomp *et al.* 1991; Wilson 1993; Bolton 1996; Perriman and Steen 2000; Johannesen *et al.* 2002), and the provision or restoration of seabird nesting habitat (Priddel and Carlile 1995; Gaston 1996; Houston 1999; Lalas *et al.* 1999; Kemper *et al.* 2007). However, in many cases artificial nests are deployed with limited knowledge on the suitability of the microclimate or the associated risks of providing suboptimal environments for inhabitants (a population 'sink'; Pulliam, 1988). The provision of artificial nests could be problematic if significant differences in their microclimate result in reproductive failure, especially for those species that are restricted to, or preferentially use, artificial structures for reproduction (Catry *et al.* 2011).

Nest microclimate is critically important to egg and chick development; nest temperature and humidity have been linked to a number of reproductive parameters including clutch size, embryonic development, chick growth and survival (Wiebe 2001; Larson *et al.* 2015; Bobek *et al.* 2018). Artificial nests are often limited in their buffering capacity and inadequate at replicating conditions of natural nests; generally, they experience more variable temperatures and are hotter and drier than natural nests across a range of habitat types and climates (Ropert-Coudert *et al.* 2004; Lei *et al.* 2014; Maziarz *et al.* 2017; Rowland *et al.* 2017). In order to be successful, artificial nests ideally need to offer microclimates conditions that are similar to, if not more favourable than, their natural equivalents (Isaac *et al.* 2008). Thus, careful consideration of the potential impact a change in climate may have on the microclimate of artificial nests is paramount (Maziarz *et al.* 2017).

In penguins, cold-water adaptations make them particularly vulnerable to high temperature during the nesting and moulting phase of their life cycle and thus rely on a suite of physiological and behavioural adaptations to maintain heat balance (Simeone *et al.*2004; Gerson *et al*. 2014). To dissipate heat, birds usually rely on a combination of both cutaneous and respiratory evaporative water loss. Increases in both temperature and humidity can impair heat dissipation (Gerson *et al*. 2014). In little penguins, this could quickly lead to hyperthermia as tolerance for temperatures exceeding 35 ˚C is thought to be only a few hours for adults (likely less for chicks) (Stahel and Nicol 1982). The ability of little penguins to dissipate heat through cutaneous evaporation is limited thus they rely on hyperventilating along with additional behavioural traits (e.g. landing at night and burrow nesting) to maintain thermal homeostasis (Stonehouse 1967; Stahel and Nicol 1982; Baudinette *et al.* 1986). In addition to thermoregulatory demands, changes in temperature and humidity could also affect little penguins ability to breed successfully (Stahel and Gales 1987; Dann and Chambers 2013). Temperature is accepted to be a critical mechanism affecting viability of eggs (Grant 1982; Webb 1987; Beissinger *et al.* 2005). Extended exposure to high temperatures can affect the development and hatchability of eggs or cause hyperthermia in nestlings (Webb 1987; Beissinger *et al.* 2005). Relative humidity can also be important for egg survival due to its role in egg water loss (Walsberg 1980; Grant 1982). For many avian taxa, thermal tolerance during incubation ranges between 16 to 41 ˚C (Webb 1987). Humidity requirements also vary significantly between species ranging between 30 – 70% (Robertson 1961; Lomholt 1976; Lin *et al.* 2005; El-Hanoun *et al.* 2012) although the majority of quantitative studies have centered on requirements for incubation of domestic poultry eggs and few have examined incubation microclimates of wild birds.

Penguin Island, Western Australia, is home to a genetically distinct population of little penguins (*Eudyptula minor)* (Cannell *et al.* 2012) at the extreme northwestern limit of the species range. This 'rear edge' population is highly valuable for exploring climate change effects on this species. Recent estimates suggest that in the last decade Penguin Island's little penguin colony has undergone a considerable population decline of more than 50% (Cannell 2018). This decline is largely attributed to lowered breeding performance; resulting from reduced prey abundance and distribution caused by warmer ocean conditions (Cannell *et al.* 2012, Cannell pers. comm.). However, in addition to marine-based impacts, warmer and drier terrestrial conditions could have compounding effects by altering nest microclimate and reducing both the quality and availability of important nesting vegetation further degrading the demographic stability of this colony.

Little penguins nest in soil or vegetation burrows across the majority of their range (Stahel and Gales 1987; Marchant and Higgins 1990; Dann 2013). However, the friability of the substrate on Penguin Island means little penguin here are restricted to nesting under vegetation or in artificial nest boxes (Klomp *et al.* 1991; Wienecke *et al.* 1995). Timber nesting boxes have been present at Penguin Island since 1986 and have been fundamental in facilitating research and monitoring of this colony. However, past evidence suggests their environments are hotter and drier than the surrounding vegetation (Ropert-Coudert *et al.* 2004). Their need to remain on land during incubation, chick rearing and moulting means exposure to unfavourable thermal conditions is unavoidable highlighting the challenges of artificial habitat provision in an isolated rear-edge population.

Given the sensitivity of this species to multiple aspects of climate change and its importance as a rear edge population, it is critical to enhance our understanding of the implications of increasing temperature within both natural and artificial habitats at all life history stages. Thus I sought to address the following objectives: (1) to quantify microclimate in artificial nest boxes and how they differ from natural nest burrows; (2) investigate the influence of climate and nest attributes (location and vegetation cover) on nest microclimate; and (3) explore future nest temperatures under a 2 ˚C temperature stabilisation target (2 ˚C of warming, as per the Paris Agreement) and the implications of this temperature increase for this range edge population. This study aims to provide insight into how predicted changes in climate may impact populations living at their thermal limit and seeks to inform management decisions concerning the suitability of artificial habitats under changing climate.

4.3 Methods

4.3.1 Study area

A description of the study area is outlined in Chapter 3.

4.3.2 Study Species

A description of the study species is outlined in Chapter 3.

4.3.3 Study design

To compare microclimatic properties of natural and artificial nests, I measured air temperature and relative humidity of 46 artificial nest boxes and 51 natural nests for 3.5 years from July 2013 – January 2017. I then quantified nest attributes and their capacity to ameliorate microclimate.

4.3.3.1 Nest identification and monitoring

Natural nests were identified using several signs of occupancy including recent excavation, fresh faeces, obvious entrance, presence of nest material, presence of adult or presence of chicks/eggs (Figure 4.1). Once identified as having nesting activity, the sites were marked with a GPS. Twenty natural nests were located in 2013 with an additional 33 nests identified and monitored in 2014, 2015 and 2016. Most penguin nesting occurs on the leeward (eastern) side of Penguin Island (Dunlop *et al.* 1988; Klomp and Wooller 1991), consequently, the majority (60%) of the natural nest sites sampled were located within this area.

Artificial nests boxes were installed on Penguin Island between 1986 and 2006 (55 in 1986, 25 in 2001 and 46 in 2006). The boxes vary in both shape and construction material, dependent on installation year (Figure 4.2). Boxes installed in 1986 were placed in the main breeding area (groups of 17, 13, 13 and 12 in areas differing in levels of human activity) with the entrance oriented towards a known little penguin access route (Klomp *et al.* 1991). There is limited information available for how boxes installed in subsequent years were placed, however it is likely they were positioned following similar methods (Cannell pers. comm.). Only artificial nest boxes in functional condition were included in the sample. All nest sites included in the study (i.e. artificial and natural) were marked, labelled and their position recorded using a Getac differential global positioning system (dGPS) which ensured a horizontal accuracy of <1 m (at best 0.1 m). Points representing each nest were entered into a geographic information system (GIS) database (Figure 4.3). Both natural and artificial nests were monitored fortnightly through the year for presence of penguins and breeding activity. Penguins were present for a portion of the sampling in 20 nest boxes and 35 natural nests. The remaining sample nests remained unoccupied.

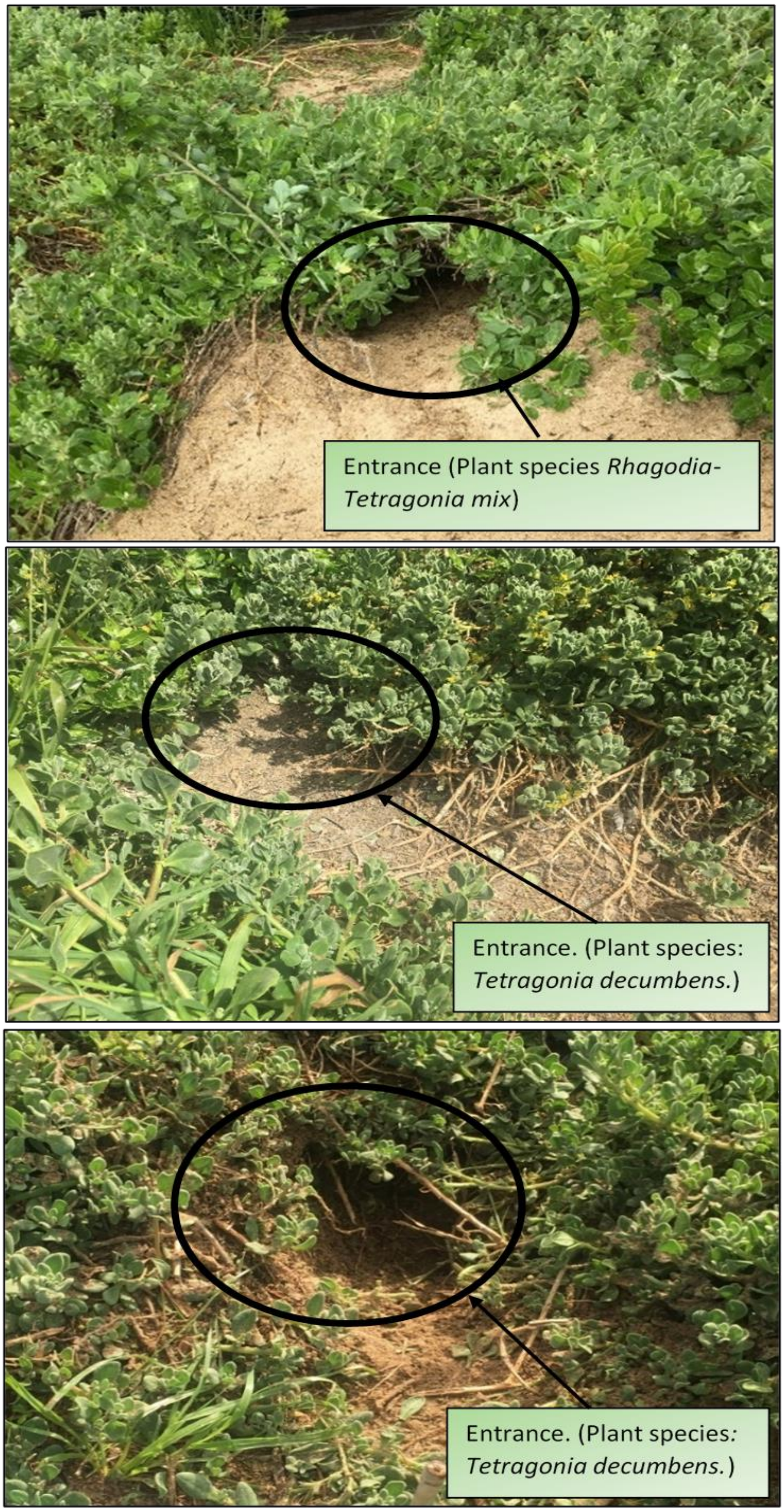

Figure 4.1: Examples of natural penguin nests on Penguin Island, Western Australia

Figure 4.2: Three artificial nest types available on Penguin Island. **Top**: Box type installed in 1986. **Middle**: box type installed in 2001. **Bottom**: Box type installed in 2006.

Figure 4.3: Aerial photograph of Penguin Island showing location of natural nests (green) and nest boxes (red)

4.3.3.2 Nest characteristics

For each nest, a suite of nest habitat variables thought to influence nest microclimate was recorded. These were stratified to represent, (1) characteristics describing the position of the nest within the landscape (hereafter landscape position), and (2) characteristics directly associated with the nest (hereafter nest site). Landscape position characteristics included topographical measurements (slope, aspect and elevation). Nest site measurements included both physical dimensions and attributes of the nest and vegetation characteristics (vegetation cover and species). As this study covered multiple years and seasons, vegetation characteristics were measured accordingly. Vegetation cover was defined at three spatial scales, (1) nest box lid cover (for nest boxes only), (2) within one m of the nest, and (3) in the broader surrounding habitat (within approximately four meters of the nest). These measurements included a combination of visual cover estimates and automated estimation of digital images. The latter allows for more precise data than those collected through visual estimation (Macfarlane (2011). To calculate a percentage foliage cover, photos were analysed using routines coded in MATLAB outlined in Macfarlane (2011) and Macfarlane and Ogden (2012). Descriptions of all measurements recorded at nests are outlined in Table 4.1.

Table 4.1: Nest attributes measured, description of attribute and frequency of measurement for natural nests and artificial nest boxes on Penguin Island, Western Australia 2013-2016.

Nest Attribute	**Description**	**Frequency of measurement**	**Artificial nest (box)**	**Natural nest**	**Random nest**
Landscape position					
Slope†	Slope of the ground on which the nest is located (degrees)	Once only	✓	✓	✓
Elevation†	Elevation of the of the position where the nest is located (m)	Once only	✓	✓	✓
Aspect†	Aspect of the hill face on which the nest is located (degrees)	Once only	✓	✓	✓
Nest site					
Vegetation attributes					
Discrete bush	Natural nest is either a discrete bush or part of a larger vegetation patch	Annual measurement during winter	NA	✓	✓
Bush wall	Thickness of vegetation measured from the nest cavity ‘ceiling’ to the outside edge of the vegetation (mm)	Annual measurement during winter	NA	✓	✓
Species Composition	Species of plant that dominated the vegetation surrounding or covering the nest.	Annual measurement during winter	✓	✓	✓
Nest bush height	Maximum height of the vegetation directly over the nest (mm)	Annual measurement during winter	NA	✓	✓

Nest Attribute	Description	Frequency of measurement	Artificial nest (box)	Natural nest	Random nest
Nest bush length	Length of nest shrub from the edge containing the entrance to the opposite edge of bush (mm). For unused natural nest and random sites this was recorded as width 1.	Annual measurement during winter		✓	✓
Nest bush width	Width of nest shrub (mm). For unused natural nest and random sites this was recorded as width 2.	Annual measurement during winter	NA	✓	✓
Cavity cover	Percentage vegetation directly over the nest cavity measured using a Gopro HERO4 camera positioned in the centre of the nest bowl facing upwards.	Bi-annual measurement in summer and winter	NA	✓	✓
Box cover	Percentage of vegetation cover covering the nest box lid, categorised into: *Low* = <5% cover, *Moderate* = 5 – 74% cover and *Full* = 75 – 100% cover)	Seasonally (winter, spring, summer, autumn)	✓	NA	NA
Quadrat cover	Percentage of vegetation cover within a circular plot (1 m diameter) centred over the nest, categorised into: 1 = <5% cover, 2 = 5- 24% cover, 3 = 25 – 49% cover, 4 = 50 – 74% cover and 5 = 75 – 100% cover)	Seasonally (winter, spring, summer, autumn)	✓	✓	✓
Surrounding ground cover	Percentage of green vegetation within a rectangular quadrat centred over the nest site. This was achieved using a pole-camera fashioned by attaching a Cannon G12 digital camera to the end of a 4-metre aluminium pole. The camera was positioned directly over the centre of the nest and a photo was remotely taken. The area captured by the photos was approximately 14.5 m^2. The position where the pole contacted the ground	Annually at the beginning of Autumn (before annual weed growth) for all old boxes in 2013, 2014, 2015, and 2016. Natural burrows were included in 2015 and 2016.	✓	✓	X

Nest Attribute	**Description**	**Frequency of measurement**	**Artificial nest (box)**	**Natural nest**	**Random nest**
	was recorded using a differential GPS to ensure accurate repeatability. The compass bearing from which the photo was taken was also recorded to ensure data were comparable across years.				
Nest/ box attributes					
Entrance bearing	The bearing (degrees) recorded using a compass	Once only for boxes and annually in winter for natural nests	✓	✓	✓
Cavity volume					
Vents	Presence or absence of ventilation holes	Once only	✓	NA	NA

† elevation, slope and aspect data retrieved from Department transport (2009) Composite Surfaces - Multibeam LIDAR Laser (DOT-022) dataset https://services.slip.wa.gov.au/public/rest/services/SLIP_Public_Services/Imagery_and_Maps/MapServer/19 under active and use licence creative commons attribution 4.0 https://creativecommons.org/licenses/by/4.0/legalcode

4.3.3.3 Nest microclimate

Temperature and humidity data loggers (DS1923 Hygrochron iButtons http://www.maximintegrated.com/en/products/comms/ibutton/DS1923.html) were set to continuously record temperature (˚C) and relative humidity (%) inside both natural nests and artificial nest boxes at 30 minute intervals until the logger was removed from the nest. As there were fewer loggers than nests, loggers were rotated between nests over the course of two and a half years with most nests containing a logger for approximately 12 months. Data loggers were inserted into a plastic key fob and mounted in the rear left of both artificial and natural nest types, approximately 10 cm off the ground. iButtons mounted in boxes were attached using cable ties (Figure 4.4A). The iButtons mounted in natural nests were attached to a bamboo stake using a cable tie and positioned at the rear edge of the nest cup (Figure 4.4B).

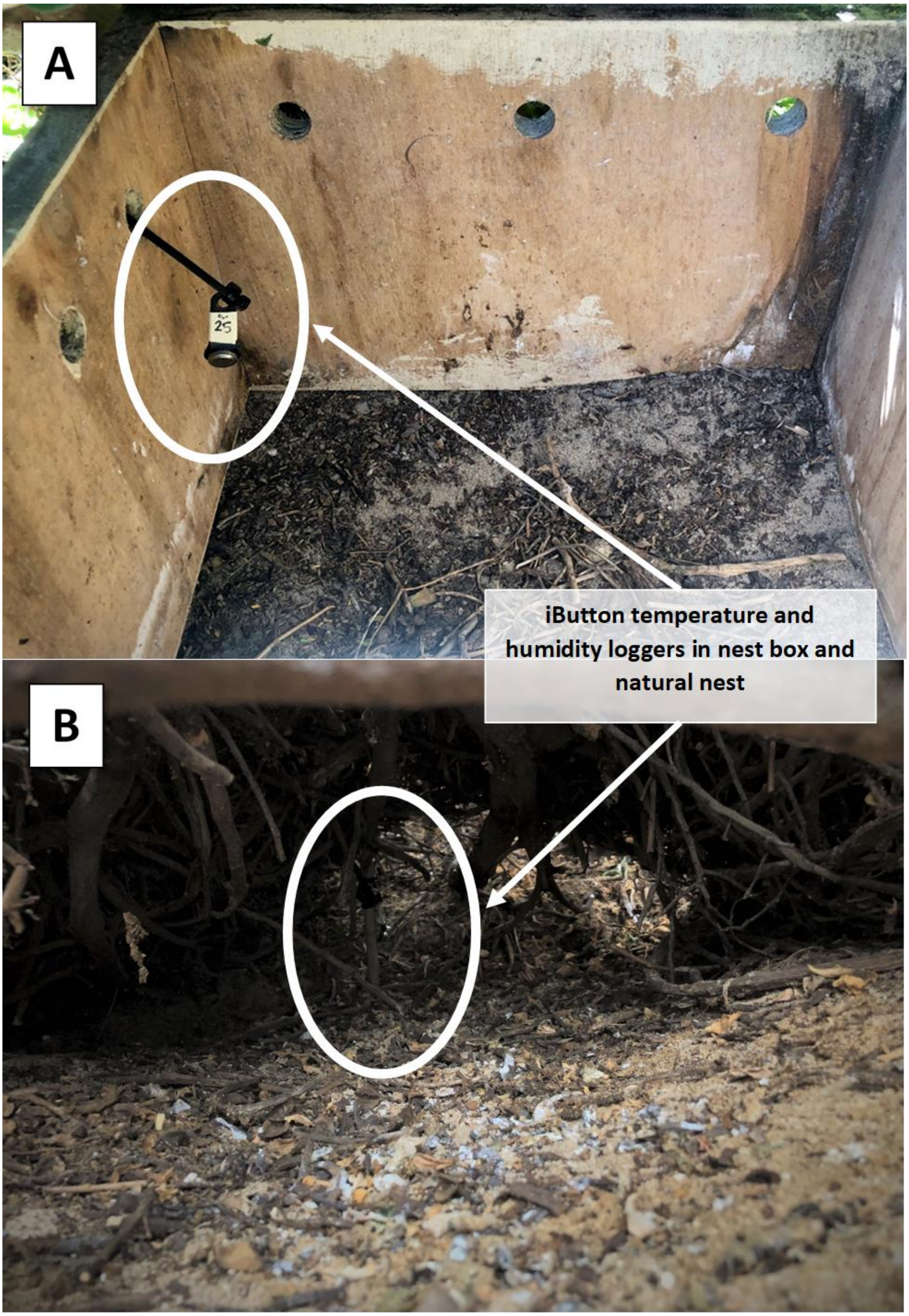

Figure 4.4: Location of iButton temperature and humidity logger inside **(A)** artificial nest boxes and **(B)** natural nests.

Nests were monitored fortnightly to ensure iButtons remained secure and did not become buried or dislodged. Data recorded by the iButtons were uploaded every two and a half months to a laptop computer using the Java™ application, *OneWireViewer* (http://onewire-viewer.software.informer.com/). Over the three years some data losses occurred due to equipment failure and loss. As a result, temperature and humidity data were recorded half-hourly for 51 boxes and 46 natural nests (Appendix 4.1; Figure A4.1).

4.3.3.4 Local weather conditions

To compare nest microclimate with local meteorological conditions, half-hourly measurements of ambient temperature, relative humidity, precipitation, wind speed and direction were sourced from the Bureau of Meteorology (BoM) meteorological station at Garden Island, approximately 10 km north of Penguin Island. This weather station is located at a height of approximately 6m above the ground.

4.3.4 Data Analysis

4.3.4.1 Preparation of data and construction of variables

The objective of this study was to describe and quantify microclimate in artificial nest boxes and how they differ from natural nest burrows, examine the influence of climate and nest attributes (location and vegetation cover) on nest microclimate and predict future nest temperatures under a 2 ˚C climate change scenario and implications for this range edge population. The focus was on maximum daily temperature and hours of exposure to potentially harmful thermal conditions while accounting for weather conditions (wind, ambient temperature, humidity). Therefore, I constructed variables at time scales allowing quantification of maximum temperature and heating duration. To do this, half-hourly temperature and humidity measurements were first averaged by hour for each day for each individual nest. To account for local climatic influences on nest microclimate, half hourly measurements of ambient conditions including temperature, relative humidity, wind speed and wind direction recorded at the BOM Garden Island weather station were also averaged by hour for each day. Several daily microclimate metrics were then constructed to compare temperature and humidity patterns and variation. For each sampling date (24-hour period), I calculated the following metrics of relative humidity and temperature for ambient conditions and individual nests: mean, maximum, minimum and range. Days were also categorised into either warm (ambient temperatures exceeded 25 ˚C) or cool (ambient temperatures were below 25 ˚C) days, hereafter referred to as '*temperature category*'. This cut point was identified from visual inspection of data where beneath 25 ˚C, ambient temperature was unlikely to induce nest box warming over 30 ˚C, a physiological threshold for stress in little penguins (Stahel and Nicol 1982; Horne 2010). For daily wind speed and direction, I isolated data at four times during the day: 6am, 9am, 12pm and 3pm. Departure of daily nest measurements from ambient conditions were extracted for each sampling date and nest by subtracting daily ambient measure from the daily nest measure. To assess and compare hours of exposure to critical temperatures, the number of hours each nest recorded temperatures from ≥ 30 ˚C, and ≥ 35 ˚C were calculated for each sampling day. These temperature thresholds were chosen as they represent the upper thermoneutral limit and the temperature at which adult little penguins become hyperthermic respectively (Stahel and Nicol 1982). Hourly and daily measurements were pooled to assess differences microclimate conditions.

4.3.4.2 *Data exploration.*

Prior to any statistical analysis, data exploration was carried out following the protocol recommended in Zuur *et al.* (2010). Cleveland dotplots were used to identify outliers and multi-panel pair-plots were used to screen for collinearity of variables, assessed using Pearson's correlation coefficient. If the Pearson's correlation coefficient was >0.6 then one variable from the pair was eliminated (Booth *et al.* 1993). Nest temperature and nest relative humidity were highly correlated (r = -0.7), therefore while descriptive statistics are presented for both, modelling was done on temperature data only as these were better measured by loggers and variation in nest humidity is likely to be largely a reflection of changes in temperature. A significant correlation (r >0.6) was found between daily ambient temperature measures (maximum, minimum, mean and range) as well as between daily humidity measures (maximum, minimum, mean and range). Subsequently, daily ambient maximum temperature and daily ambient maximum relative humidity were the only ambient temperature and humidity predictors used for statistical analysis. As many of the nest characteristics variables measured were correlated and to avoid over parametrising models during analysis, collinear variables were removed and only those variables that were thought to be biologically relevant were retained.

The influence of adult presence within a nest on temperature was also examined. True adult occupancy for each sample nest could only be obtained for 26 days/ year for each sample nest (i.e. when the adult was observed during fortnightly monitoring sessions). A naive adult occupancy measure was inferred through nesting activity (i.e. each day during a breeding attempt from egg lay until fledging was considered ‘occupied’). Preliminary analysis revealed negligible evidence of an effect of adult presence on nest temperature and was not included in further analyses.

All analyses were performed within the statistical software program R version 3.6.1 (R Core Team 2018) and using RStudio version 1.2.1335 (RStudio Team 2018) Data manipulation and plotting was carried out using packages within tidyverse (ggplot2; dplyr; Wickham 2017). Descriptive statistics are reported as means ± standard error (SE) or ± 95 % confidence interval (CI) for tables and graphs, respectively. Tests where $P<0.05$ were considered significant and as evidence of an effect.

4.3.4.3 Modelling framework

Nest type models. To detect and quantify relationships between Daily maximum temperature and nest type (natural nest vs artificial nest box) while accounting for local climatic conditions, I modelled four temperature response variables: daily maximum, daily minimum, exposure hours over 30 ˚C and exposure hours over 35 ˚C. To model daily maximum and minimum temperature, Linear Mixed Models (LMM) were constructed using the package glmmTMB [function: glmmTMB; (Brooks *et al.* 2017)]. Daily maximum nest temperature was modelled against the fixed effects of nest type and local climate conditions including: maximum ambient temperature, temperature category (‘warmer’ vs ‘cooler’ days), maximum ambient relative humidity, wind speed and wind direction and included two interaction terms between maximum ambient temperature and temperature category, and wind speed and wind direction. Daily minimum nest temperature was modelled against nest type and local climate conditions including minimum ambient temperature, maximum ambient relative humidity, wind speed and wind direction and the interaction between wind speed and direction. All models included the random effect of nest ID. As expected, temporal correlation was detected during initial model validation procedures and was accounted for by using the first-order autoregressive (AR1) error structure with date nested within nest ID.

Exposure hours over 30 ˚C and 35 ˚C were modelled separately using Generalized Linear Mixed Models (GLMMs) with a logit link function and Poisson distribution to represent the count of hours above the threshold temperature (measurements were hourly and therefore a discrete count). Explanatory variables for both models included maximum ambient temperature, maximum ambient relative humidity, wind speed, wind direction and the interaction between wind speed and wind direction. Nest ID was used as the random effect.

Nest attribute models. To detect and quantify relationships between temperature and nest attributes (location and vegetation) each nest type (natural nest or artificial nest box) was modelled separately against nest type specific attributes. Modelling framework was similar to nest type model set however minimum temperature was not assessed as minimum temperatures were not considered low enough to have a negative impact on the thermoregulatory capacity of little penguins (Stahel and Nicol 1982). Furthermore, preliminary data exploration and analyses revealed little variation in minimum nest temperatures between nest type. In addition to local climate variables, nest box models also included fixed effect of vegetation cover, box cover, aspect, slope and vents. Models examining natural nest type included local climate variables and additional fixed effects of bush wall depth, species, aspect and slope.

All models also accounted for the effect of year. While not a factor of interest for this study, year could not be included as a random effect as it was limited to four levels (i.e. 2013, 2014, 2015 and 2016) and therefore was included as a fixed effect. An overview of all model sets is given in (Appendix 4.2; Figure A4.2).

4.3.4.4 General approach to analysis

During data analysis, I applied an information-theoretic approach (Burnham and Anderson 2003) whereby support for predictors given the data was examined. Due to the exploratory nature of this study, a balanced *all subsets* approach was used whereby all possible combinations of the predictor variables were tested to examine the effect of local climate variables and nest characteristics on nest maximum temperature, nest minimum temperature and hours of exposure to upper thermoneutral limits of 30 ˚C and 35 ˚C. This approach is recommended practice in model selection ensuring all important sub-models are included in the candidate model set and performs better than other ad hoc model selection strategies when defining variable importance (Doherty et al 2012; Morin et al 2020). Selected explanatory variables were fitted to a global model that included all predictors (see below for specifics) and all possible combinations were tested using the 'dredge' function in the MuMIN package (Barton 2016). Model residuals were visually evaluated for issues with fit or assumptions; no violations were detected. Variance explained by the fixed effects (marginal pseudo R^2) was estimated using methods described by Nakagawa and Schielzeth (2013) and the function 'r.squaredGLMM' in the package MuMIN (Barton 2016).

Models were evaluated using Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2003; Symonds and Moussalli 2011; Barton 2016). AICc weight (ω_i) was used to select the best of the competing models. Models with a ΔAICc <5 are presented and models with a ΔAICc <2 were considered as having substantial support (Burnham and Anderson 2003; Burnham et al. 2011). To account for model uncertainty and enable more robust inferences, model averaging was applied across all models and parameter and error estimates were derived from a weighted average across multiple models (Burnham and Anderson 2003; Johnson and Omland 2004; Symonds and Moussalli 2011). Prior to averaging, model parameters were standardised based on partial standard deviations to remove effects of collinearity among predictors (Cade 2015). I examined two types of model averaged coefficients to assess strength of evidence for an effect: the conditional model average (where estimates are generated from only the models each covariate appears), and the full model average (where covariates not present in the model contribute zero to the calculation) (Symonds and Moussalli 2011). Full model averaged estimates consequently shrink towards zero; the difference between full and conditional model estimates is referred to as shrinkage and represents the degree by which covariates are informative (Symonds and Moussalli 2011; Cade 2015). Shrinkage was examined to assess strength of covariates present in top models (Burnham et al. 2011; Grueber et al. 2011; Symonds and Moussalli 2011). Predictions and graphical representations of full and conditional model averaged coefficients were produced through the packages ggeffects (Lüdecke and Lüdecke 2017) and sjplot (Lüdecke 2018). Variables were considered to have the strongest evidence of effect if the disparity between the full and conditional estimates (shrinkage) was small and 95% confidence intervals of model-averaged coefficients did not include zero (Johnson and Omland 2004; Burnham et al. 2011; Symonds and Moussalli 2011).

4.3.4.5 Predicting nest temperature under 2 ˚C increase scenario

The chances of limiting global temperature increase to below 2 ˚C by 2100 (the stabilisation target adopted by the Paris agreement) is 5% and 2 ˚C of warming will likely be the minimum change observed over the next 8 decades (Raferty *et al.* 2017). To explore how this minimum increase in ambient temperature could affect nest temperatures in the future I simulated a simple 2 ˚C mean increase of daily maximum temperature during the study period by applying this increase to daily maximum temperatures recorded by BOM at the Garden Island weather station for every calendar day of the year between 2013 and 2016 for all nests. Other daily climate and nest attribute variables were kept the same as there is far less certainty of effect of climate change on relative humidity and wind conditions. These inputs were then run through the daily maximum and exposure models to generate predictions using the R base function predict() (R Core Team 2018). Results from these predictions are presented graphically.

4.4 Results

4.4.1 Daily patterns of nest temperature and relative humidity

Temperature inside natural nests and nest boxes followed a similar daily pattern increasing steadily from a minimum around 0500 hrs and reaching a maximum between 1200-1300 hrs before dropping in the afternoon (Figure 4.5). Temperatures inside both artificial and natural nests were similar to ambient temperature from ~1700 – 0800 hrs. Thereafter temperatures departed from and exceeded ambient temperature, with the maximum difference occurring at 1200 hrs for natural nests and 1300 hrs for artificial nest boxes. The degree to which the nest temperature departed from the ambient temperature varied depending on ambient maximum temperature with greater deviation from ambient conditions observed at lower maximum temperatures. At 25 – 29.9 ˚C ambient temperatures, both nest types reached temperatures that are thermally stressful for adult penguins (Figure 4.6B). Nest boxes reached temperatures that resulted in hyperthermic conditions for incubating penguins when ambient temperatures reached or exceeded 30 ˚C (Figure 4.6C). When ambient temperatures reached or exceeded 35 ˚C, both natural nests and nest boxes entered hyperthermic conditions (Figure 4.6D).

Daily relative humidity (RH) peaked at ~0600 hrs and then steadily dropped to a daily minimum between 1200 – 1300hrs before increasing again in the afternoon (Figure 4.5). Natural and artificial nests were more humid than ambient conditions except for a period in the afternoon between 1200 – 1600 hrs during which conditions were drier for both nest types.

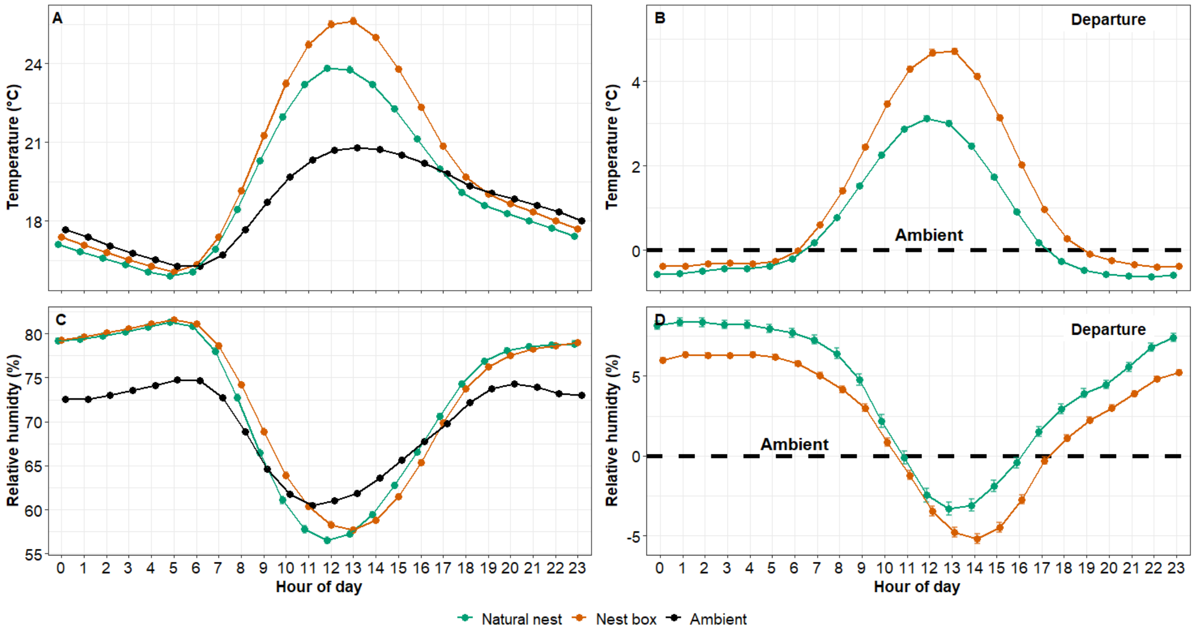

Figure 4.5: Pattern of temperature (˚C) and relative humidity (%) change throughout the day. Mean ± 95% CI of **(A)** hourly nest temperature; **(B)** departure from ambient temperature; **(C)** hourly nest relative humidity; **(D)** departure from ambient relative humidity recorded inside natural nests and artificial nests (boxes) on Penguin Island

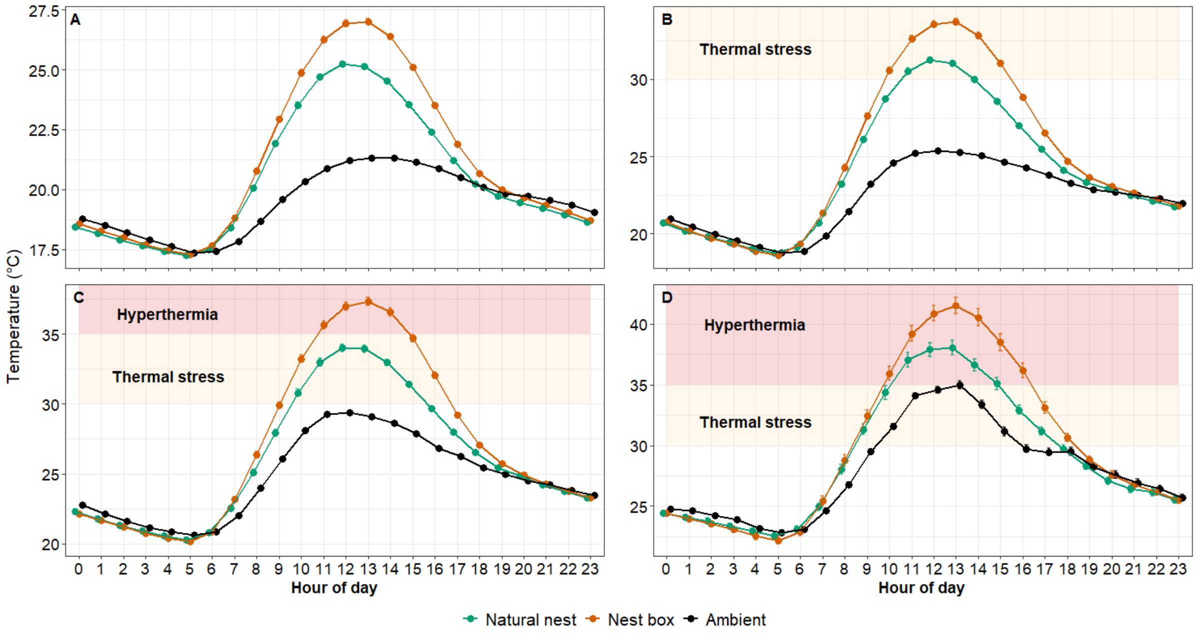

Figure 4.6: Mean ± 95% CI of hourly nest temperature at differing ambient temperature ranges: (A) Ambient Max = 20-25˚C ; **(B)** Ambient Max = 25- 30˚C; **(C)** Ambient Max = 30-35˚C; **(D)** Ambient Max = >=35˚C) for natural nest and artificial nests (boxes).

Artificial nests reached higher daily maximum temperatures than natural nests (mean = 26.5 ± 0.1; range = 11.9 – 56.0 and mean = 24.7 ± 0.1; range = 10.8 – 51.3 respectively) and experienced a greater daily temperature range (mean = 11.1 ± 0.04; range = 0 – 36.7 and mean = 9.5 ± 0.04; range = 0 – 34.0 respectively) (Table 4.2). Nest boxes and natural nests experienced similar daily minimum temperatures (mean = 15.4 ± 0.03; range = 1.6 – 27.0 and mean = 15.2 ± 0.03; range = 1.8 – 27.3 respectively; Table 4.2). Nest boxes were consistently warmer throughout the year during both the breeding (April – December) and non-breeding (January – May) seasons (Appendix 4.3; Figure A4.3; Appendix 4.4; Figure A4.4). Artificial nest boxes exceeded upper thermoneutral limits (30 ˚C and 35 ˚C) more often and maintained extreme temperatures for longer periods (mean = 5.6 ± 0.03 hrs day^{-1}, range = 1 – 16 hrs day^{-1} ; mean = 4.1 ± 0.04 hrs day^{-1}, range = 1 – 11 hrs day^{-1}, for 30 ˚C and 35 ˚C respectively) than natural nests (mean = 4.7 ± 0.04 hrs day^{-1}, range = 1 – 14 hrs day^{-1} ; mean = 3.0 ± 0.04 hrs day^{-1}, range = 1 – 8 hrs day^{-1}, 30 ˚C and 35 ˚C respectively), (Figure 4.7; Table 4.2).

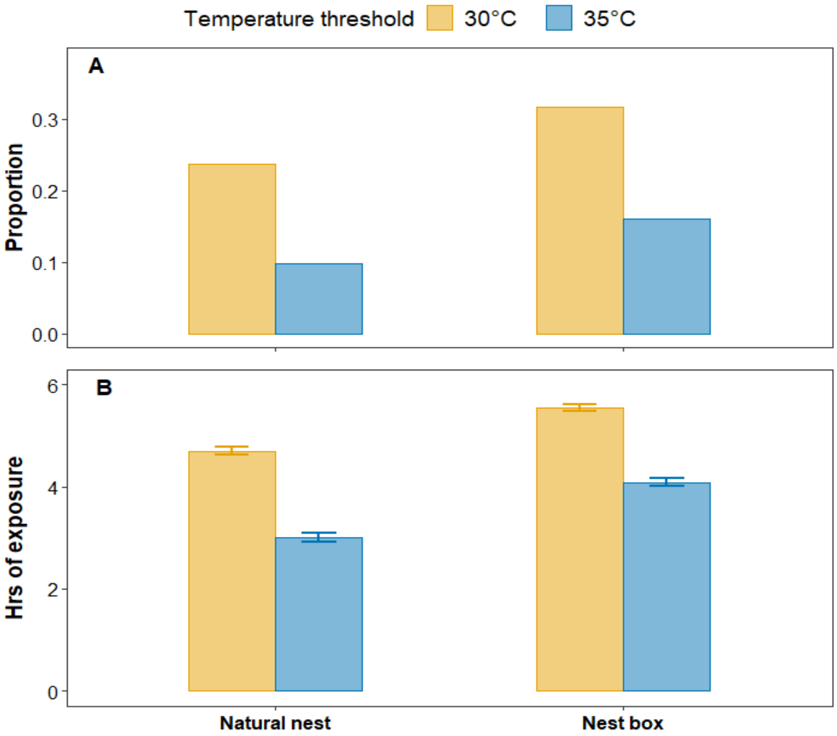

Figure 4.7: (A) proportion of total sampling days where daily temperature exceeded upper thermoneutral limits of 30 ˚C (thermal stress zone) and 35 ˚C (Hyperthermic zone) for natural nests and nest boxes. **(B)** For days exceeding 30 ˚C; mean duration in hours per day that exceeded thermal threshold limits of 30 ˚C and 35 ˚C for natural nests and artificial nests (boxes).

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Table 4.2: Summary (mean ± standard error, range in parentheses) of daily maximum, minimum, mean, range nest temperature (˚C), departure from Garden Island relative humidity (nest – ambient) and hours of exposure over 30 ˚C and over 35 ˚C for natural and artificial nests.

Temperature variable	**Natural nest** **(N_{nest}= 51; N_{daily}= 18325)**	**Nest box** **(N_{nest} = 46; N_{daily}= 17142)**
Max Temperature$_{(nest)}$	24.7 ± 0.1 (10.8 – 51.3)	26.5 ± 0.1 (11.9 – 56.0)
Max Temperature$_{(departure)}$	2.9 ± 0.03 (-13.1 – 19.9)	4.6 ± 0.04 (-7.1 – 24.3)
Min Temperature$_{(nest)}$	15.2 ± 0.03 (1.8 – 27.3)	15.4 ± 0.03 (1.6 – 27.0)
Min Temperature$_{(departure)}$	-0.2 ± 0.01 (-6.8 – 8.4)	0.1 ± 0.01 (-6.7 – 6.7)
Mean Temperature$_{(nest)}$	19.1 ± 0.03 (0.1 – 19.1)	19.9 ± 0.04 (6.5 – 35.4)
Mean Temperature$_{(departure)}$	0.5 ± 0.01 (-4.5 – 7.6)	1.2 ± 0.01 (-5.5 – 8.1)
Range Temperature$_{(nest)}$	9.5 ± 0.04 (0 – 34.0)	11.1 ± 0.04 (0 – 36.7)
Range Temperature$_{(departure)}$	3.1 ± 0.03 (-12.4 – 26.2)	4.6 ± 0.04 (-8.7 – 25.6)
Hours ≥30 ˚C	4.7 ± 0.04 (1 – 14)	5.6 ± 0.03 (1 – 16)
Hours ≥35 ˚C	3.0 ± 0.04 (1 – 8)	4.1 ± 0.04 (1 – 11)

Relatively humidity of natural and artificial nests. Natural nests and artificial nest boxes both experienced a similar range of relative humidity (RH) observations with a mean daily humidity of 72.3 ± 0.1 (range = 9.9 – 97.8) and 72.7 ± 0.1 (range = 36.4 – 98.5) respectively (Table 4.3; Figure 4.8). While both nest types observed similar daily RH patterns the response differed depending on the time of year. From September to March, artificial nests were generally drier than the natural nests but during the wetter months (April to August) artificial nests were more humid (Appendix 4.3; Figure A4.3).

Table 4.3: Summary (mean ± standard error, range in parentheses) of daily maximum, minimum, mean and range nest relative humidity (%) and departure from Garden Island relative humidity (nest – ambient) for natural nests and nest boxes pooled across the study period (2014-2016).

Humidity variable	**Natural nest (N$_{nest}$= 31 N$_{daily}$= 5825)**	**Nest box (N$_{nest}$ = 45 N$_{daily}$= 12599)**
Max Humidity$_{(nest)}$	86.1 ± 0.1 (13.8 – 99.9)	85.1 ± 0.1 (51.1 – 100.0)
Max Humidity $_{(departure)}$	3.2 ± 0.1 (-71.3 – 29.9)	3.5 ± 0.1 (-35.8 – 32.7)
Min Humidity $_{(nest)}$	52.8 ± 0.2 (2.5 – 96.4)	54.7 ± 0.2 (9.1 – 97.9)
Min Humidity $_{(departure)}$	2.8 ± 0.2 (-76.0 – 56.0)	1.6 ± 0.1 (-64.3 – 52.1)
Mean Humidity $_{(nest)}$	72.3 ± 0.1 (9.9 – 97.8)	72.7 ± 0.1 (36.4 – 98.5)
Mean Humidity $_{(departure)}$	4.1 ± 0.1 (-72.4 – 40.5)	2.3 ± 0.1 (-31.2 – 37.5)
Range Humidity $_{(nest)}$	33.4 ± 0.2 (0.8 – 74.7)	30.4 ± 0.1 (0 – 76.0)
Range Humidity $_{(departure)}$	0.4 ± 0.2 (-67.2 – 57.1)	-1.2 ± 0.1 (-51.5 – 57.3)

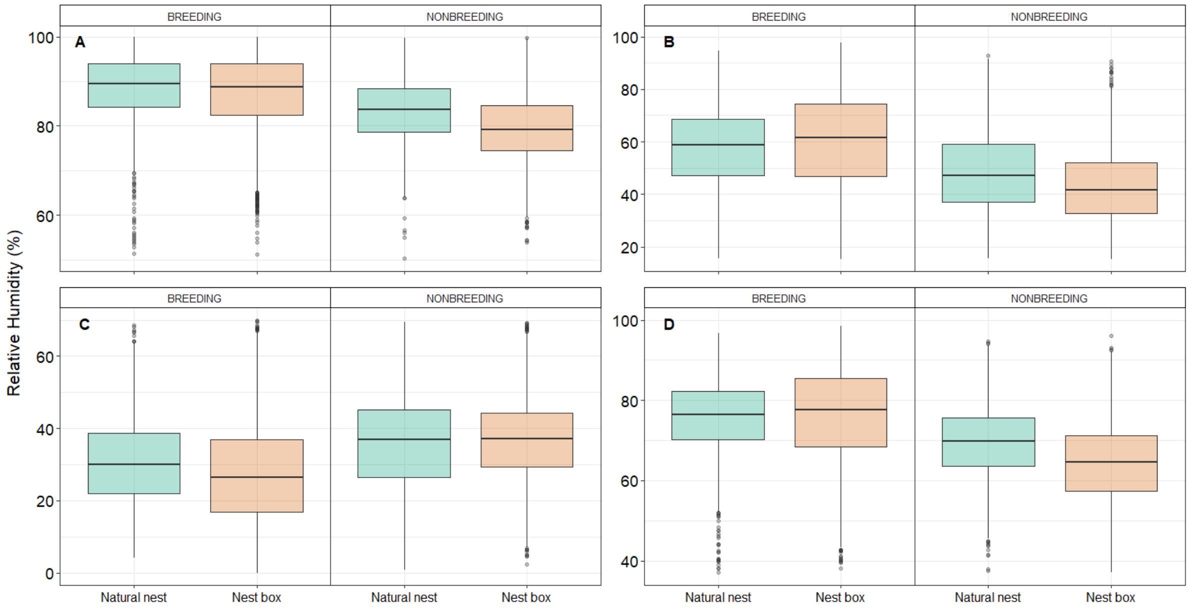

Figure 4.8: Box plots of mean daily humidity observations for natural nests and nest boxes during the breeding (April – December) and non-breeding seasons (December - March. **(A)** Daily maximum; **(B)** daily minimum; **(C)** daily range; **(D)** daily mean.

4.4.2 Effect of nest type and local climate on daily nest maximum temperature

Model comparisons showed substantial support for models containing nest type. The top two competing models included this term with the most parsimonious model having an Akaike weight of 0.67 (Table 4.4). The next model that excluded nest type was >15 ΔAICc units from the top model and with a weight <0.0001, supporting the importance of nest type in explaining variation in maximum nest temperature. Artificial nests were around 2 ˚C warmer than natural nests (β = 2.04 ˚C, CI [1.11 – 2.97 ˚C]; Figure 4.9A-B; Appendix 4.5; Table A4.5).

All local climate predictors were included in the top model (Table 4.4). As expected, ambient daily max temperature had a significant positive effect on nest temperature however the effect of ambient temperature depended on whether or not ambient daily maximum exceeded 25 ˚C (Figure 4.9A-B). Nests were approximately 3 ˚C and 4.2 ˚C warmer than ambient on 'warm' and 'cool' days respectively. Wind speed had a negative effect on nest temperature however the strength of effect was dependent on wind direction with a significantly stronger cooling effect of wind speed being observed in onshore winds (Figure 4.9C). Maximum ambient relative humidity had a weak but significant negative effect on nest maximum temperature (β = -0.19 ˚C, CI [-0.21 – -0.17 ˚C]; Figure 4.9A; Appendix 4.5; Table A4.5).

Table 4.4: Top models (ΔAICc < 5) for all subsets linear regression model set predicting mean daily maximum temperature of natural nests and artificial nest boxes on Penguin Island based on nest type and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*234703.1*	*87135.9*	*0.00*	*4*	*0*
Nest type + ambient temp max + temperature category+ ambient RH max + wind speed at 12pm + wind direction at 12pm + wind speed at 12pm * wind direction at 12pm + ambient temp max*temperature category	147567.2	0	0.67	14	0.46
Nest type + ambient temp max + temperature category+ ambient RH max + wind speed at 12pm + wind direction at 12pm + wind speed at 12pm * wind direction at 12pm + ambient temp max*temperature category +year	147568.6	1.42	0.33	17	0.46

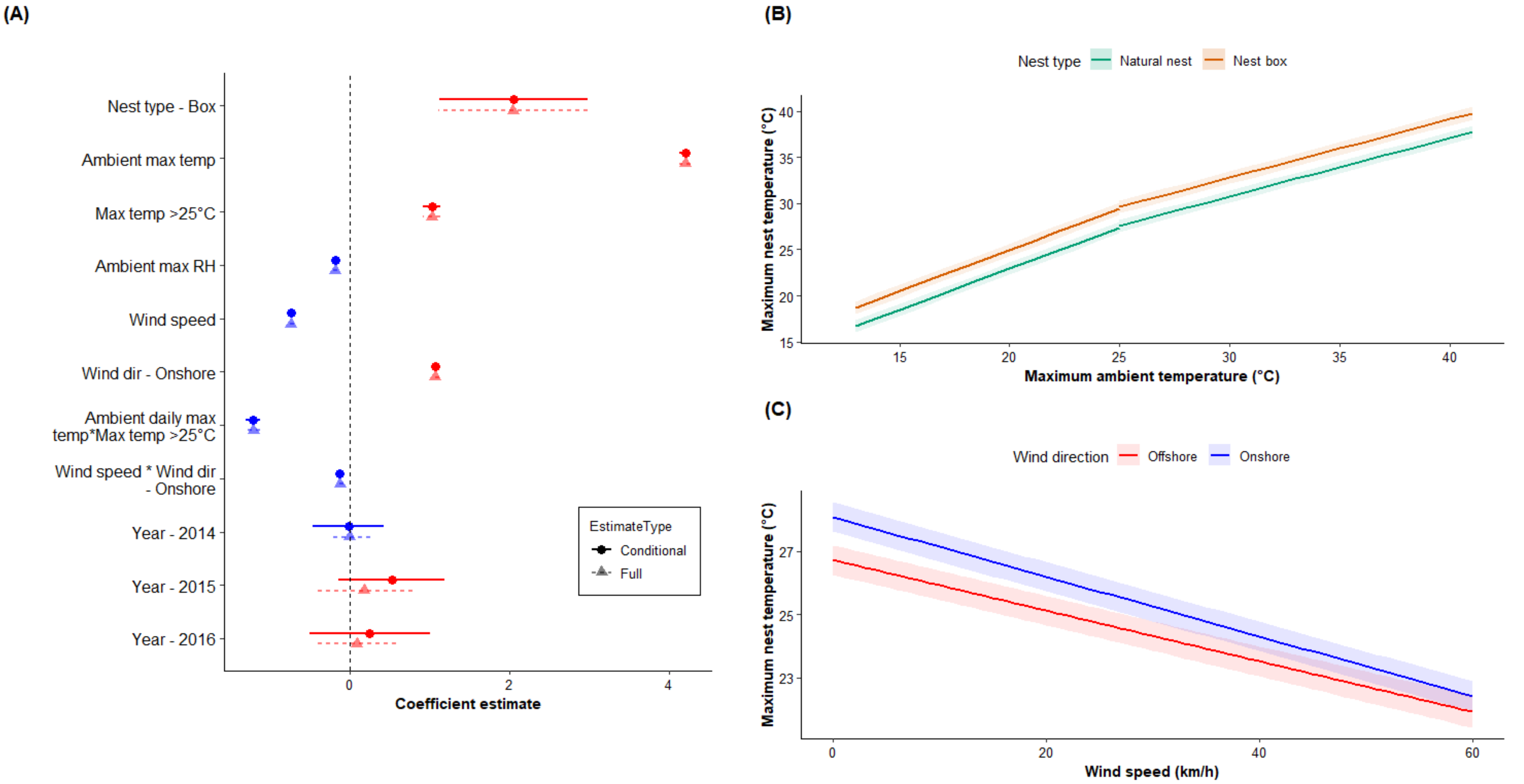

Figure 4.9: **(A)** Coefficient effects of top performing model for effect of nest type and local climatic conditions on nest maximum temperature. **(B)** Predictions from Linear Mixed Models of the effect of nest type and maximum ambient air temperature on nest maximum temperature (mean ± 95% CI). **(C)** Predictions from Linear Mixed Models of the interactive effect of wind speed and direction on nest maximum temperature (shaded areas represent 95% CI).

4.4.3 Effect of nest type and local climate on daily nest minimum temperature

Model comparisons investigating predictors of minimum nest temperature revealed nest type was less likely to be a significant predictor of daily minimum nest temperature. While the top model (Akaike weight=0.78; Table 4.5) included nest type, examination of model averaged coefficients (Appendix 4.6; Table A4.6) suggested that the strength of the effect was small (Figure 4.10A) and that variation in minimum nest temperature could be better explained by other factors.

All local climate predictors were included in the two top performing models (Table 4.5). Effect of ambient temperature was similar to what was observed in maximum temperature models; higher ambient temperatures lead to greater nest temperatures (β = 3.16 ˚C [3.15 – 3.18 ˚C]; Figure 4.10A-B; Appendix 4.6; Table A4.6). A greater cooling effect of wind speed was observed for onshore winds when compared to offshore winds (Figure 4.10C) however the effect on nest minimum temperature was marginal (-0.16 ˚C per 10km/hr increase of wind speed and -0.06 ˚C per 10km/hr respectively). Relative humidity had a weak positive effect on nest temperature (β = 0.23 [0.22 – 0.24]; Figure 4.10A; Appendix 4.6; Table A4.6).

Table 4.5: Top models (ΔAICc < 5) for all subsets linear regression model set predicting mean daily minimum temperature of natural nests and artificial nest boxes on Penguin Island based on nest type and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*89952.54*	*259.08*	*0.00*	*4*	*0*
Nest type + ambient temp min + ambient RH max + wind speed at 6am + wind direction at 6am + wind speed at 12pm * wind direction at 12pm + year	89693.46	0	0.78	15	0.84
Ambient temp min + ambient RH max + wind speed at 6am + wind direction at 6am + wind speed at 12pm * wind direction at 12pm + year	89696.00	2.54	0.22	14	0.84

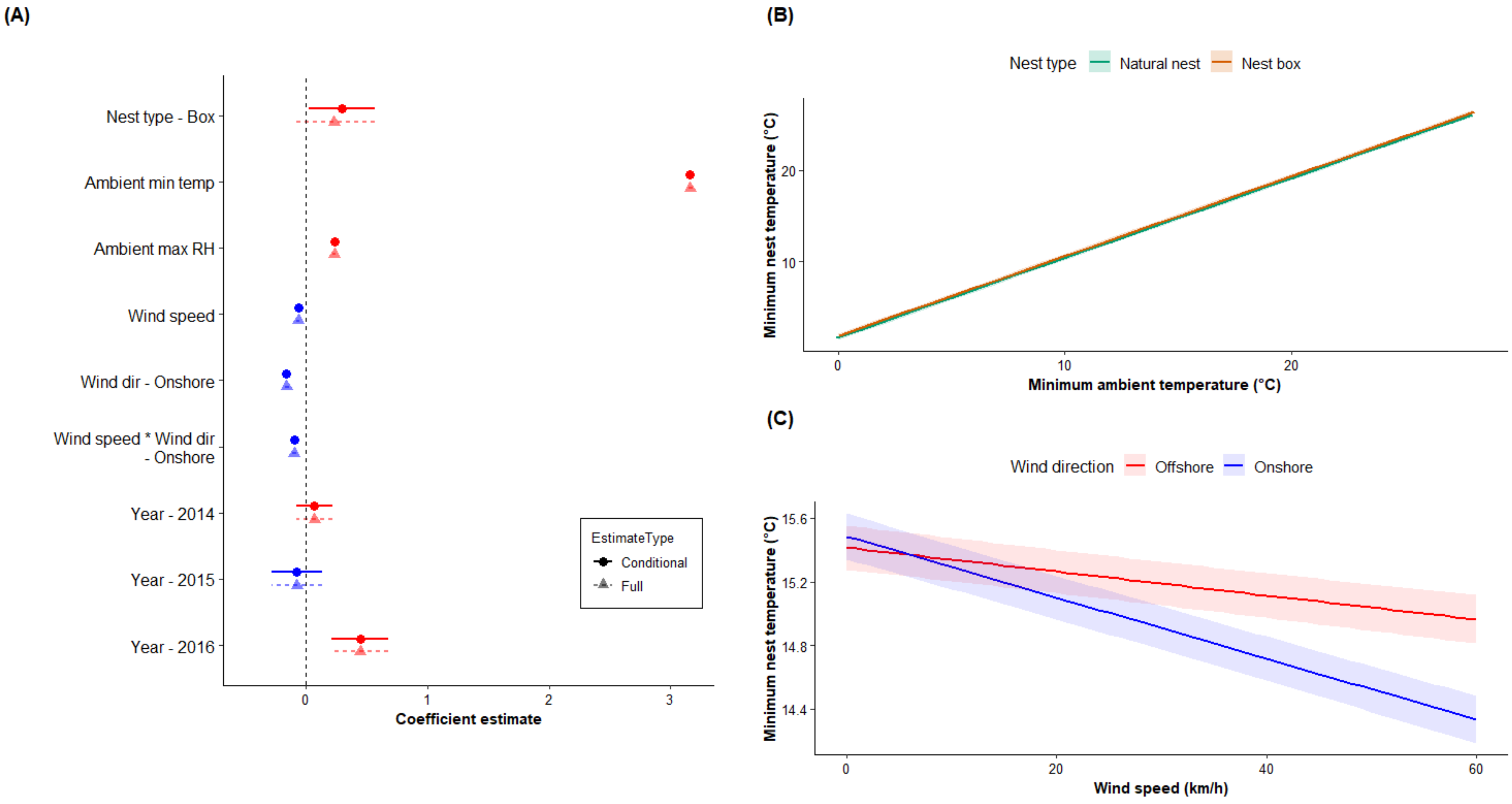

Figure 4.10: (A) Coefficient effects of top performing model for effect of nest type and local climatic conditions on nest minimum temperature. **(B)** Predictions from Linear Mixed Models of the effect of minimum ambient temperature and nest type on nest minimum temperature (Shaded area represent 95% CI).**(C)** Predictions from Linear Mixed Models of the interactive effect of wind speed and direction on nest minimum temperature (Shaded areas represent 95% CI).

4.4.4 Effect of nest type and local climate on nest exposure hours ≥30 ˚C and ≥35 ˚C

Nest type was supported as an important predictor for explaining variation in nest exposure hours over both 30 ˚C and 35 ˚C. Nest type was included in the top three candidate models investigating exposure hours to temperatures ≥30 ˚C accounting for >98% of total Akaike weight; the most parsimonious model having a weight of 0.50 (Table 4.6). While model comparisons were more competitive in the ≥35 ˚C model set, nest type remained well supported, present in the top 12 models accounting for >99% of the total Akaike weight (Table 4.7). Compared to natural nests, artificial nest boxes spent more time exposed to temperatures exceeding 30 ˚C(β = 0.18 CI [0.07 – 0.28] (Figure 4.11A-B; Appendix 4.7; Table A4.7) and temperatures exceeding 35 ˚C (β = 0.28 CI [0.15 – 0.41] , Figure 4.12A-B; Appendix 4.8; Table A4.8).

The top models for exposure ≥30 ˚C indicated that all local climate predictors were influential on the hours of nest exposure (Table 4.6). As anticipated, high maximum ambient temperature were associated with significantly longer exposure (β = 0.38 [0.37 – 0.39]; Figure 4.11A-B; Appendix 4.7; Table A4.7) while ambient relative humidity was associated with slightly reduced exposure time (β = -0.02 [-0.03 – -0.01]; Figure 4.11A; Appendix 4.7; Table A4.7). Likewise, ambient maximum temperature had a comparable effect on hours of exposure to nest temperatures exceeding 35 ˚C (β = 0.38 [0.36 – 0.40]; Figure 4.12A- B; Appendix 4.8; Table A4.8)

The effect of wind on exposure hours was less clear. Wind speed was present in the top competing models however the effect was negligible and examination of model averaged coefficients (Appendix 4.7 & 4.8) indicated some uncertainty in the importance of wind speed as a predictor suggesting variation in exposure hours could be better explained by other factors. Wind direction was a stronger predictor of exposure hours than wind speed and had a positive effect on hours of exposure over 30 ˚C (β = 0.30 CI[0.27 – 0.33]; Figure 4.11C; Appendix 4.7; Table A4.7), and 35 ˚C (β = 0.24 CI[0.20 – 0.28]; Figure 4.12C; Appendix 4.8; Table A4.8). There was a level of uncertainty in the importance of the interaction between wind speed and direction in models examining exposure hours ≥30 ˚C and ≥35 ˚C suggesting the role of wind in influencing nest exposure hours was less important once nest temperatures exceeded 30 ˚C (Appendix 4.7 & 4.8).

Table 4.6: Top models (ΔAICc < 5) for all subsets linear regression model set predicting hours of exposure per day exceeding 30 ˚C of natural nests and artificial nest boxes on Penguin Island based on nest type and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ω_i) (ωi), number of parameters (k) and marginal (R^2_{marg}.) pseudo R2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*44774.07*	*5628.46*	*0.00*	*3*	*0*
Nest type + ambient temp max + ambient RH max + wind direction +year	39145.61	0.00	0.50	10	0.31
Nest type + ambient temp max + ambient RH max + wind speed + wind direction + wind speed * wind direction +year	39146.82	1.21	0.27	12	0.31
Nest type + ambient temp max + ambient RH max + wind speed + wind direction + year	39147.26	1.66	0.22	11	0.31

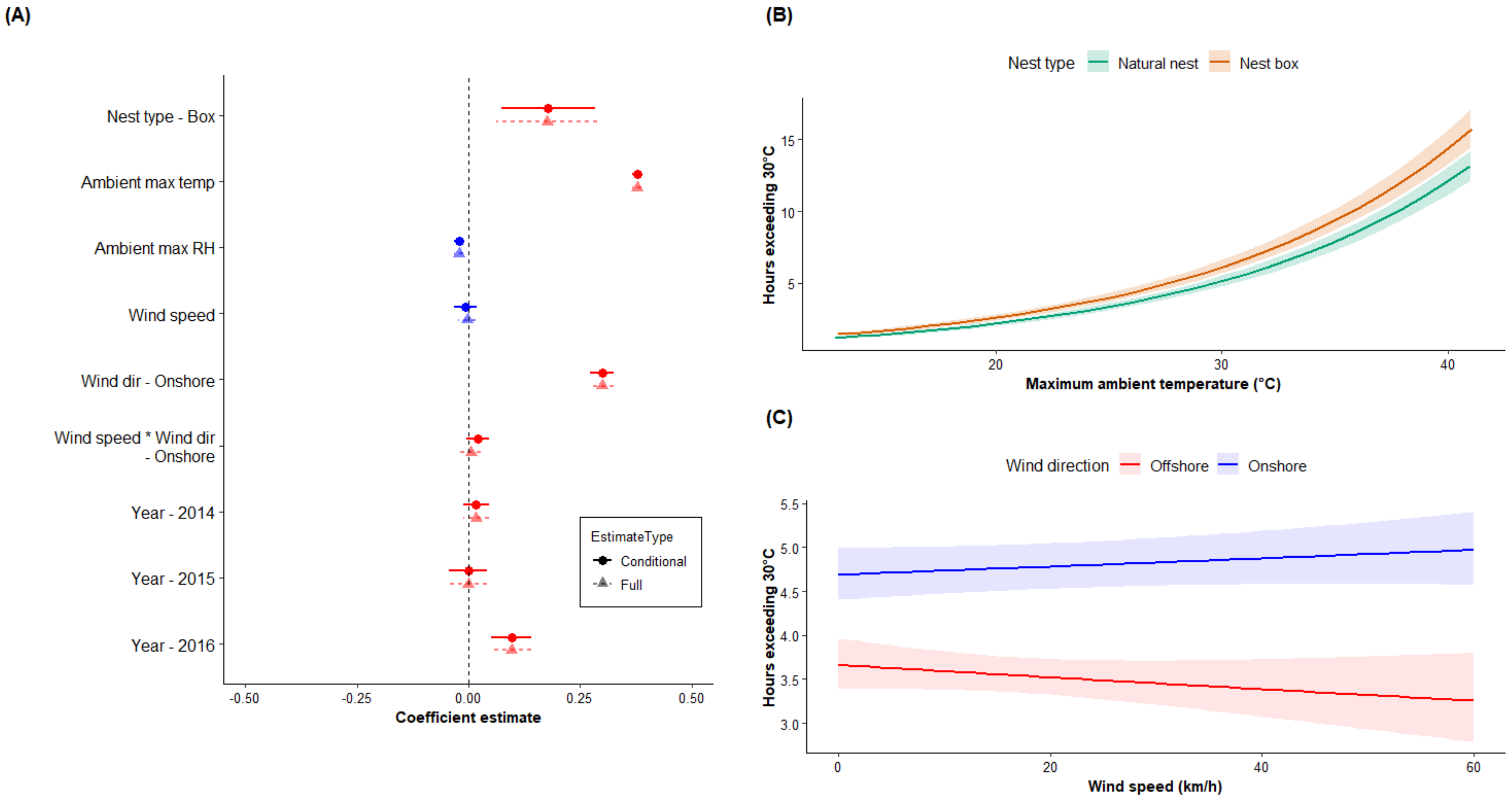

Figure 4.11. (A) Full and conditional model averaged coefficient estimates for effect of nest type and local climatic conditions on hours of exposure to temperatures exceeding 30 ˚C. **(B)** Predictions from Generalised Linear Mixed Models of the effect of nest type and maximum ambient air temperatures on hours of exposure to temperatures exceeding 30 ˚C (mean ± 95%CI). **(C)** Predictions from Generalised Linear Mixed Models of the interactive effect of wind speed and direction on hours of exposure to temperatures exceeding 30˚C (shaded areas represent 95% CI).

Table 4.7: Top models (ΔAICc < 5) for all subsets linear regression model set predicting hours of exposure per day exceeding 35 ˚C of natural nests and artificial nest boxes on Penguin Island based on nest type and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ω_i), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*18077.68*	*1696.08*	*0.00*	*3*	
Nest type + ambient temp max + wind speed at 12pm + wind direction at 12pm + year	16381.60	0.00	0.28	10	0.25
Nest type + ambient temp max + wind speed at 12pm + wind direction at 12pm + year + wind speed 12pm * wind direction 12pm	16382.70	1.09	0.16	11	0.25
Nest type + ambient temp max + wind speed at 12pm + wind direction at 12pm	16382.98	1.37	0.14	7	0.25
Nest type + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm + year	16383.22	1.61	0.12	11	0.25
Nest type + ambient temp max + wind speed at 12pm + wind direction at 12pm+ wind speed 12pm * wind direction 12pm	16383.99	2.39	0.08	8	0.25
Nest type + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm+ wind speed 12pm * wind direction 12pm + year	16384.49	2.89	0.07	12	0.25
Nest type + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm	16384.50	2.90	0.07	8	0.25
Nest type + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm+ wind speed 12pm * wind direction 12pm	16385.70	4.10	0.04	9	0.25

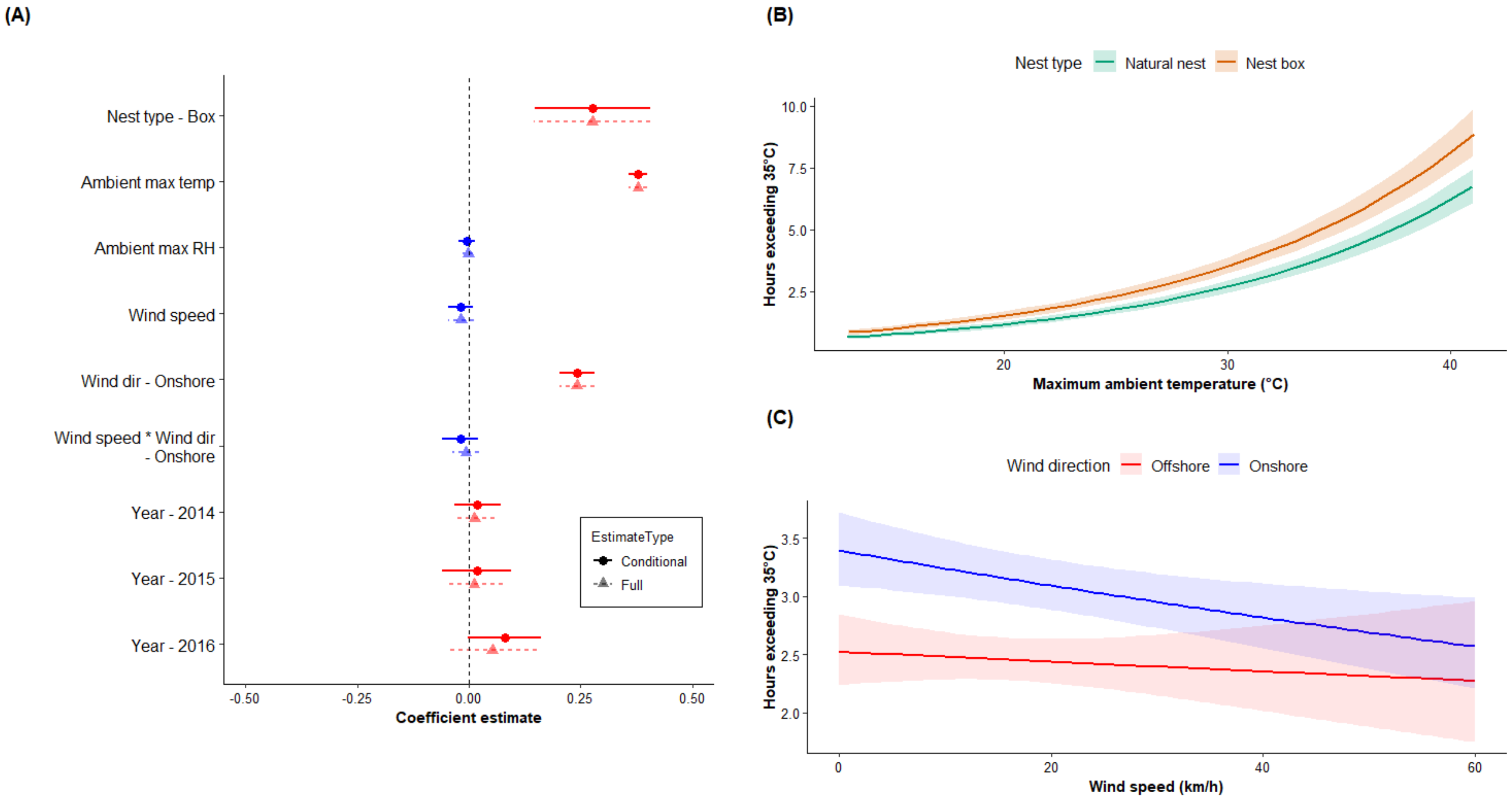

Figure 4.12: (A) Full and conditional model averaged coefficient estimates for effect of nest type and local climatic conditions on hours of exposure to temperatures exceeding 35 ˚C. **(B)** Predictions from Generalised Linear Mixed Models of the effect of nest type and maximum ambient air temperature on hours of exposure to temperatures exceeding 35 ˚C (shaded area represent 95% CI). **(C)** Predictions from Generalised Linear Mixed Models of the interactive effect of wind speed and direction on hours of exposure to temperatures exceeding 35 ˚C (shaded area represent 95% CI).

4.4.5 Effect of nest site attributes on mean daily maximum temperature of natural nests

As expected, model comparisons revealed that nest temperature in natural nests was best predicted by climate variables, in particular ambient maximum temperature and wind direction. However, vegetation and location attributes were also influencing nest temperature of natural nests. Model selection (Table 4.8) suggested bush wall was a moderate predictor of maximum nest temperature and model averaged coefficients indicated thicker walls were associated with lower maximum nest temperature (β = -0.51 CI [-0.06 – 0.03]; Figure 4.13A&B; Appendix 4.9; Table A4.9). While bush wall was present in two of the top three competing models, examination of full and conditional model averages showed a minor degree of shrinkage and conditional model confidence interval slightly overlapped zero suggesting a minor level of uncertainty for this predictor. Slope was indicated as a strong predictor of nest temperature and was present in the top three competing models and top 16 candidate models accounting for >94% of total Akaike weight. Model coefficients based on model averaging suggested steeper slopes were associated with warmer maximum temperature (β = 1.08 CI [0.16 – 2.01]; Figure 4.13A&C; Appendix 4.9; Table A4.9). There was less support for aspect or species composition as important predictors of maximum nest temperature. While model selection suggested aspect may influence nest temperature, this was not supported by model averaged coefficients (Appendix 4.9; Table A4.9). Species composition was not present in any competing models, model averaged coefficients were not consistent and conditional model coefficient estimates overlapped zero (Figure 4.13A; Appendix 4.9; Table A4.9).

Table 4.8: Top models (ΔAICc < 5) for all subsets linear regression model set predicting mean daily maximum temperature of natural nests on Penguin Island based on vegetation, exposure and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	73024.00	13919.83	0.00	6	0
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + aspect + year + ambient temp max*temperature category + wind speed 12pm * wind direction	59104.17	0.00	0.19	19	0.53
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + year + ambient temp max*temperature category + wind speed * wind direction	59104.30	0.14	0.17	17	0.52
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + aspect + year + ambient temp max*temperature category + wind speed * wind direction	59105.99	1.82	0.07	18	0.52
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + year + ambient temp max*temperature category + wind speed 12pm * wind direction	59106.19	2.03	0.07	16	0.51
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + Species Composition + year + ambient temp max*temperature category + wind speed 12pm * wind direction	59106.35	2.18	0.06	19	0.53
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + Species composition + aspect + year +	59106.53	2.36	0.06	21	0.53

Model	**AICc**	**ΔAICc**	**ω_i**	***k***	**$R^2_{marg.}$**
ambient temp max*temperature category + wind speed 12pm * wind direction					
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + aspect + ambient temp max*temperature category + wind speed 12pm * wind direction	59106.80	2.64	0.05	17	0.52
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + Species Composition + ambient temp max*temperature category + wind speed 12pm * wind direction	59106.86	2.69	0.05	15	0.51
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + Species Composition + ambient temp max*temperature category + wind speed 12pm * wind direction	59107.17	3.00	0.04	14	0.50
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + aspect + ambient temp max*temperature category + wind speed 12pm * wind direction	59107.25	3.09	0.04	16	0.51
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + Species Composition + aspect + ambient temp max*temperature category + wind speed 12pm * wind direction	59107.76	3.59	0.03	19	0.52
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + bush wall + Species Composition + ambient temp max*temperature category + wind speed 12pm * wind direction	59107.83	3.66	0.03	17	0.52
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + Species	59108.20	4.03	0.02	18	0.52

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Composition + aspect + ambient temp max*temperature category + wind speed 12pm * wind direction					
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + Species Composition + ambient temp max*temperature category + wind speed 12pm * wind direction	59108.42	4.25	0.02	16	0.51
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + Species Composition + aspect + ambient temp max*temperature category + wind speed 12pm * wind direction + year	59108.74	4.58	0.02	20	0.52
Ambient temp max + temp category + ambient RH max + wind speed at 12pm + wind direction at 12pm + slope + Species Composition + ambient temp max*temperature category + wind speed 12pm * wind direction +year	59109.05	4.88	0.02	18	0.51

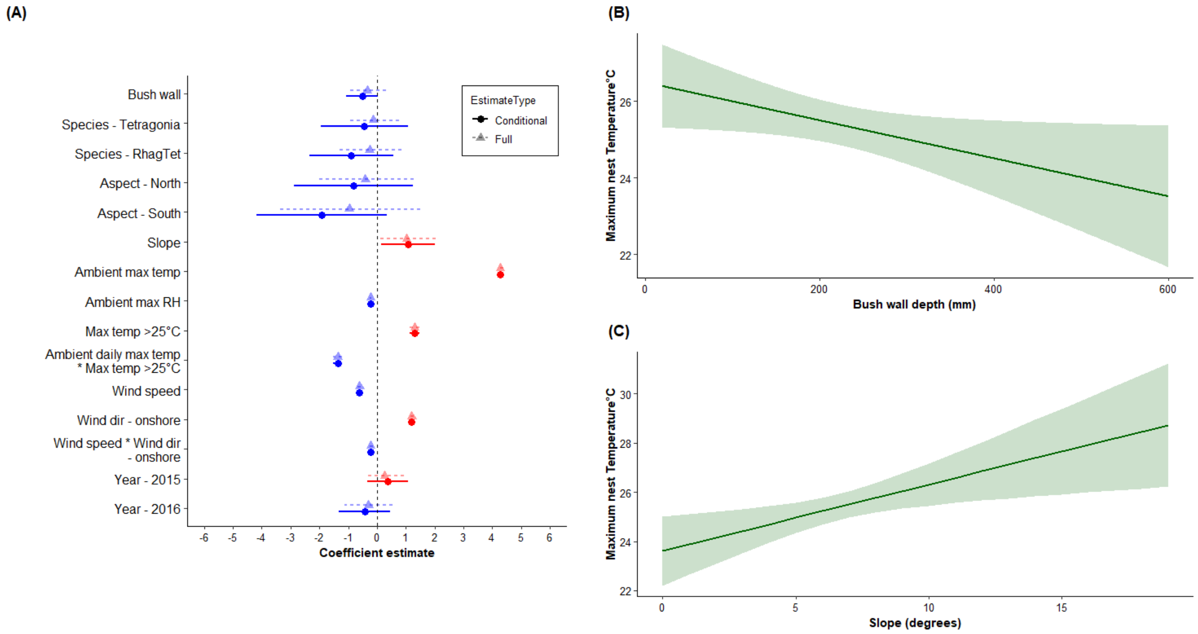

Figure 4.13: (A) Full and conditional model averaged coefficient estimates for effect of vegetation, exposure and local climatic conditions on mean daily maximum nest temperature of natural nests. **(B)** Predictions from Linear Mixed Models of the effect of bush wall depth on mean daily maximum nest temperature (Shaded area represent 95% PI). **(C)** Predictions from Linear Mixed Models of the effect of slope on mean daily maximum nest temperature (Shaded area represent 95% CI).

4.4.6 Effect of nest site attributes on natural nest exposure hours ≥30 ˚C and ≥35 ˚C

Model comparisons revealed that exposure time to temperatures exceeding 30 ˚C was best predicted by local climate variables and the thickness of a nest bush wall. Bush wall was included in top four competing models (Table 4.9). Model averaged coefficients indicated that thicker bush wall was negatively associated with number of hours exposed to 30 ˚C (β = -0.13 CI [-0.18 – -0.08]; Figure 4.14A&B; Appendix 4.10; Table A4.10). There was no evidence supporting effects of other vegetation or location attributes for the 30 ˚C models set. While slope appeared in two of the four top competing models, examination of full and conditional model averaged coefficients revealed little support for this predictor (Appendix 4.10; Table A4.10). The absence of species composition and aspect from all top competing models suggest they poorly describe variation in hours of exposure to temperatures exceeding 30 ˚C.

Model comparisons of the 35 ˚C model set revealed more competitive results, however, similar to the 30 ˚C models set, bush wall was present in all top competing models (Table 4.10). Examination of full and conditional model averaged coefficients revealed minor shrinkage however CIs did not overlap zero (Figure 4.15A; Appendix 4.11; Table A4.11). Thicker bush wall was negatively associated with number of hours exposed to 35 ˚C (β = -0.11 CI [-0.20 – -0.03]; Figure 4.15A&B; Appendix 4.11; Table A4.11). There was little support for remaining vegetation and location predictors in the 35 ˚C model set.

Table 4.9: Top models (ΔAICc < 5) for all subsets generalised linear regression model set predicting hours of exposure per day exceeding 30 ˚C of natural nests on Penguin Island based on vegetation, exposure and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*15992.01*	*2212.475*	*0*	*3*	*0*
Ambient temp max + ambient RH max + wind direction + bush wall + year	13779.53	0.00	0.20	9	0.36
Ambient temp max + ambient RH max + wind direction + bush wall + slope + year	13780.00	0.47	0.16	10	0.35
Ambient temp max + ambient RH max + wind direction + wind speed + bush wall + year	13780.56	1.02	0.12	10	0.36
Ambient temp max + ambient RH max + wind direction + wind speed + slope + bush wall + year	13781.00	1.47	0.10	11	0.35
Ambient temp max + ambient RH max + wind direction + wind speed + bush wall + year + wind direction*wind speed	13782.46	2.92	0.05	11	0.36
Ambient temp max + ambient RH max + wind direction + aspect + bush wall + year	13782.54	3.01	0.05	11	0.36
Ambient temp max + ambient RH max + wind direction + species composition + bush wall + year	13782.69	3.16	0.04	11	0.36
Ambient temp max + ambient RH max + wind direction + wind speed + slope + bush wall + year + wind direction*wind speed	13783.40	3.87	0.03	12	0.35
Ambient temp max + ambient RH max + wind direction + slope + bush wall + species composition + year	13783.40	3.87	0.03	12	0.35

Model	AICc	ΔAICc	ω_i	k	$R^2_{marg.}$
Ambient temp max + ambient RH max + wind direction + wind speed + aspect + bush wall + year	13783.55	4.01	0.03	12	0.35
Ambient temp max + ambient RH max + wind direction + wind speed + bush wall + species + year	13783.74	4.21	0.02	12	0.36
Ambient temp max + ambient RH max + wind direction + slope + aspect + bush wall + year	13783.91	4.38	0.02	12	0.35
Ambient temp max + ambient RH max + wind direction + wind speed + slope + bush wall + species + year	13784.44	4.90	0.02	13	0.35

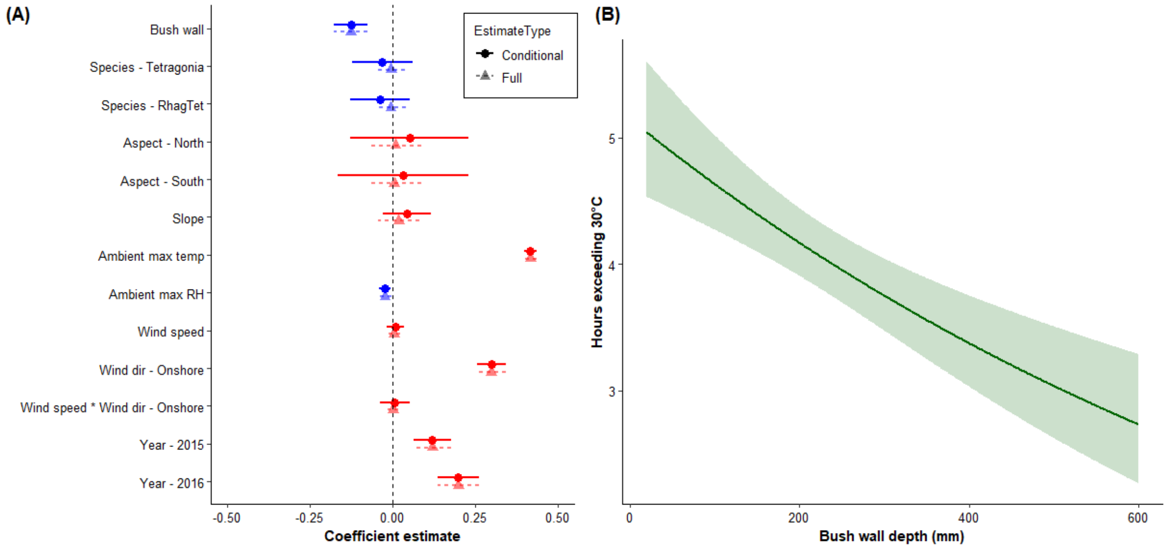

Figure 4.14: (A) Full and conditional model averaged coefficient estimates for effect of vegetation, exposure and local climatic conditions on exposure hours exceeding 30 ˚C of natural nests. **(B)** Predictions from Linear Mixed Models of the effect of bush wall depth on mean daily maximum nest temperature (shaded area represents 95% CI).

Table 4.10: Top models (ΔAICc < 5) for all subsets generalised linear regression model set predicting hours of exposure per day exceeding 35 ˚C of natural nests on Penguin Island based on vegetation, exposure and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*5583.40*	*552.46*	*0.00*	*3*	*0*
Ambient temp max + wind direction + bush wall + year	5030.94	0.00	0.09	8	0.29
Ambient temp max + wind direction + wind speed + bush wall + year	5031.64	0.71	0.06	9	0.29
Ambient temp max + wind direction + bush wall + slope + year	5031.70	0.77	0.06	9	0.28
Ambient temp max + wind direction + bush wall + species + year	5032.01	1.07	0.05	10	0.29
Ambient temp max + wind direction + wind speed + bush wall + year + wind speed * wind direction	5032.04	1.10	0.05	10	0.29
Ambient temp max + wind direction + bush wall + species + slope + year	5032.24	1.31	0.05	11	0.28
Ambient temp max + wind direction at 12pm + wind speed + bush wall + slope + year	5032.43	1.50	0.04	10	0.28
Ambient temp max + wind direction at 12pm + wind speed + bush wall + species + year	5032.75	1.82	0.04	11	0.29
Ambient temp max + wind direction at 12pm + wind speed + bush wall + slope + year + wind speed 12pm * wind direction	5032.78	1.84	0.03	11	0.29
Ambient temp max + ambient RH max + wind direction at 12pm + bush wall + year	5032.87	1.94	0.03	9	0.29
Ambient temp max + wind direction at 12pm + wind speed + bush wall + slope + year	5033.03	2.09	0.03	12	0.28

Model	**AICc**	**ΔAICc**	**ω_i**	**k**	**$R^2_{marg.}$**
Ambient temp max + wind direction at 12pm + wind speed + bush wall + year + wind speed 12pm * wind direction	5033.20	2.27	0.03	12	0.29
Ambient temp max + ambient RH max + wind direction at 12pm + wind speed + bush wall + year	5033.41	2.48	0.03	10	0.29
Ambient temp max + wind direction at 12pm + wind speed + bush wall + species + slope + year + wind speed 12pm * wind direction	5033.42	2.48	0.03	13	0.29
Ambient temp max + ambient RH max + wind direction at 12pm + bush wall + slope + year	5033.64	2.70	0.02	10	0.28
Ambient temp max + ambient RH max + wind direction at 12pm + bush wall + species + year	5033.99	3.05	0.02	11	0.29
Ambient temp max + ambient RH max + wind direction at 12pm + wind speed + bush wall + year + wind speed 12pm * wind direction	5034.01	3.08	0.02	11	0.29
Ambient temp max + ambient RH max + wind direction at 12pm + wind speed + bush wall + slope + year	5034.21	3.27	0.02	11	0.28
Ambient temp max + ambient RH max + wind direction at 12pm + wind speed + bush wall + species + year	5034.22	3.29	0.02	12	0.28
Ambient temp max + wind direction at 12pm + species + year	5034.60	3.66	0.01	9	0.29
Ambient temp max + ambient RH max + wind direction at 12pm + wind speed + bush wall + species + year	5034.60	3.67	0.01	12	0.29
Ambient temp max + ambient RH max + wind direction at 12pm + wind speed + bush wall + slope + year + wind speed 12pm * wind direction	5034.76	3.82	0.01	12	0.29
Ambient temp max + wind direction at 12pm + bush wall + aspect + year	5034.80	3.87	0.01	10	0.29

Model	**AICc**	**∆AICc**	**ω_i**	***k***	**$R^2_{marg.}$**
Ambient temp max + ambient RH max + wind direction at 12pm + wind speed + bush wall + species + slope + year	5034.88	3.94	0.01	13	0.28
Ambient temp max + wind direction + slope + aspect + bush wall + year	5035.03	4.09	0.01	11	0.28
Ambient temp max + ambient RH max + wind direction + wind speed + bush wall + species + year + wind direction*wind speed	5035.21	4.28	0.01	13	0.29
Ambient temp max + wind direction + slope +aspect + bush wall + species + year	5035.24	4.30	0.01	13	0.28
Ambient temp max + wind direction + slope + species + year	5035.32	4.38	0.01	10	0.28
Ambient temp max + wind direction + wind speed + species + year	5035.41	4.48	0.01	10	0.29
Ambient temp max + ambient RH max + wind direction + wind speed + slope + bush wall + species + year + wind direction*wind speed	5035.43	4.49	0.01	14	0.29
Ambient temp max + wind direction + wind speed + aspect + bush wall + year	5035.52	4.59	0.01	11	0.29
Ambient temp max + wind direction + wind speed + slope +aspect + bush wall + year	5035.76	4.83	0.01	12	0.29
Ambient temp max + wind direction + wind speed + species + year + wind direction*wind speed	5035.85	4.92	0.01	11	0.29
Ambient temp max wind direction + aspect + bush wall + species + year	5035.86	4.92	0.01	12	0.29
Ambient temp max + wind direction + wind speed + aspect + bush wall + year + wind direction*wind speed	5035.91	4.97	0.01	12	0.29

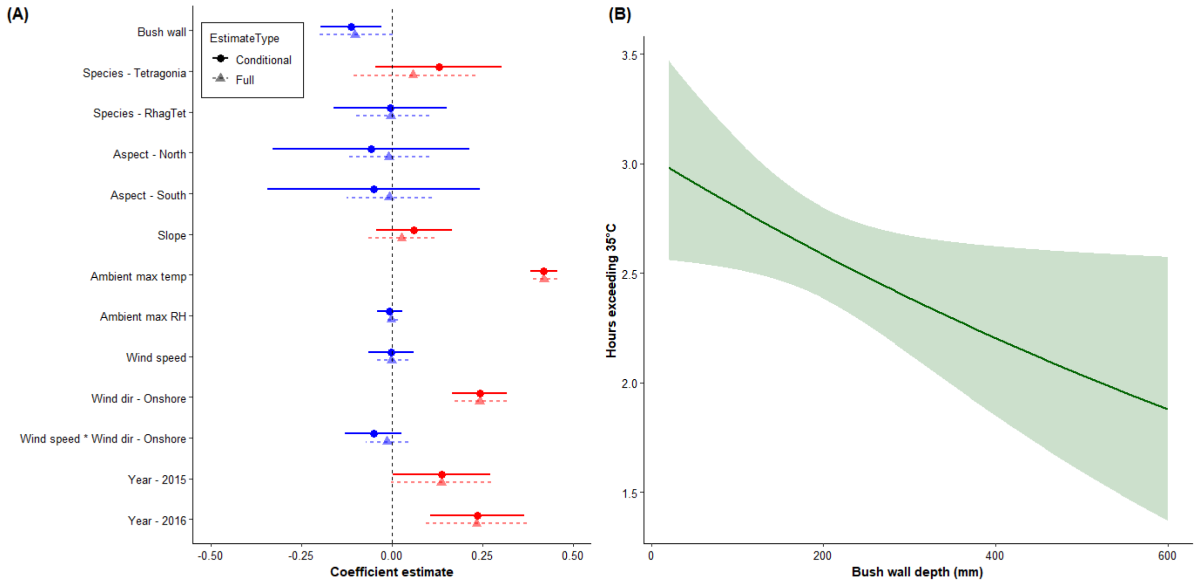

Figure 4.15: (A) Full and conditional model averaged coefficient estimates for effect of vegetation, exposure and local climatic conditions on exposure hours exceeding 35 ˚C of natural nests. **(B)** Predictions from Linear Mixed Models of the effect of bush wall depth on mean daily maximum nest temperature (shaded area represents 95% CI).

4.4.7 Effect of nest site attributes on mean daily maximum temperature of nest boxes

Model selection resulted in 12 competing models and suggested that in addition to daily climate variables, vegetation cover and the presence of vents were influencing maximum nest box temperature (Table 4.11). Models including vegetation cover were well supported, as they were present in all 12 competing models (combined Akaike weight of 0.63). Model averaged coefficients indicated greater vegetation cover was associated lower daily maximum temperature (β = -0.93 CI [-1.77 – -0.09]; Figure 4.16A &B; Appendix 4.12; Table A4.12). While model selection supported the presence of vents as predictor of maximum nest temperature (included in the top five models), this was not reflected in the model averaged coefficients which overlapped zero (β = -1.49 CI [-3.25 – 0.27]; Figure 4.16A-B; Appendix 4.12; Table A4.12) suggesting vents were less important compared to other predictors. There was little evidence to support slope, aspect or box cover as predictors of nest box maximum temperature. While aspect and slope were present in some competing models, model averaged coefficients revealed little support for these predictors. Box cover was not present in any of the top competing models.

Table 4.11: Top models (ΔAICc < 5) for all subsets linear regression model set predicting mean daily maximum temperature of artificial nests (boxes) on Penguin Island based on vegetation, exposure and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R2.

Model	**AICc**	**ΔAICc**	ω_i	***k***	$R^2_{marg.}$
Intercept	*67360.8*	*13896.97*	*0.00*	*5*	*0*
Vegetation cover + vents +aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53463.83	0.00	0.07	19	0.49
Vegetation cover + vents + slope + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53463.92	0.09	0.07	16	0.47
Vegetation cover + vents + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53464.00	0.18	0.07	15	0.46
Vegetation cover + vents + slope + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53464.08	0.25	0.06	18	0.48

Model	AICc	∆AICc	ω_i	k	$R^2_{marg.}$
Vegetation cover + vents + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53464.32	0.49	0.06	17	0.48
Vegetation cover + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53464.45	0.62	0.05	18	0.48
Vegetation cover + slope + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53464.62	0.80	0.05	15	0.46
Vegetation cover + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53464.71	0.88	0.05	16	0.47
Vegetation cover + slope + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53464.82	0.99	0.04	17	0.47
Vegetation cover + vents + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53464.97	1.14	0.04	17	0.47
Vegetation cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53465.40	1.57	0.03	14	0.44

Model	**AICc**	**∆AICc**	ω_i	k	$R^2_{marg.}$
Vegetation cover + vents + slope + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53465.73	1.91	0.03	20	0.49
Vegetation cover + vents + slope + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53466.25	2.42	0.02	18	0.48
Vents + slope + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53466.28	2.45	0.02	15	0.46
Vegetation cover + slope + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53466.40	2.57	0.02	19	0.48
Vegetation cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53466.49	2.66	0.02	16	0.45
Vegetation cover + slope + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53466.68	2.85	0.02	17	0.47
Vents + aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53466.84	3.02	0.02	16	0.47

Model	**AICc**	**∆AICc**	**ω_i**	***k***	**$R^2_{marg.}$**
Vents + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53466.92	3.10	0.02	14	0.45
Vegetation cover + aspect +box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53467.08	3.26	0.01	20	0.49
Vegetation cover + slope + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53467.19	3.37	0.01	17	0.47
Vegetation cover + aspect +box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53467.24	3.41	0.01	18	0.48
Vegetation cover + slope + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53467.29	3.47	0.01	19	0.48
Vegetation cover + vents + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53467.31	3.48	0.01	17	0.47
Vegetation cover + vents + aspect +box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53467.32	3.49	0.01	21	0.49

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Vegetation cover + vents + slope + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53467.34	3.51	0.01	18	0.48
Vegetation cover + vents + slope + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53467.37	3.55	0.01	20	0.49
Vegetation cover + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53467.63	3.80	0.01	16	0.45
Vegetation cover + vents + aspect +box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53467.73	3.90	0.01	19	0.48
Slope + ambient temp max + temp category + ambient RH max + wind speed + wind direction + ambient temp max*temperature category + wind speed* wind direction	53468.18	4.35	0.01	14	0.44
Vegetation cover + vents + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53468.19	4.37	0.01	19	0.47
Aspect + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction	53468.32	4.49	0.01	15	0.45

Model	AICc	ΔAICc	ω_i	k	$R^2_{marg.}$
Vegetation cover + box cover + ambient temp max + temp category + ambient RH max + wind speed + wind direction +ambient temp max*temperature category + wind speed* wind direction +year	53468.66	4.83	0.01	18	0.46

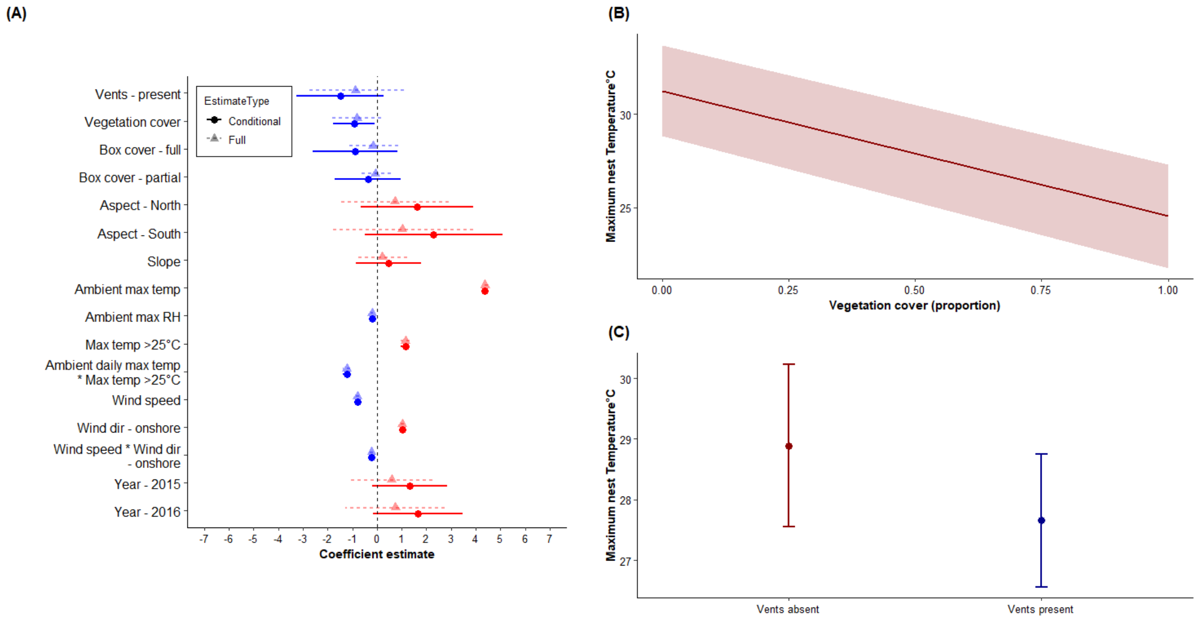

Figure 4.16: (A) Full and conditional model averaged coefficient estimates for effect of vegetation, exposure and local climatic conditions on mean daily maximum temperature in artificial nest boxes. **(B)** Predictions from Linear Mixed Models of the effect of vegetation cover on mean daily maximum nest temperature (Shaded area represent 95% CI). **(C)** Predictions from Linear Mixed Models of the effect nest ventilation on mean daily maximum nest temperature (Shaded area represent 95% CI).

4.4.8 Effect of nest site attributes on nest box exposure hours ≥30 ˚C and ≥35 ˚C

Model selection resulted in seven competing models explaining exposure time to temperatures exceeding 30 ˚C. Model comparisons suggested that in addition to climate predictors, vegetation cover and the presence of vents were the only other important predictors determining nest box exposure hours. Models with the vegetation cover and vents were well supported, with both variables present in all seven competing models (combined Akaike weight of 0.62; Table 4.12). Model averaged coefficients indicated greater vegetation cover limited exposure to temperatures exceeding 30 ˚C (β = -0.12 CI [-0.17 – -0.07]; Figure 4.17A&B; Appendix 4.13; Table A4.13). Vents had a similar effect and were associated with reduced exposure time (β = -0.15 CI [-0.27 – -0.02]; Figure 4.17A&C; Appendix 4.13; Table A4.13).

Comparisons of the best models relating exposure time to temperatures exceeding 35 ˚C revealed seven competing models. In addition to ambient temperature, wind direction and year, models including vegetation cover and vents were well supported, with both variables present in all seven competing models (combined Akaike weight of 0.62; Table 4.13). Model averaged coefficients indicated greater vegetation cover limited exposure to temperatures exceeding 35 ˚C (β = -0.12 CI [-0.20 – -0.04]; Figure 4.18A&B; Appendix 4.14; Table A4.14). Vents had a slightly larger effect, limiting exposure time (β = -0.24 CI [-0.43 – -0.05]; Figure 4.18A&C; Appendix 4.14; Table A4.14).

Table 4.12: Top models (ΔAICc < 5) for all subsets generalised linear regression model set predicting hours of exposure per day exceeding 30 ˚C of artificial nest boxes on Penguin Island based on vegetation, exposure and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo $R^{2.}$

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*19978.29*	*2638.83*	*0.00*	*3*	*0*
Vegetation cover + vents + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17339.46	0.00	0.13	15	0.37
Vegetation cover + vents + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17339.59	0.12	0.12	14	0.37
Vegetation cover + vents + slope + aspect + ambient temp max + ambient RH max + wind direction + year	17339.97	0.51	0.10	13	0.37
Vegetation cover + vents + aspect + ambient temp max + ambient RH max + wind direction + year	17340.09	0.63	0.09	12	0.37
Vegetation cover + box cover + vents + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17340.73	1.26	0.07	17	0.37
Vegetation cover + box cover + vents + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17341.17	1.71	0.06	16	0.37
Vegetation cover + box cover + vents + slope + aspect + ambient temp max + ambient RH max + wind direction + year	17341.23	1.77	0.05	15	0.37

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Vegetation cover + vents + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction +year	17341.98	2.52	0.04	14	0.37
Vegetation cover + box cover + vents + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17342.10	2.63	0.03	13	0.37
Vegetation cover + box cover + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17343.05	3.58	0.02	16	0.37
Vegetation cover + box cover + vents + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction +year	17343.24	3.78	0.02	16	0.37
Vegetation cover + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17343.31	3.85	0.02	14	0.37
Vegetation cover + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17343.32	3.86	0.02	13	0.36
Vegetation cover + box cover + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	17343.40	3.93	0.02	15	0.36
Vegetation cover + box cover + slope + aspect + ambient temp max + ambient RH max + wind direction + year	17343.54	4.07	0.02	14	0.36
Vegetation cover + box cover + vents + aspect + ambient temp max + ambient RH max + wind speed + wind direction + year	17343.69	4.23	0.02	15	0.37

Model	AICc	ΔAICc	ω_i	k	$R^2_{marg.}$
Vegetation cover + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + year	17343.78	4.32	0.01	12	0.37
Vegetation cover + slope + aspect + ambient temp max + ambient RH max + wind direction + year	17343.78	4.32	0.01	11	0.36
Vegetation cover + box cover + aspect + ambient temp max + ambient RH max + wind direction + + year	17343.89	4.42	0.01	13	0.36

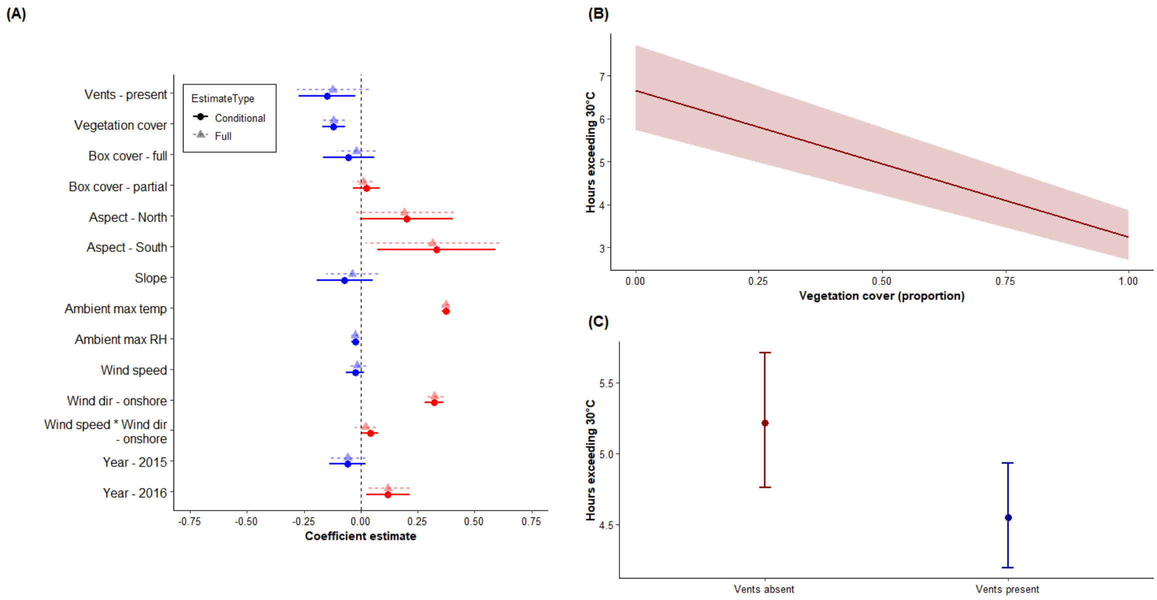

Figure 4.17: (A) Full and conditional model averaged coefficient estimates for effect of vegetation, exposure and local climatic conditions on exposure hours exceeding 30˚C of artificial nest boxes. **(B)** Predictions from Generalised Linear Mixed Models of the effect of vegetation cover on exposure hours exceeding 30˚C (Shaded area represent 95% CI). **(C)** Predictions from Generalised Linear Mixed Models of the effect nest ventilation on exposure hours exceeding 30˚C (shaded area represents 95% CI).

Table 4.13: Top models (ΔAICc < 5) for all subsets generalised linear regression model set predicting hours of exposure per day exceeding 35 ˚C of artificial nest boxes on Penguin Island based on vegetation, exposure and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), model weight (ωi), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Intercept	*9118.17*	*900.99*	*0.00*	*3*	*0*
Vegetation cover + vents + slope + aspect + ambient temp max + wind speed + wind direction +year	8217.18	0.00	0.10	13	0.30
Vegetation cover + vents + aspect + ambient temp max + wind speed + wind direction +year	8217.35	0.17	0.09	12	0.28
Vegetation cover + vents + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction +year	8218.28	1.11	0.06	14	0.30
Vegetation cover + vents + aspect + ambient temp max + ambient RH max + wind speed + wind direction +year	8218.45	1.27	0.05	13	0.28
Vegetation cover + vents + ambient temp max + wind speed + wind direction +year	8218.69	1.51	0.05	10	0.26
Vegetation cover + vents + slope + aspect + ambient temp max + wind speed + wind direction + wind speed* wind direction +year	8218.86	1.68	0.04	14	0.30
Vegetation cover + vents + aspect + ambient temp max + wind speed + wind direction + wind speed* wind direction +year	8219.02	1.84	0.04	13	0.28
Vegetation cover + vents + slope + aspect + ambient temp max + wind speed + wind direction +year	8219.77	2.59	0.03	11	0.26
Vegetation cover + vents + ambient temp max + ambient RH max + wind speed + wind direction +year	8219.79	2.61	0.03	11	0.26

Model	**AICc**	**ΔAICc**	**ω_i**	***k***	**$R^2_{marg.}$**
Vegetation cover + vents + slope + aspect + ambient temp max + wind speed + wind direction + box cover + year	8219.94	2.76	0.03	15	0.29
Vegetation cover + vents + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	8220.11	2.93	0.02	15	0.30
Vegetation cover + vents + aspect + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	8220.27	3.09	0.02	14	0.28
Vegetation cover + vents + aspect + box cover + ambient temp max + wind speed + wind direction + year	8220.34	3.16	0.02	14	0.28
Vegetation cover + vents + ambient temp max + wind speed + wind direction + wind speed* wind direction +year	8220.37	3.19	0.02	11	0.26
Vegetation cover + vents + slope + ambient temp max + ambient RH max + wind speed + wind direction + year	8220.87	3.69	0.02	12	0.26
Vegetation cover + vents + slope + aspect ambient temp max + wind direction + year	8221.00	3.83	0.02	12	0.29
Vegetation cover + vents + slope + aspect + box cover + ambient temp max + ambient RH max + wind speed + wind direction + year	8221.04	3.87	0.01	16	0.29
Vegetation cover + vents + aspect + ambient temp max + wind direction + year	8221.17	3.99	0.01	11	0.28
Vegetation cover + vents + slope + ambient temp max + wind speed + wind direction + wind speed* wind direction +year	8221.44	4.26	0.01	12	0.26
Vegetation cover + vents + box cover + ambient temp max + wind speed + wind direction + year	8221.44	4.26	0.01	12	0.26

Model	**AICc**	**ΔAICc**	ω_i	k	$R^2_{marg.}$
Vegetation cover + vents + aspect + box cover + ambient temp max + ambient RH max + wind speed + wind direction + year	8221.45	4.27	0.01	15	0.28
Vegetation cover + slope + aspect + ambient temp max + ambient RH max + wind speed + wind direction + year	8221.57	4.39	0.01	12	0.28
Vegetation cover + vents + ambient temp max + ambient RH max + wind speed + wind direction + wind speed* wind direction +year	8221.60	4.43	0.01	12	0.26
Vegetation cover + vents + slope + aspect + box cover + ambient temp max + wind speed + wind direction + wind speed* wind direction +year	8221.63	4.46	0.01	16	0.29
Vegetation cover + aspect + ambient temp max + wind speed + wind direction + year	8221.79	4.61	0.01	11	0.26
Vegetation cover + vents + aspect + box cover + ambient temp max + wind speed + wind direction + wind speed* wind direction +year	8222.02	4.85	0.01	15	0.28

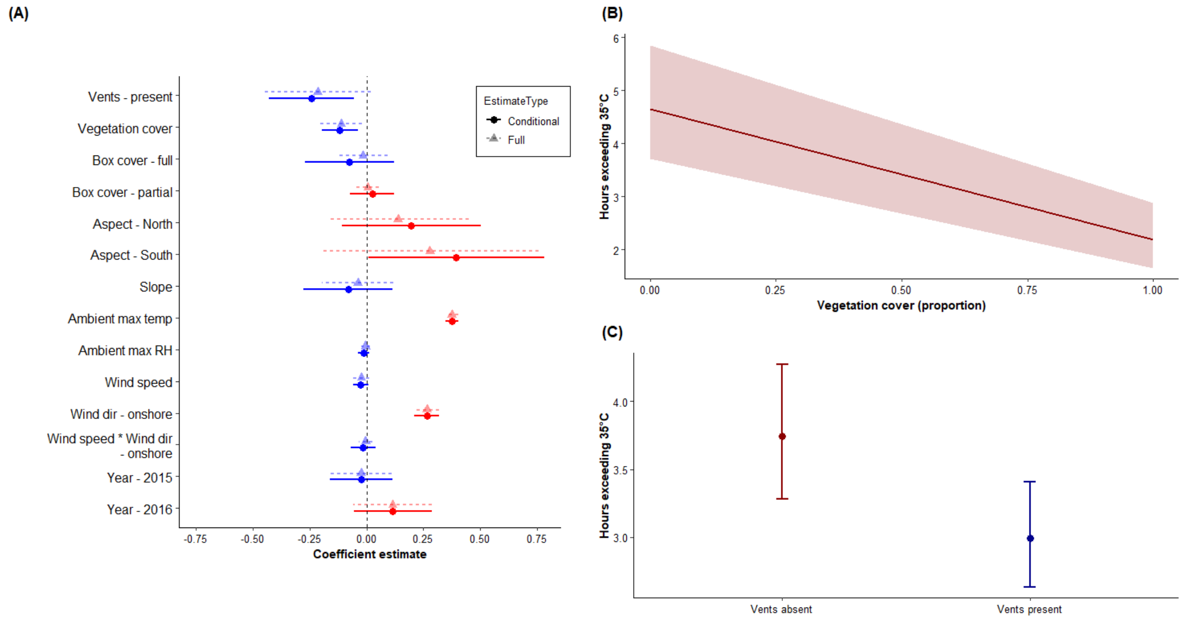

Figure 4.18: (A) Full and conditional model averaged coefficient estimates for effect of vegetation, exposure and local climatic conditions on exposure hours exceeding 35˚C of artificial nest boxes. **(B)** Predictions from Generalised Linear Mixed Models of the effect of vegetation cover on exposure hours exceeding 35˚C (shaded area represent 95% CI). **(C)** Predictions from Generalised Linear Mixed Models of the effect nest ventilation on exposure hours exceeding 35˚C (shaded area represent 95% CI).

4.4.9 Future nest climate predictions

An increase by 2 ˚C of ambient temperature led to nest boxes exceeding 30 ˚C in all months with the greatest frequency being observed in January (82% / ~25 days) and February (85% / ~24 days) (Figure 4.19). The frequency of days will increase across all months with large increases predicted between May and August; the largest increase (>600%) predicted for July. Days exceeding 35 ˚C are predicted to occur from September through April. The highest frequency of days predicted to occur in January (42% / ~13 days) and February (43% / ~12 days).

Natural nests are predicted to record days exceeding 30 ˚C in all months except June, July and August (Figure 4.19). January and February are predicted to record the highest frequency of days (66% / ~20 days and 68% / ~ 19 days respectively). The largest predicted increases from current conditions will occur in April and May. Days exceeding 35 ˚C are predicted to occur between November and April. As with nest boxes, January and February are likely to record the greatest frequency of days (25% / ~7 days and 22% / ~6 days respectively). The greatest predicted increase from current conditions will be observed in April.

The mean number of hours per day exceeding 30 ˚C is predicted to be greatest in nest boxes during the months of January and February (~7 hours and ~6 hours respectively; Figure 4.20). However, all months are predicted to record at least one hour above this threshold. An increase from current conditions is predicted to occur in all months with May, June, July, August and September predicting the largest increases. Hours exceeding 35 ˚C will also be greatest in January (~4.5 hours) and February (~4 hours). The number of hours will increase from current conditions in all months except July.

In natural nests, all months except July are predicted to observe increases in the number of hours exceeding 30 ˚C (Figure 4.20). In January nests are predicted to be exposed to an average of 7.5 hours. Natural nests are likely to observe greater increases than nest boxes across all months of the year except July. The time spent over 35 ˚C will exceed two hours in January and February.

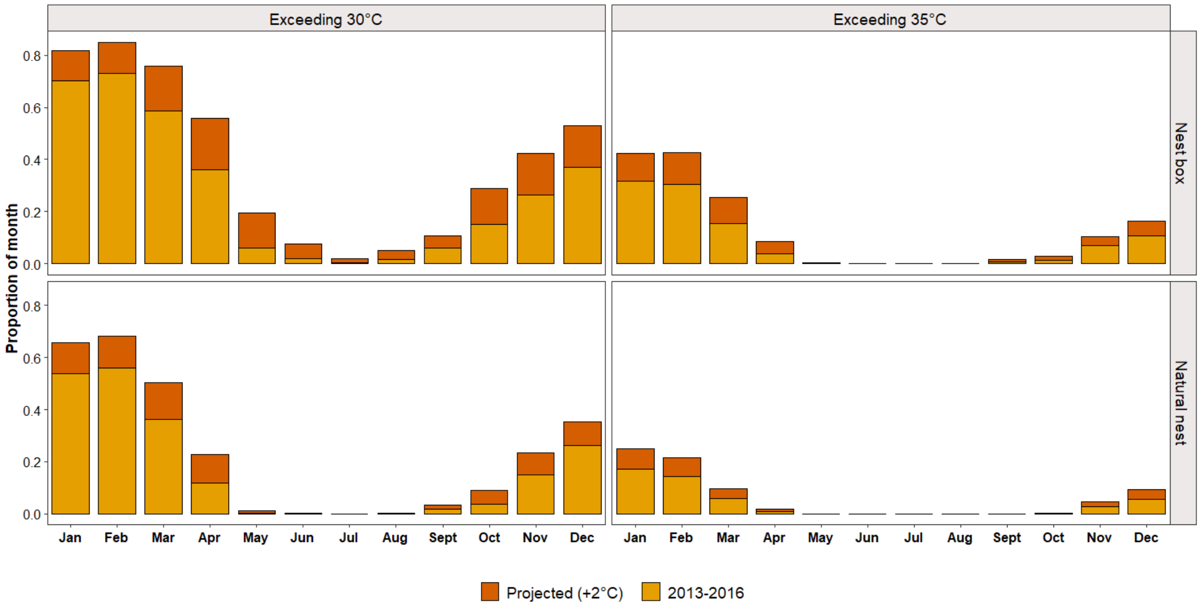

Figure 4.19: Model predicted mean proportion of days per month exceeding 30˚C and 35C at current climate and 2˚C increase in daily maximum temperatures.

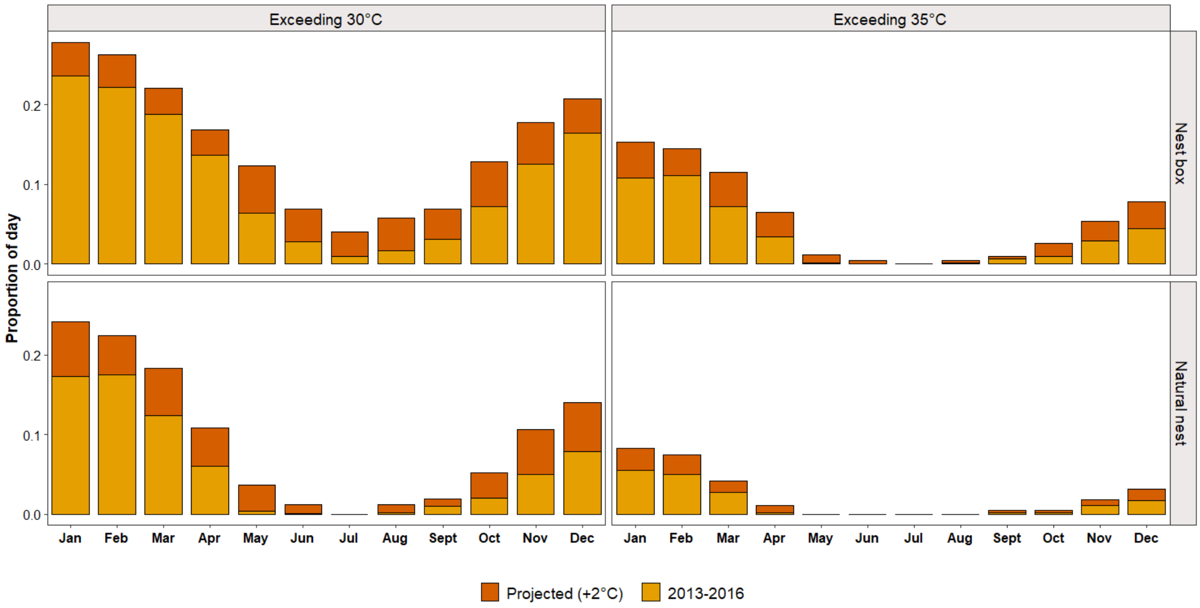

Figure 4.20: Model predicted mean proportion of hours per days exceeding 30˚C and 35˚C at current climate and 2˚C increase in daily maximum temperatures.

4.5 Discussion

Results from this study demonstrate that artificial nest boxes provided for little penguins on Penguin Island did not provide microclimate conditions representative of natural nests and had a narrower daily and annual window with thermoneutral nest conditions. Artificial nest boxes experienced consistently higher daily maximum temperature and longer hours exposed to temperatures exceeding upper thermoneutral limits. Despite this, both nest types were limited in their buffering capacity, exposing penguins to potentially dangerous thermal conditions, particularly as revealed by modelling of a 2 ˚C climate change impact. As expected, thermal properties of nests were strongly influenced by local climate conditions, specifically ambient temperature. However fine scale biotic and abiotic nest characteristics also influenced the maximum daily temperature and hours of exposure to upper thermoneutral limits. Nest temperature is likely to rise under future climate scenarios and extreme conditions inside little penguin nests are predicted to increase in frequency and intensity. Results from my study highlight the need to continue to investigate the suitability of both natural and artificial nesting habitat under current and future climate scenarios and emphasises that careful consideration be given to the design and placement of artificial nests to ensure conditions remain within thermoneutral limits.

4.5.1 Microclimate of artificial nest boxes and natural nests

Natural and artificial nests followed a similar daily thermal profile and had a comparable response to changes in local climate conditions. However, artificial nests invariably reached higher maximum temperatures and more frequently exceeded temperatures likely to cause significant thermal stress (30 ˚C) or hyperthermia (35 ˚C). Furthermore, for nests that exceeded thermoneutral limits, artificial nests maintained these temperatures for longer periods of time. The difference in thermal properties of artificial and natural nests reported here augment findings of Ropert-Coudert *et al.* (2004) who found little penguin artificial nest box temperatures on Penguin Island were warmer than surrounding bushes by 2.73 ± 1.65 ˚C. Similar results have been observed in other little penguin colonies. In Tasmania, artificial little penguin nests recorded higher temperatures than nests located in vegetation (Marker 2016). Similarly, artificial nests of African penguins (*Spheniscus demersus*) were consistently hotter than natural burrows and maintained elevated temperatures for longer periods of time (Lei *et al.* 2014). These findings support the growing literature highlighting the inadequacy of many artificial nests at replicating conditions of natural nests for a range of vertebrate fauna (Isaac *et al.* 2008; Lei *et al.* 2014; Rowland *et al.* 2017; Griffiths *et al.* 2018).

The elevated temperature observed in artificial nests meant that upper thermoneutral limits were exceeded earlier in the breeding season than natural nests, often during spring, when penguins are still actively nesting. This effectively shortens the annual thermoneutral zone in artificial nests thus limiting the period where conditions may be considered optimal for nesting. An increase in daily maximum temperature predicted under future climate scenarios would shorten this period further, reducing the optimal nesting period to only 6 months. This may have significant reproductive consequences. For adults and chicks present in nests during spring, thermostatic demands are heightened thus reducing energy allocation to reproduction and consequently reproductive success (Bryan and Bryant 1999; Pérez *et al.* 2008). Furthermore, annual changes in oceanographic conditions and food availability often influence the timing and duration of breeding in many seabirds (Numata *et al.* 2000; Perriman *et al.* 2000; Ramos *et al.* 2002; Cullen *et al.* 2009; Wanless *et al.* 2009; Cannell *et al.* 2012). Therefore, a shift to breeding later in the year coupled with warmer nest temperatures could result in significant asynchrony between food availability and optimal nesting conditions for this colony.

The length of time artificial nests maintained thermal extremes was concerning. Temperatures above 30 ˚C are considered stressful for adult little penguins (and thus probably chicks as their ability to thermoregulate is limited) and extended periods (more than two hours) exceeding 35 ˚C are likely to induce hyperthermia (Stahel and Nicol 1982; Horne 2010). Furthermore, prolonged exposure to very extreme temperatures could inhibit proper egg development (Webb 1987). Once reaching 30 ˚C or 35 ˚C, artificial nests maintained temperatures above these thresholds on average 5.6 hours and 4.1 hours, respectively. This far exceeds what might be considered safe for penguin occupants and in some cases may be fatal. The direct effect of extreme heat on penguin reproduction was observed in an African penguin colony where extreme temperature resulted in significant egg and chick mortality (Kemper *et al.* 2007) and several authors report nest abandonment during periods of excessive heat (e.g. Pichegru 2012; Sherley *et al.* 2012).

It was expected that natural nests would be cooler than boxes however they too had limited buffering capacity particularly when ambient temperatures were high. This is inconsistent with observed thermal properties reported for many other cavity nesting seabirds where burrow conditions are generally reported to be more stable than ambient conditions (Boersma 1986; Marker 2016; Kulaszewicz and Jakubas 2018). Many cavity nesting seabirds excavate deep soil burrows thus the high thermal inertia of soil assists in maintaining a stable internal environment. While little penguins are often described as burrow nesting, they inhabit a variety of cavity types including soil burrows, rock crevices artificial structures and vegetation (Stahel and Gales 1987; Marchant and Higgins 1990; Dann 2013). This plasticity allows them to occupy a wider range of environments. However, Marker (2016) found the temperature profiles varied substantially between different burrow types. Grass and soil burrows had more stable daily temperatures than nests located in other vegetated nest types. For penguins inhabiting regions where temperatures are unlikely to fall below lower thermoneutral limits, it is possible that stability of the nest environment may be less important and, in some cases, could even promote development of unattended eggs during cooler months

(Boersma 1982). While this may be true for population existing at higher latitudes, for those populations at warmer climates, acquiring a nest that can protect contents from unfavourable environmental conditions will become critical.

Natural nests could reach extreme temperatures considered stressful and potentially lethal to little penguins. Nests frequently exceeded upper thermoneutral limits and often recorded temperatures more than 40 ˚C. Natural nests remained at temperatures above 30 ˚C and 35 ˚C for on average 4.7 and 3 hours, respectively. Most of these records occurred outside of the nesting season and such are unlikely to be significantly impacting nesting penguins. Nonetheless, little penguins on Penguin Island continue to utilise nest sites during the summer months to carry out their annual moult (December to March). Under current conditions more than half of days in January and February exceed 30 ˚C and 20% of days exceed 35 ˚C. This means that penguins moulting during this time could potentially spend almost their entire moult (~17 days; Reilly and Cullen 1983) with daily exposure to thermally stressful conditions and four to five days of their moult exposed to potentially lethal conditions. Under future climate scenarios, risk of exposure to thermally stressful or lethal conditions increases further still.

To sustain their moult little penguins use 15% more energy than they would under normal rest conditions (Gales *et al.* 1988). As air temperature rises, hyperventilation can further enhance energy demands (Baudinette *et al.* 1986). Little penguins are unable to forage during moult, consequently using excess energy could increase the risk of starvation. On Penguin Island, hyperthermia accounted for 5% of mortality of dead penguins necropsied from 2003 - 2012 (Cannell *et al.* 2016). While heat stressed little penguins have been observed retreating to the water to cool down, this has only been observed when there is no perceived threat such as the presence of humans (E Clitheroe, pers. obs.) thus during the summer months when visitation is high, the risk of mortality from hyperthermia is exacerbated. On Phillip Island, Victoria, the number of days exceeding 27 ˚C was found to negatively affect adult little penguin survival (Ganendran *et al.* 2016; Ganendran 2017) and heat stress accounted for 1.7% of land based mortality of little penguins between 1986 - 1989 (Dann 1992). Increased mortality is a key factor driving population stability of little penguins thus management strategies should focus on minimising mortality during moult (Dann 1992).

4.5.2 Predictors of nest temperature in natural nests and nest boxes

Natural nest temperature was strongly influence by local climate conditions as well as the slope of the ground and the thickness of the nest bush wall. Natural nests located on steeper slopes reached higher daily maximum temperatures however slope was not an important predictor on the exposure hours above thermoneutral limits. This was unexpected as typically, steeper slopes receive lower solar radiation (Buffo 1973). However, slope gradient strongly influences the availability of water for plants thus a steeper slope may affect temperature through influencing the amount and condition of vegetation (Zhang *et al.* 2013). Nests located within bushes with thicker walls reached lower daily maximum temperatures. More importantly, bush wall was significantly influential in reducing the number of hours exceeding thermoneutral limits indicating that bush wall is an important factor in moderating nest temperatures. Thicker vegetation likely provides greater insulation and has additional cooling properties through evapotranspiration (Huang *et al.* 1987). Several authors have demonstrated the importance of vegetation in moderating nest temperature. For example, a study on lesser black backed gulls reported reduced daily nest temperatures with increased vegetation height (Kim and Monaghan 2005).

In nest boxes, local climate was also the most important factor driving temperature. However, vegetation cover and the presence of ventilation holes were found to attenuate nest box temperatures. High vegetation cover decreased daily maximum temperatures in nest boxes and had significant negative effect on the hours a nest exceeded thermoneutral limits. Higher vegetation cover likely limits solar insolation thus nest temperatures are reduced; an effect reported by several authors (Isaac *et al.* 2008; Rowland *et al.* 2017; Larson *et al.* 2018). However, in addition to shading, areas with high vegetation cover are likely to lower ambient temperature through evapotranspiration, limiting heat transfer to a box and thus lowering nest temperature. Contrary to expectations, the vegetation cover directly over the box lid was not found to be an important predictor of nest box temperature. This is possibly due to many nest boxes with low box cover over the lid being positioned under a canopy vegetation thus masking the effect of lid cover. Further investigation assessing the effect of direct cover over nest boxes on nest temperature would be beneficial to help understand these effects.

In addition to biotic variables, the presence of ventilation holes had a strong effect on the exposure hours of a nest to upper thermoneutral limits. Ventilation holes reduced the time a nest box maintained temperature above 30 ˚C and 35 ˚C by approximately one hour. Ventilation allows for more effective air flow through the nest thus hot air can escape sooner than it would if ventilation were absent. The effect of ventilation on artificial nest temperature has not been extensively examined, but some authors have suggested ventilation to be an important factor for reducing temperature of artificial penguin nests (Ropert-Coudert *et al.* 2004; Lei *et al.* 2014). In contrast to this, a study examining temperature of little penguin nests in Tasmania found no significant difference between thermal properties of nest boxes with and without holes. (Marker 2016). This may be due to the different thermal ranges experienced at the two locations.

4.5.3 Management Implications

Nest boxes are an important tool used in the conservation and management of seabird colonies globally and in many cases have proven successful in increasing breeding effort, breeding success and population in little penguins and other seabirds (Perriman and Steen 2000;

de León and Mínguez 2003; Bolton *et al.* 2004; Libois *et al.* 2012; Sutherland *et al.* 2014). Here, I have demonstrated that nest boxes on Penguin Island do not reflect the thermal conditions of natural nests and potentially expose penguin occupants to thermally stressful conditions. Many artificial nests currently used by little penguins on Penguin Island potentially present an ecological trap as these seemingly poor quality habitats are readily used by little penguins potentially leading to reduced fitness for individuals using boxes over natural nest sites. This could have potential negative effects on survival and breeding outcome and thus overall stability of the population. While some nest boxes did not provide thermal conditions representative of natural nests, their use as a conservation tool remains critically relevant. However, careful consideration must be given to the design and placement of artificial nests to ensure conditions remain within thermoneutral limits. Future use of artificial nests on Penguin Island may necessitate either the application of an alternative design or modification of existing boxes. Ensuring artificial nests have high vegetation cover and increased ventilation could potentially reduce box temperatures to reflect natural nest conditions more closely.

This study also highlighted that under current conditions natural habitat available to little penguins may not be adequate throughout all stages of their annual life cycles. Climate models predict increased ambient temperature and reduced rainfall for this region which will certainly decrease quality and availability of little penguin nesting and moulting habitat. Given the importance of thick vegetation in moderating temperature of natural nests, the potential for climate change to reduce vegetation quality is concerning. Mitigation efforts might seek to ensure focus on the conservation and restoration of quality vegetation however must consider how this habitat will be modified under future climate change scenarios. Ideally future revegetation should include establishment of drought tolerant species which can provide thickness and durability required for minimising nest temperatures throughout the year.

The persistence of rear edge populations will require the implementation of adaptation strategy based on a comprehensive understanding of how climate change is altering microhabitat conditions and thus habitat suitability at range edges (Hannah *et al.* 2002; Mawdsley *et al.* 2009; Hannah *et al.* 2014; Varner and Dearing 2014). This study provides insight into how predicted changes in climate may impact edge populations living at their thermal limit and highlights the conservation implications of informed habitat management and use of artificial nests.

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CHAPTER 5

Artificial nests as a climate adaptation tool: buffering climate change effects on the little penguin (*Eudyptula minor)*

5.1 Abstract

Climate change is likely to result in increased frequency and intensity of extreme weather events, posing a significant threat to biodiversity and ecosystem functioning. Populations inhabiting the latitudinal margins of a species' range are particularly susceptible to negative effects posed by climate change and their persistence may rely on implementation of effective adaptation strategies. Provision of artificial nests has a long history of use in the conservation and management of a wide range of fauna. Climate change is certain to continue to change habitat availability and quality thus the reliance on artificial nests is becoming more pertinent. Despite recent evidence that artificial nests are inadequate at replicating conditions of natural cavities, there has been remarkably little investigation into ways in which to modify artificial nests such that they more effectively replicating the microclimate of natural cavities. This study quantified the effectiveness of two nest designs and shading methods in buffering artificial nest temperature. Experimental manipulation of boxes and shading revealed nest design and shading methods were effective at reducing nest temperature. Compared to exposed boxes, artificial shading and shading vegetation had the greatest buffering effect, significantly lowering maximum nest temperature by around 4.5 ˚C and reducing the hours of exposure to upper thermoneutral limits by up to approximately one hour. These findings highlight the importance of shading vegetation in moderating nest temperature and provide insight into the

potential consequences of uninformed provision of artificial nests. Future work should continue to investigate alternate methods of insulating or shading artificial nests.

5.2 Introduction

Effects of climate change on biotic systems will be profound. The IPCC (2018) estimate that global temperature is currently increasing at 0.2 ˚C per decade with average global air temperature likely to rise by 1.5 ˚C above pre-industrial levels between 2030 and 2052. Amongst other effects, the frequency and intensity of extreme weather events, such as heat waves, droughts, and tropical cyclones, will increase, posing a significant threat to biodiversity and ecosystem functioning (Jentsch and Beierkuhnlein 2008; Wernberg *et al.* 2013; IPCC 2018). Impacts on biotic systems are expected to intensify resulting in significant changes in the physiology, phenology and distribution of taxa around the world (Chambers *et al.* 2005; Lawler 2009; Hoegh-Guldberg and Bruno 2010; Dawson *et al.* 2011; Young *et al.* 2012; Cahill *et al.* 2013; Diffenbaugh and Field 2013; Jones and Cheung 2015).

Understanding and predicting the effects of climate change is a critical component in responding to challenges associated with climate change (Hannah *et al.* 2002; Mawdsley *et al.* 2009). However, an area gaining considerable interest, is the identification and anticipatory implementation of adaptation strategies which are aimed at reducing negative effects posed by climate change (Mawdsley *et al.* 2009; Stein *et al.* 2013; IPCC 2018). This will be of particular significance in the conservation of populations inhabiting the latitudinal margins of a species' range and particularly so for species that have limited dispersal capacity or a narrow habitat niche (Thomas *et al.* 2004; Rehm *et al.* 2015). Reports of local extinctions and reduced population growth at range edges are growing (Jump *et al.* 2006; Jiguet *et al.* 2010; Wiens 2016). For example, the common guillemot (*Uria aalge*) which once had its largest breeding population at the low latitude limit of the species breeding range, is now considered quasi-extinct at this location (Munilla *et al.* 2007). Edge populations are becoming increasingly important for predicting species' responses to expected trends in climate change (Hampe and

Petit 2005; Grémillet and Boulinier 2009). Furthermore, *in situ* adaptation of edge populations may be critical in avoiding climate driven extinction (Thomas *et al.* 2004; Rehm *et al.* 2015).

The use of artificial nests or refuges is fundamental in the conservation and management of a variety of taxa (Bolton *et al.* 2004; Harley 2006; Priddel *et al.* 2006; Corrigan *et al.* 2011; Libois *et al.* 2012; Goldingay *et al.* 2015; Macak 2020). In seabirds they are used in a number of contexts including the establishment or translocation of seabird colonies (Priddel *et al.* 2006; Miskelly *et al.* 2009; Carlile *et al.* 2012), monitoring/research (Wilson 1986; Podolsky and Kress 1989; Klomp *et al.* 1991; Wilson 1993; Bolton 1996; Perriman and Steen 2000; Johannesen *et al.* 2002), and the provision or restoration of seabird nesting habitat (Priddel and Carlile 1995; Gaston 1996; Houston 1999; Lalas *et al.* 1999; Kemper *et al.* 2007). However, in many cases artificial nests are deployed with limited knowledge on the suitability of the microclimate and the potential consequences and associated risks of providing suboptimal environments for inhabitants.

The microclimate of a nest is critically important to egg and chick development and may have significant influence on the outcome of a breeding attempt. Nest temperature and humidity have been linked to a number of reproductive parameters including clutch size, embryonic development, chick growth and survival (Wiebe 2001; Larson *et al.* 2015; Bobek *et al.* 2018). Artificial nests are often limited in their buffering capacity and inadequate at replicating conditions of natural nests; generally, they experience more variable temperatures and are hotter and drier than natural nests across a range of habitat types and climates (Ropert-Coudert *et al.* 2004; Lei *et al.* 2014; Maziarz *et al.* 2017; Rowland *et al.* 2017). Despite the growing evidence supporting the apparent mismatch between the microclimate of artificial and natural nests, there has been remarkably little investigation into ways in which to modify artificial nests such that they are providing suitable nesting environments. The few recent studies have suggested modifications and aspects of design and placement that may be beneficial for improving the thermal properties of nest boxes including, using heat reflective paint (Griffiths *et al.* 2017) ; carving nests from natural logs (Griffiths *et al.* 2018); the use of insulative materials (Larson *et al.* 2018); and positioning nests to reduce sub exposure (Griffiths *et al.* 2017). However, few of these studies examined the degree to which modified nests effectively replicate the microclimate of natural cavities. Furthermore, consideration should be given to the potential for conditions within natural nests to become unfavourable under climate change. Thus ultimately, the persistence of some populations may require artificial nests to perform better thermally.

Like most seabirds, the little penguin (*Eudyptula minor*) is vulnerable to the effects of changing climate in multiple, complex dimensions given their reliance on both marine (foraging) and terrestrial (breeding) habitats. Their need to remain on land during incubation, chick rearing and moulting means exposure to potentially unfavourable thermal conditions is unavoidable. Cold-water adaptations make little penguins more vulnerable to high temperature during the nesting and moulting phase of their life cycle. Little penguins rely on hyperventilating along with additional behavioural traits (e.g. landing at night and burrow nesting) to maintain thermal homeostasis (Stonehouse 1976; Stahel and Nicol 1982; Baudinette *et al.* 1986) with increases in both temperature and humidity impairing heat dissipation (Gerson *et al*. 2014). In little penguins, hyperthermia may develop quickly as tolerance for temperatures exceeding 35 ˚C is thought to be only a few hours for adults (likely less for chicks) (Stahel and Nicol 1982). Furthermore, temperature is accepted to be a critical mechanism affecting viability of eggs (Grant 1982; Webb 1987; Beissinger *et al.* 2005). For many avian taxa thermal tolerance during incubation ranges between 16 to 41 ˚C (Webb 1987) and extended exposure to high temperatures can affect the development and hatchability of eggs or cause hyperthermia in nestlings (Webb 1987; Beissinger *et al.* 2005). Projected rises in temperatures combined with the increased frequency and intensity of extreme weather events could have profound consequences for this species including increased adult and chick mortality and reduced breeding success (Dann and Chambers 2009).

Penguin Island, Western Australia, is home to a genetically distinct population (Cannell *et al.* 2012) of little penguins at the extreme northwestern limit of the species range. This 'rear edge' population is highly valuable for exploring climate change effects on this species. In the last decade Penguin Island's little penguin colony has undergone a considerable population decline of more than 50% (Cannell 2018). This decline is largely attributed to lowered breeding performance; resulting from reduced prey abundance and distribution caused by warmer ocean conditions (Cannell *et al.* 2012, Cannell pers. comm.). However, in addition to marine based impacts, warmer and drier terrestrial conditions could have compounding effects, reducing both the quality and availability of important nesting vegetation further degrading the demographic stability of this colony. Consequently, the provision of artificial nests has gained prominence as a conservation and management strategy.

Timber nesting boxes have been present at Penguin Island for 30+ years but evidence suggests their environments are becoming hotter (DBCA. Unpub. Data). Future use of artificial nests may necessitate either the application of an alternative design or modification of existing boxes, the latter being the preferred option for currently occupied boxes. One possible method for influencing nest temperature of existing nest boxes is reducing solar exposure through artificial shading (Kelsey *et al.* 2016b; Olson 2017). Given accelerating temperature change, this study set out to experimentally test the most important determinants of nest box temperature and identify key elements of design and placement. Using two designs and three methods of shading, I monitored nest boxes for 2.5 years over three little penguin breeding cycles. Therefore, I sought to determine the nest box climate in relation to box type/design and shading type. Such information provides critical insight into appropriate management measures for little penguin persistence and to provisioning of artificial habitats globally, especially seabirds.

5.3 Methods

5.3.1 Study area

A description of the study area is outlined in Chapter 3.

5.3.2 Study Species

A description of the study species is outlined in Chapter 3.

5.3.3 Study design

To test the effects of design and shading on the microclimatic properties of artificial nests, 36 artificial nests encompassing two nest designs and four shading treatments (total six combinations) were installed on Penguin Island in 2014. Temperature and relative humidity were recorded continuously between June 2014 and January 2017 (three breeding cycles).

5.3.3.1 Artificial nest design

The artificial nests consisted of two designs, (1) a free-standing timber box (N=30), and (2) a recycled fibreglass plastic tunnel (N=18). The designs were based on artificial nests used successfully in other penguin colonies and utilised materials that were affordable and readily available.

The timber box design was comparable to those being used successfully for little penguins on Garden Island, WA; Phillip Island, Victoria; and at Oamaru, New Zealand as well as some of those already available on Penguin Island (Klomp *et al.* 1991; Houston 1999; Sutherland *et al.* 2014). Boxes were constructed using 25 mm thick exterior grade plywood (box dimensions = 450 mm L x 425 mm W x 300 mm H; entrance dimension = 200 mm L x

200 mm W x 150 mm H; Figure 5.1; Figure 5.2). The bottom remained open to allow penguins to exhibit normal digging and nesting behaviour. Boxes were painted using a light-coloured heat reflective paint to increase heat reflectance (Griffiths *et al.* 2017).

The plastic tunnels, constructed from fibreglass recycled plastic, were based on structures provided for African penguins in Namibia and South Africa (Kemper *et al.* 2007). The dimensions roughly conformed to measurements of the current nest boxes deployed on Penguin Island (dimensions = 450 mm L x 300 mm W x 200 mm H; entrance dimension = NA; Figure 5.2). Tunnels were long enough to provide adequate nesting space while still allowing easy access into the rear of the nest for monitoring and research purposes. The tunnels were buried on an angle of approximately 20° and to a depth of 100 mm at the rear end of the tunnel. The tunnel was then covered with soil. As the entryway to this design was relatively open, brushwood screening was attached to the front to partially hide the entry to the burrow (Figure 5.2). Like the timber boxes, the bottom of the tunnel was left open to facilitate normal digging behaviour.

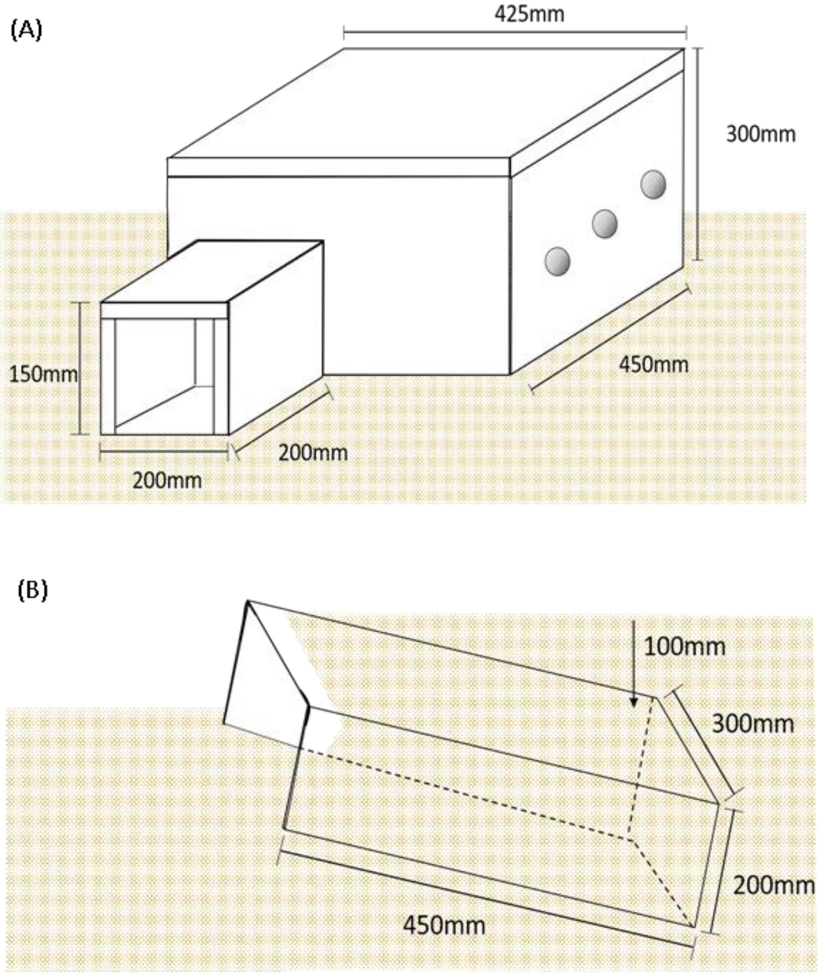

Figure 5.1: Dimensions of **(A)** timber box nest design, and **(B)** plastic tunnel nest design

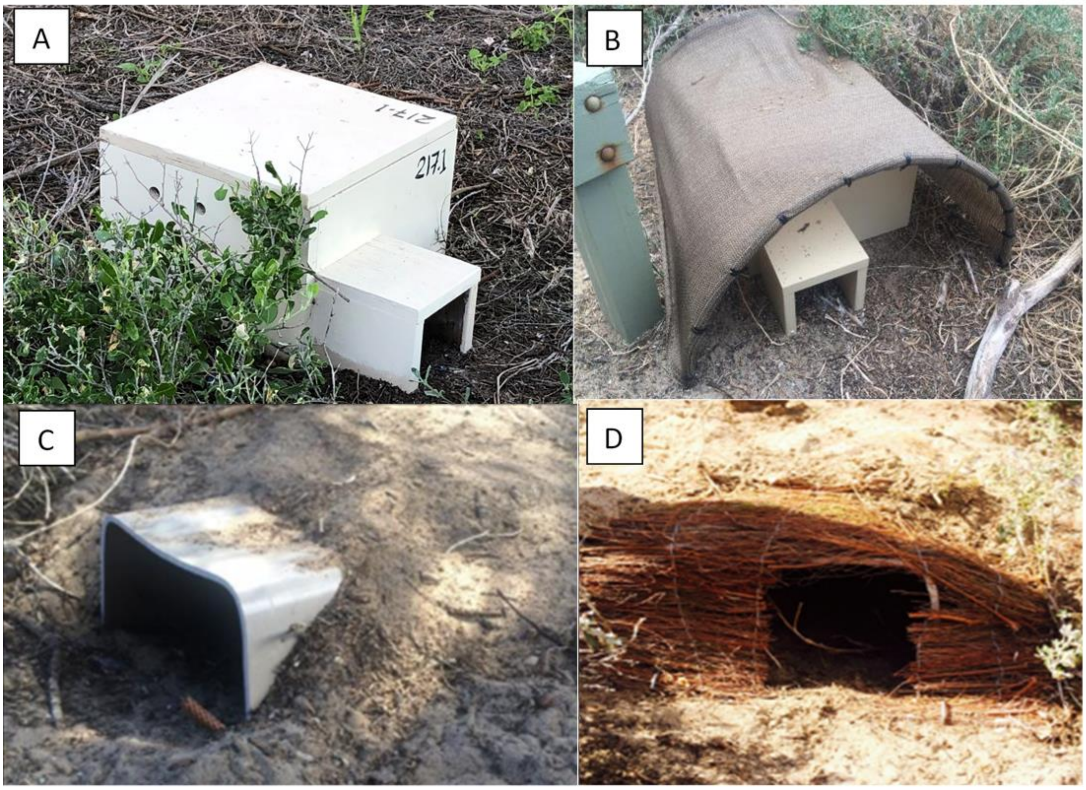

Figure 5.2: **(A)** Timber box nest design with no shading treatment (exposed). **(B)** Timber box nest deisgn with artificial shading treatment. **(C)** Plastic tunnel design before brushing is in place. **(D)** Plastic tunnel design with brushing in place to conceal entrance.

The artificial nests were placed *in situ* and exposed to different shading scenarios (Table 5.1). Boxes were placed under the following four shade conditions: (1) exposed; boxes were placed in full sun with no or minimal shading directly over the box. (2) shade cloth; boxes were placed in full sun but covered with shade cloth. This was achieved by stretching 90% shade cloth over a semicircular frame made of 25 mm flexible plastic tubing. The shade cloth frames were then anchored into the ground over nest boxes using timber garden stakes leaving approximately 10 cm between the box and the cloth at the highest point. (3) shading vegetation; boxes were installed under vegetation providing a minimum 75% cover over the box, or (4) shading vegetation and shade cloth; boxes were placed underneath both shade cloth and shading vegetation. Plastic tunnels were placed in either (1) full sun, or (2) shaded under vegetation.

To encourage use of the new nests and to facilitate future monitoring and management of Penguin Island's breeding population of little penguins, the artificial nests were placed within three areas adjacent to major penguin landfall sites. The first area was located on the north-east side of the island, the second on the south-east side while the third was west facing (Figure 5.3). In areas one and two, twelve boxes (three of each shade treatment) and six tunnels (three of each shade treatment) were installed (Table 5.1). In area three, treatments involving shading vegetation could not be tested as vegetation was not tall enough to adequately shade boxes and tunnels therefore, only six boxes (three exposed, three under artificial shade) and six tunnels (all exposed) were installed (Table 5.1). Nests entrance was oriented in a direction that would allow easy access by penguins.

All nest sites were marked, labelled and their position recorded using a Getac differential global positioning system (dGPS) which ensured a horizontal accuracy of <1 m (at best 0.1 m). Points representing each nest were entered into a geographic information system (GIS) database (Figure 5.3).

Table 5.1: Number of replicates of each nest type and shading treatment deployed on Penguin Island

	Timber box				**Buried plastic tunnel**	
	Exposed	Shade cloth	Shading vegetation	Shading vegetation plus shade cloth	Soil and exposed	Soil and shading vegetation
Area 1	x3	x3	x3	x3	x3	x3
Area 2	x3	x3	x3	x3	x3	x3
Area 3	x3	x3	n/a	n/a	x6	n/a

Figure 5.3: Location of the three areas that tested designs were placed (yellow dots = boxes; red dots = plastic tunnels).

5.3.3.2 Nest microclimate

Temperature and humidity data loggers (DS1923 Hygrochron iButtons http://www.maximintegrated.com/en/products/comms/ibutton/DS1923.html) were set to record temperature (˚C) and relative humidity (%) inside the artificial nests at 30-minute intervals during the sampling periods. As there were fewer loggers than nests, loggers were rotated between nests over the course of two and a half years with most nests containing a logger for approximately 12 months. Data loggers were inserted into a plastic key fob and mounted in the rear left of both artificial nest types (approximately 10 cm off the ground). iButtons mounted in boxes were attached using cable ties (Figure 5.4A). The iButtons mounted in plastic burrows were attached to metal pegs using a cable tie (Figure 5.4B).

Figure 5.4: Location of iButton temperature and humidity logger inside **(A)** timber boxes, and **(B)** plastic tunnels.

Nests were monitored fortnightly to ensure iButtons remained secure and did not become buried or dislodged. Nests were also checked for occupancy and nesting activity. Penguins were present for a portion of the sampling in 19 nests. The remaining sample nests remained unoccupied. Data recorded by the iButtons were uploaded every two and a half months to a laptop computer using the Java™ application, *OneWireViewer* (http://onewire-viewer.software.informer.com/). Over the three years some data losses occurred due to equipment failure and loss. As a result, temperature and humidity data were recorded half-hourly for 30 boxes and 14 plastic tunnels (Appendix 5.1; Figure A5.1).

5.3.3.3 Local weather conditions

To compare nest microclimate with local meteorological conditions, half-hourly measurements of ambient temperature, relative humidity, precipitation, wind speed and direction local were sourced from the Bureau of Meteorology (BOM) meteorological station at Garden Island (approximately 10 km north of Penguin Island).

5.3.4 Data Analysis

Preparation of data and construction of variables. The objective of this study was to describe and quantify the effects of design and shading modifications on microclimate conditions of artificial nests with a central focus on maximum daily temperature and hours of exposure to potentially harmful thermal conditions while accounting for weather conditions (wind, ambient temperature, humidity). Therefore, I had to construct variables at time scales allowing quantification of maximum and heating duration. To do this, half-hourly temperature and humidity measurements were first averaged by hour within each sampling date for each individual nest. To account for local climatic influences on nest microclimate, half hourly measurements of ambient conditions including temperature, relative humidity, wind speed and wind direction recorded at the BOM Garden Island weather station were also averaged by hour for each day. Several daily microclimate metrics were then constructed to compare temperature and humidity patterns and variation. For each sampling date, I calculated the daily mean, maximum, minimum and range for both individual nests and ambient temperature and humidity. Days were also categorised into either warm day (ambient temperatures exceeded 25 ˚C) or cool days (ambient temperatures were below 25 ˚C) hereafter referred to as '*temperature category'*. This cut point was identified from visual inspection of data where beneath 25 ˚C, ambient temperature was unlikely to induce nest box warming over 30 ˚C, a physiological threshold for stress in little penguins (Stahel and Nicol 1982; Horne 2010). For daily wind speed and direction, I isolated data at four points during the day at 6am, 9am, 12pm and 3pm. Departure of daily nest measurements from ambient conditions were extracted for each sampling date and nest by subtracting daily ambient measure from the daily nest measure. To assess and compare hours of exposure to critical temperatures, the number of hours each nest recorded temperature over 30 ˚C and 35 ˚C respectively was calculated for each sampling day. These temperature thresholds were chosen as they represent the upper thermoneutral limit and the temperature at which little penguins become hyperthermic respectively (Stahel and Nicol 1982). Hourly and daily measurements were pooled to assess differences in nest type - treatment groups.

Data exploration. Prior to any statistical analysis, data exploration was carried out following the protocol recommended in Zuur *et al.* (2010). Cleveland dotplots were used to identify outliers and multi-panel pair-plots were used to screen for collinearity of variables, assessed using Pearson's correlation coefficient. If the Pearson's correlation coefficient was >0.6 then one variable from the pair was eliminated (Booth *et al.* 1993). Nest temperature and nest relative humidity were highly correlated (r >0.6), therefore while descriptive statistics are presented for both, modelling was done on temperature data only as these were better measured by loggers and hold greater biological importance. A significant correlation (r >0.6) was found between daily ambient temperature measures (maximum, minimum, mean and range) as well as between daily humidity measures (maximum, minimum, mean and range). Subsequently, daily ambient maximum temperature and daily ambient maximum relative humidity were the only ambient temperature and humidity predictors used for statistical analysis.

The influence of adult presence within a nest on temperature was also examined. True adult occupancy for each sample nest could only be obtained for 26 days/ year for each sample nest (i.e. when the adult was observed during fortnightly monitoring sessions). A naive adult occupancy measure was inferred through nesting activity (i.e. each day during a breeding attempt from egg lay until fledging was considered ‘occupied’). Preliminary analysis revealed negligible evidence of an effect of adult presence on nest temperature and was not included in further analyses.

All analyses were performed within the statistical software program R version 3.6.1 (R Core Team 2018) and using RStudio version 1.2.1335 (RStudio Team 2018). Data manipulation and plotting was carried out using packages within tidyverse (ggplot2; dplyr; Wickham 2017). Descriptive statistics are reported as means ± standard error (SE) or ± confidence interval (CI) for tables and graphs respectively. Tests where $P<0.05$ were considered significant and as evidence of an effect.

General approach to analysis. During data analysis, I applied an information-theoretic approach (Burnham and Anderson 2003) whereby support for predictors given the data was examined. Due to the observational nature of some of the variables included in this study, a balanced *all subsets* approach was used whereby all possible combinations of the predictor variables were tested to examine the effect of local climate variables and nest type - treatment on nest maximum temperature, nest minimum temperature and hours of exposure to upper thermoneutral limits of 30 ˚C and 35 ˚C. This approach is recommended practice in model selection and ensures that all important sub-models are included in the candidate model set and performs better than other ad hoc model selection strategies when defining variable importance (Doherty et al 2012; Morin et al 2020). Selected explanatory variables were fitted to a global model that included all predictors (see below for specifics) and all possible combinations were tested using the ‘dredge’ function in the MuMIN package (Barton 2016). Model residuals were visually evaluated for issues with fit or assumptions; no violations were detected. Variance explained by the fixed effects (marginal pseudo R^2) was estimated using methods described by Nakagawa and Schielzeth (2013) and the function ‘r.squaredGLMM’ from the package MuMIN (Barton 2016).

Models were evaluated using Akaike’s information criterion corrected for small sample size (AICc) (Burnham and Anderson 2003; Symonds and Moussalli 2011; Barton 2016). AICc weight (ω_i) was used to select the best of the competing models. Models with a ΔAICc <5 are presented and models with a ΔAICc <2 were considered as having substantial support (Burnham and Anderson 2003; Burnham *et al.* 2011). Predictions and graphical representations of the top model were produced through the packages ggeffects (Lüdecke and Lüdecke 2017) and sjplot (Lüdecke 2018) and are presented here. However, to account for model uncertainty and enable more robust inferences, model averaging was applied across all models and parameter and error estimates were derived from a weighted average across multiple models (Burnham and Anderson 2003; Johnson and Omland 2004; Symonds and Moussalli 2011). I examined two types of model averaged coefficients to assess strength of evidence for an effect: the conditional model average (where estimates are generated from only the models each covariate appears), and the full model average (where covariates not present in the model contribute zero to the calculation) (Symonds and Moussalli 2011). Full model averaged estimates consequently shrink towards zero; the difference between full and conditional model estimates is referred to as *shrinkage* and represents the degree by which covariates are informative (Symonds and Moussalli 2011; Cade 2015). Shrinkage was examined to assess strength of covariates present in top models (Burnham *et al.* 2011; Grueber *et al.* 2011; Symonds and Moussalli 2011). Variables were considered to have the strongest evidence of effect if the disparity between the full and conditional estimates (shrinkage) was small and 95% confidence intervals of model-averaged coefficients did not include zero (Johnson and Omland 2004; Burnham et al. 2011; Symonds and Moussalli 2011). Predictions and graphical representations of full and conditional model averaged coefficients were produced through the packages ggeffects (Lüdecke and Lüdecke 2017) and sjplot (Lüdecke 2018). Full and conditional averaged model coefficient sets with 95% confidence intervals are presented in Chapter 5 Appendix.

Modelling framework. To detect and quantify relationships between daily maximum and minimum nest temperature and nest type – treatment, while accounting for local climatic conditions, Linear Mixed Models (LMM) were constructed using the package glmmTMB [function: glmmTMB; (Brooks *et al.* 2017)]. Daily maximum nest temperature was modelled against the fixed effects of nest type – treatment and local climate conditions including: maximum ambient temperature, temperature category (‘warmer’ vs ‘cooler’ days), maximum ambient relative humidity, wind speed and wind direction and included interactions between maximum ambient temperature and temperature category as well as wind speed and wind direction. Daily minimum nest temperature was modelled against nest type – treatment and local climate conditions including: Minimum ambient temperature, maximum ambient relative humidity, wind speed and wind direction and included the interaction between wind speed and wind direction. All models included the random effect of nest ID. As expected, temporal correlation was detected during initial model validation procedures and was accounted for by using the first-order autoregressive (AR1) error structure with date nested within nest ID.

Exposure hours over 30 ˚C and 35 ˚C were modelled separately using Generalized Linear Mixed Models (GLMMs) with a logit link function and Poisson distribution to represent the count of hours above the threshold temperature (measurements were hourly and therefore a discrete count). Explanatory variables for both models included maximum ambient temperature, maximum ambient relative humidity, wind speed, wind direction and the interaction between wind speed and wind direction. Nest ID was included as a random effect.

All models also accounted for the effect of year. While not a factor of interest for this study, year could not be included as a random effect as it was limited to three levels (i.e. 2014, 2015 and 2016) and therefore was included as a fixed effect.

Comparison of nest temperature between natural nests and new artificial nest designs. To assess how the daily maximum temperature and exposure hours of the new nest boxes compared to current natural nests, maximum and exposure models developed for natural nests in Chapter 4 and new artificial nests in the current chapter were used to generate daily predictions for all sample nests from January 1st 2014 until December 31st 2016 using the R base function predict() (R Core Team 2018). Results from these predictions are presented graphically.

5.4 Results

Daily patterns of nest temperature and relative humidity. Temperature inside all nest type - treatment groups followed a similar daily pattern: increasing steadily from a minimum around 0500 hrs and reaching a maximum between 1200-1300 hrs before dropping in the afternoon (exposed plastic tunnels peaked later at 1400- 1500 hrs; Figure 5.5A). Temperatures in the boxes were similar to ambient temperature from ~1800 – 0600 hrs, but exceeded ambient temperature from 0600-1800 hrs. The degree to which nest temperature departed from ambient temperatures varied depending on ambient maximum temperature with greater deviation from ambient conditions observed at lower maximum temperatures. At temps ≥ 30 ˚C , all nest types reached temperatures that were either indicative of thermal stress or hyperthermia, but even at 25 – 29.9 ˚C ambient temperatures, three treatment groups (exposed boxes and tunnels and boxes with shade cloth) reached temperatures that are thermally stressful for penguins (Figure 5.6).

Daily relative humidity (RH) peaked at ~0600hrs and then steadily dropped to a daily minimum between 1200 – 1300hrs before increasing again in the afternoon (Figure 5.5C). Plastic tunnels covered by vegetation and timber boxes shaded either solely by vegetation or combined with shade cloth were consistently more humid than the ambient RH, Additionally, these nest sites displayed relatively minimal variation in RH throughout the day and night (Figure 5.5D). The only nest site treatments in which the RH was less than ambient were; (1) boxes with shade, that became less humid than ambient conditions for a short period around midday, and (2) exposed boxes and exposed plastic tunnel that were less humid than ambient for extended periods in the afternoon (Figure 5.5D).

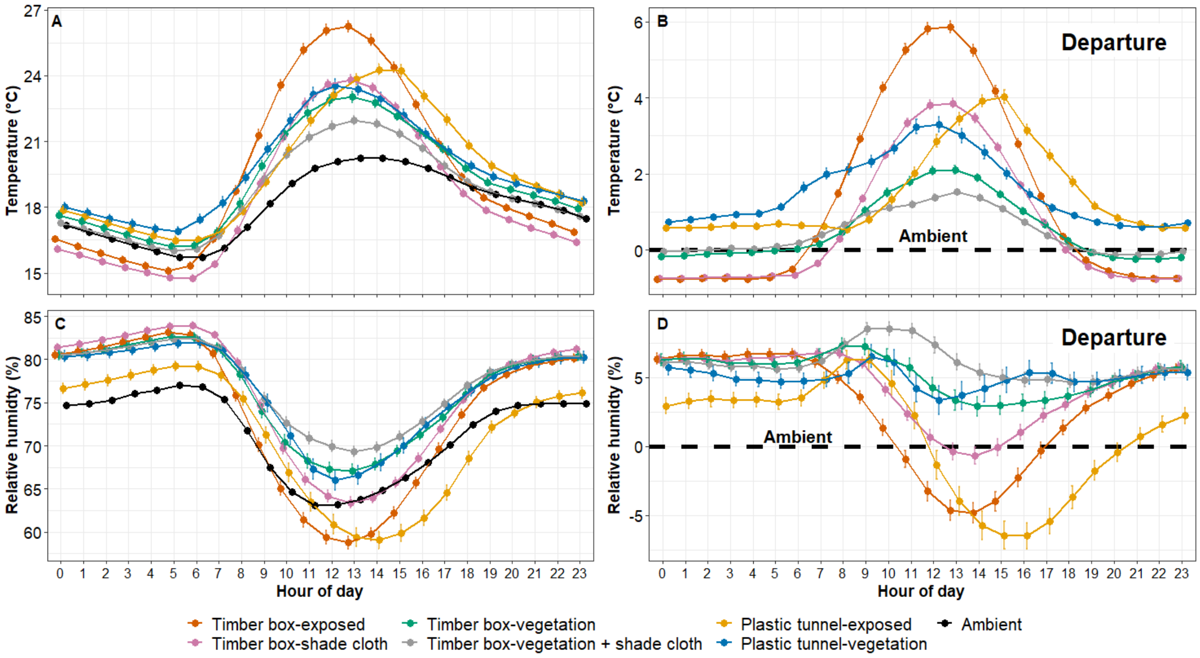

Figure 5.5: Pattern of temperature (˚C) and relative humidity (%) change throughout the day. Mean ± 95% CI of **(A)** hourly nest temperature; **(B)** departure from ambient temperature; **(C)** hourly nest relative humidity; **(D)** departure from ambient relative humidity recorded inside different nest type - treatments.

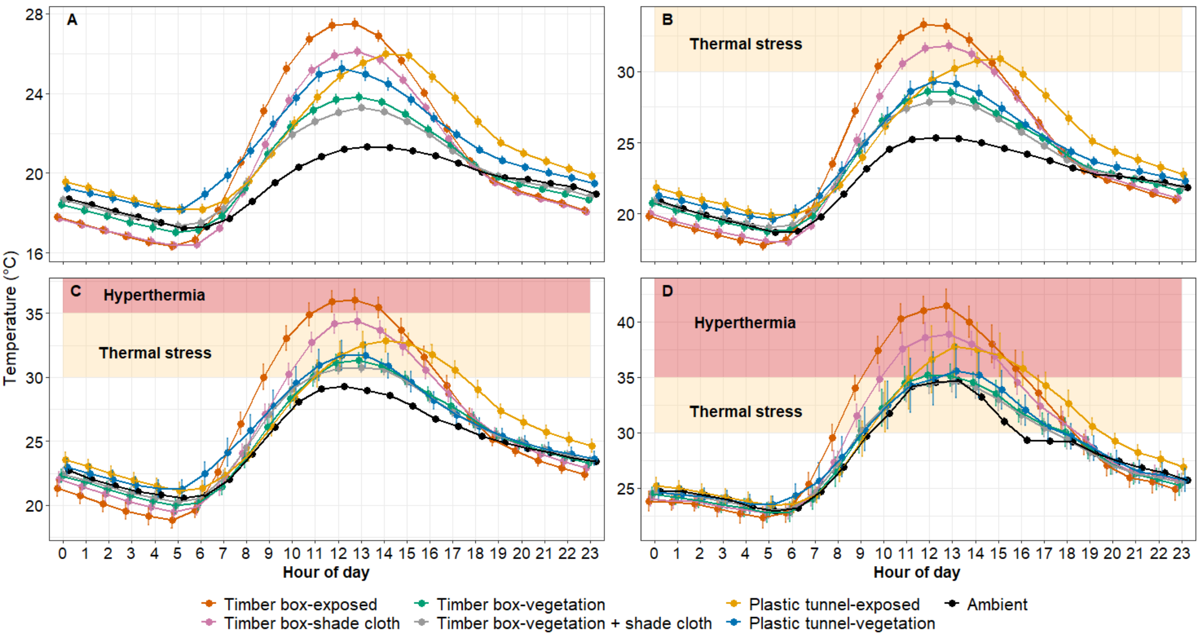

Figure 5.6: :Mean ± 95% CI of hourly nest temperature at differing ambient temperature ranges: (A) Ambient Max = 20-25˚C; (B) Ambient Max = 25- 30C; (C) Ambient Max = 30-35C; (D) Ambient Max = >=35˚C) for the different nest type - treatments tested.

Exposed and artificially shaded timber boxes and exposed plastic tunnels reached upper thermoneutral limits (30 ˚C and 35 ˚C) at lower ambient temperatures and more often than other nest type - treatments (Figure 5.6; Figure 5.7A). Exposed timber boxes reached temperature thresholds of 30 ˚C and 35 ˚C earlier in the day and maintained extreme temperatures for longer periods (mean = 5.0 ± 0.1 hrs day^{-1}, range = 1.0 – 12 hrs day^{-1} ; mean = 3.9 ± 0.1 hrs day^{-1}, range = 1.0 – 9 hrs day^{-1}, respectively; Figure 5.6). Timber boxes with shading vegetation reached thermal thresholds of 30 ˚C and 35 ˚C later and were exposed to these temperatures for a lesser amount of time (mean = 4.1 ± 0.2 hrs day^{-1}, range = 1.0 – 11 hrs day^{-1}; mean = 2.9 ± 0.2 hrs day^{-1}, range = 1.0 – 7 hrs day^{-1}, respectively; Figure 5.6; Figure 5.7).

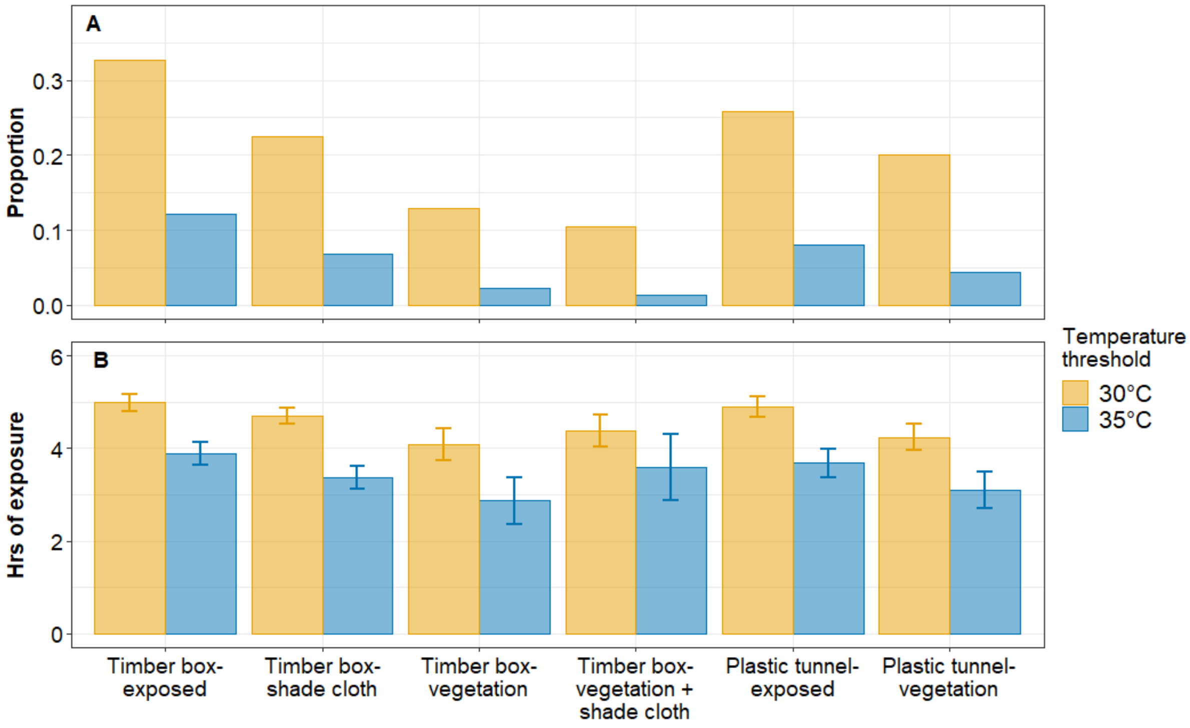

Figure 5.7: (A) Proportion of total sampling days where daily temperature exceeded upper thermoneutral limits of 30˚C (thermal stress zone) and 35˚C (Hyperthermic zone) for different nest-type treatments. **(B)** For days exceeding 30 ˚C; mean duration in hours per day that exceeded thermal threshold limits of 30˚C and 35˚C for different nest type-treatment.

Temperature of nest type - treatment groups. Timber boxes with shading vegetation or combined shade cloth and vegetation were the coolest relative to other treatment groups (mean = 23.7 ± 0.1 ˚C; range = 12.6 – 40.3 ˚C and mean = 22.6 ± 0.1 ˚C; range = 12.6 – 41.1 ˚C respectively) and had the lowest daily temperature range (mean = 8.1 ± 0.1 ˚C; range = 1.5 – 20.5 and mean = 7.3 ± 0.1 ˚C; range = 1.0 – 18.5 respectively), while exposed timber boxes were consistently warmer than all other treatments (mean = 27.2 ± 0.13 ˚C; range 13.1 – 47-1) and had a greater daily temperature range (mean = 12.7 ± 0.1 ˚C), (Table 5.2; Figure 5.8).

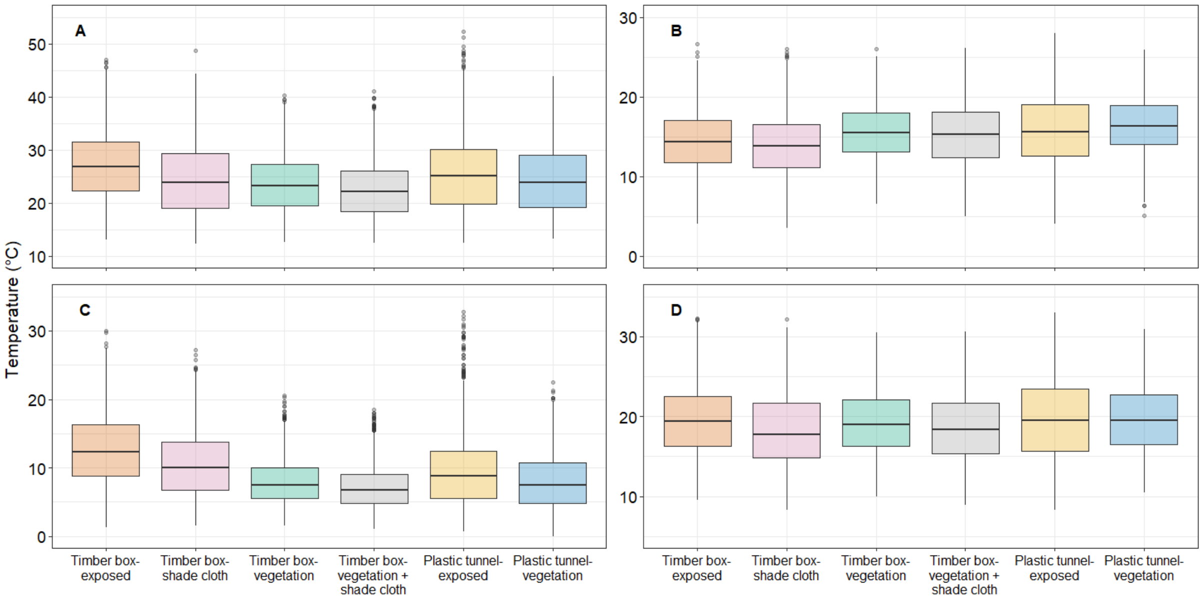

Figure 5.8: Box plots of mean daily temperature observations across all nest types- treatment groups. **(A)** Daily maximum; **(B)** daily minimum; **(C)** daily range; **(D)** daily mean.

Departure from ambient maximum temperature closely reflected the mean daily maximum temperature and varied considerably ranging from -9.4 ˚C to 23.6 ˚C (Table 5.2). Exposed timber boxes displayed the largest divergence and were on average 5.7 ± 0.1 ˚C (range = -7.50 – 17.89 ˚C) warmer than the ambient maximum temperatures while timber boxes with shading vegetation or combined shade cloth and vegetation displayed the least divergence from the ambient (mean = 1.7 ± 0.1 ˚C; range = -5.9 – 8.9 ˚C; mean = 1.2 ± 0.04 ˚C; range = -6.1 –

8.8 ˚C respectively), (Table 5.2). Mean minimum temperature between nest type - treatments showed less heterogeneity. Exposed and artificially shaded timber boxes reached cooler minimum temperatures than other nest types (mean = 14.1 ± 0.1 ˚C; range = 3.5 – 26.0 ˚C; mean = 14.5± 0.1 ˚C; range = 4.0 – 26.6 ˚C respectively) while the highest mean minimum temperature was observed in the plastic tunnels shaded by vegetation (mean = 16.4± 0.1 ˚C; range = 5.0 – 26.0 ˚C) (Table 5.2; Figure 5.8).

Table 5.2: Summary (mean ± standard error, range in parentheses) of daily maximum, minimum, mean, range nest temperature (˚C), departure from Garden Island relative humidity (nest – ambient) and hours of exposure over 30 ˚C and over 35 ˚C for different nest type – shading treatments pooled (2014-2016).

Temperature variable	**Timber box- exposed (N_{nest}= 9 N_{daily}= 2467)**	**Timber box- shade cloth (N_{nest} = 9 N_{daily}= 3222)**	**Timber box- vegetation (N_{nest} = 6 N_{daily}= 1685)**	**Timber box- vegetation + shade cloth (N_{nest} = 6 N_{daily}= 2308)**	**Plastic tunnel- exposed (N_{nest} = 9 N_{daily}= 2394)**	**Plastic tunnel - vegetation (N_{nest} = 5 N_{daily}= 1410)**
Max Temperature$_{(nest)}$	27.2 ± 0.1 (13.1 – 47.1)	24.5± 0.1 (12.4 – 48.8)	23.7 ± 0.1 (12.6 – 40.3)	22.6± 0.1 (12.6– 41.1)	25.5 ± 0.1 (12.6 – 52.3)	24.4 ± 0.2 (13.3– 43.8)
Max Temperature$_{(departure)}$	5.7 ± 0.1 (-7.5 – 17.9)	3.6 ± 0.1 (-5.6 – 14.5)	1.7 ± 0.1 (-5.9 – 8.9)	1.2 ± 0.04 (-6.1 – 8.8)	4.0 ± 0.1 (-9.4 – 23.6)	3.0 ± 0.1 (-8.6 – 15.0)
Min Temperature$_{(nest)}$	14.5 ± 0.1 (4.0 – 26.6)	14.1 ± 0.1 (3.5 – 26.0)	15.7 ± 0.1 (6.6 – 26.1)	15.4 ± 0.1 (5.0 – 26.1)	16.0 ± 0.1 (4.0 – 28.1)	16.41 ± 0.1 (5.1 – 25.9)
Min Temperature$_{(departure)}$	-0.5 ± 0.02 (-11.3 – 3.7)	-0.5 ± 0.02 (-5.1 – 6.4)	0.2 ± 0.03 (-5.1 – 4.7)	0.3 ± 0.02 (-3.3 – 3.9)	1.0 ± 0.04 (-5.1 – 10.8)	1.4 ± 0.04 (-3.0 – 9.4)
Mean Temperature$_{(nest)}$	19.5 ± 0.1 (9.6 – 32.3)	18.4 ± 0.1 (8.3 – 32.1)	19.2 ± 0.1 (10.0 – 30.5)	18.7 ± 0.1 (8.9 – 30.6)	19.7 ± 0.1 (8.3 – 33.0)	19.7 ± 0.1 (10.4 – 30.9)
Mean Temperature$_{(departure)}$	1.3 ± 0.03 (-6.6 – 6.3)	0.6 ± 0.03 (-3.3 – 5.4)	0.5 ± 0.02 (-2.4 – 3.3)	0.5 ± 0.02 (-2.9 – 4.9)	1.5 ± 0.04 (-3.4 – 9.1)	1.5 ± 0.04 (-3.2 – 8.4)
Range Temperature$_{(nest)}$	12.7 ± 0.1 (1.3 – 30.0)	10.4 ± 0.1 (1.5 – 27.2)	8.1 ± 0.1 (1.5 – 20.5)	7.3 ± 0.1 (1.0 – 18.5)	9.5 ± 0.1 (0.7 – 32.7)	8.0 ± 0.1 (0.0 – 22.5)
Range Temperature$_{(departure)}$	6.3 ± 0.1 (-6.9 – 19.9)	4.1 ± 0.1 (-5.7 – 16.5)	1.5 ± 0.1 (-7.3 – 10.5)	0.8 ± 0.1 (-6.7 – 7.9)	3.1 ± 0.1 (-12.7 – 24.2)	1.6 ± 0.1 (-12.0 – 14.5)
Hours ≥30 ˚C	5.0 ± 0.1 (1 – 12)	4.7 ± 0.1 (1 – 12)	4.1 ± 0.2 (1 – 11)	4.4 ± 0.2 (1 – 11)	4.9 ± 0.1 (1 – 14)	4.2 ± 0.1 (1 – 12)
Hours ≥35 ˚C	3.9 ± 0.1 (1 – 9)	3.4 ± 0.1 (1 – 8)	2.9 ± 0.2 (1 – 7)	3.6 ± 0.4 (1 –7)	3.7 ± 0.2 (1 – 9)	3.1 ± 0.2 (1 – 7)

Relative humidity of nest type - treatment groups. Relative humidity ranged considerably with the lowest minimum recorded being 17.3% and the highest maximum of 99.9%. Exposed plastic tunnels were consistently drier than other nest types with a mean of 71.2 ±0.3% (range = 39 – 97.2%) and observed the greatest daily range of 27.9 ±0.4% (range = 1.5 – 67.3%) (Figure 5.9; Table 5.3). Timber boxes with combined vegetation and shade cloth were the most humid with a mean relative humidity of 77.2 ± 0.2% (range = 46.4 – 97.2%) and displayed the lowest daily range (mean = 20.3 ± 0.2%; range = 2.5 – 53.6%) (Figure 5.9; Table 5.3).

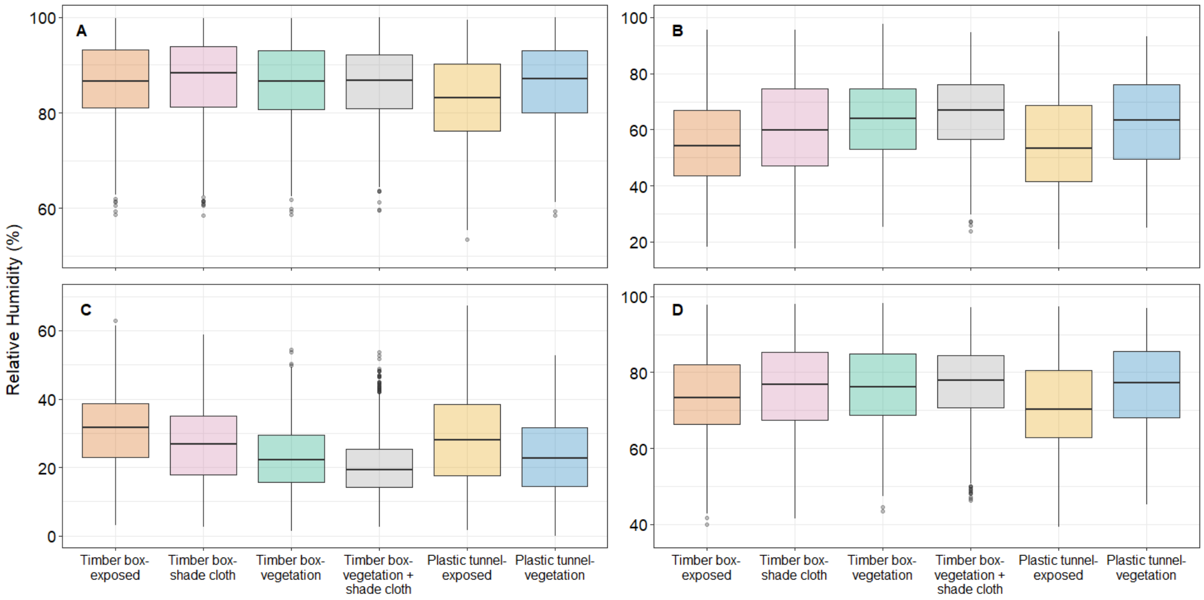

Figure 5.9: Box plots of mean daily relative humidity observations across all nest type – treatments groups. **(A)** Daily maximum; **(B)** daily minimum; **(C)** daily range; **(D)** daily mean.

Table 5.3: Summary (mean ± standard error, range in parentheses) of daily maximum, minimum, mean and range nest relative humidity (%) and departure from Garden Island relative humidity (nest – ambient) for different nest type - treatments pooled across the study period (2014-2016).

Humidity variable	**Timber box- exposed (N_{nest}= 7 N_{daily}= 1775)**	**Timber box- shade cloth (N_{nest} = 9 N_{daily}= 2633)**	**Timber box- vegetation (N_{nest} = 6 N_{daily}= 1409)**	**Timber box- vegetation + shade cloth (N_{nest} = 6 N_{daily}= 1868)**	**Plastic tunnel – exposed (N_{nest} = 5 N_{daily}= 1142)**	**Plastic tunnel - vegetation (N_{nest} = 4 N_{daily}= 912)**
Max Humidity$_{(nest)}$	86.4 ± 0.2 (58.7 – 99.8)	87.2 ± 0.2 (58.4 – 99.8)	86.3 ± 0.2 (58.7 – 99.9)	86.2 ± 0.2 (59.5 – 99.9)	82.8 ± 0.3 (53.4 – 99.5)	86.2 ± 0.3 (58.5 – 99.9)
Max Humidity $_{(departure)}$	1.5 ± 0.2 (-17.2 – 32.9)	1.6 ± 0.1 (-19.7 – 32.1)	1.4 ± 0.2 (-14.0 – 33.0)	0.9 ± 0.2 (-18.8 – 33.4)	-1.7 ± 0.2 (-22.9 – 27.5)	0.9 ± 0.2 (-16.5 – 26.1)
Min Humidity $_{(nest)}$	55.8 ± 0.4 (18.2 – 95.6)	60.5 ± 0.3 (17.7 – 95.5)	63.8 ± 0.4 (25.3 – 97.7)	65.9 ± 0.3 (23.8 – 94.7	54.9 ± 0.5 (17.3 – 95.1)	62.6 ± 0.5 (25.1 – 93.0)
Min Humidity $_{(departure)}$	1.9 ± 0.3 (-41.0 – 45.9)	5.8 ± 0.3 (-36.9 – 45.9)	10.0 ± 0.3 (-24.7 – 50.8)	11.9 ± 0.3 (-19.5 – 48.6)	1.9 ± 0.5 (-38.3 – 71.4)	8.5 ± 0.5 (-34.2 – 53.0)
Mean Humidity $_{(nest)}$	73.7 ± 0.3 (40.1 – 97.1	76.1 ± 0.2 (41.5 – 97.9)	76.4 ± 0.3 (43.5 – 98.2)	77.2 ± 0.2 (46.4 – 97.2)	71.2 ± 0.3 (39.3 – 97.2)	76.3 ± 0.4 (45.3 – 96.9)
Mean Humidity $_{(departure)}$	2.7 ± 0.2 (-23.5 – 28.6)	4.2 ± 0.2 (-22.4 – 36.6)	5.2 ± 0.2 (-14.3 – 39.0)	6.0 ± 0.2 (-14.1 – 34.6)	0.7 ± 0.3 (-21.0 – 41.8)	5.0 ± 0.3 (18.4 – 28.0)
Range Humidity $_{(nest)}$	30.7 ± 0.3 (3.1 – 62.8)	26.7 ± 0.2 (2.5 – 58.7)	22.5 ± 0.3 (1.3 – 54.4)	20.3 ± 0.2 (2.5 – 53.6)	27.9 ± 0.4 (1.5 – 67.3)	23.5 ± 04 (0.0 – 52.7)
Range Humidity $_{(departure)}$	-0.5 ± 0.3 (-38.9 – 30.9)	-4.2 ± 0.2 (-38.9 – 28.6)	-8.6 ± 0.3 (-44.9 – 24.1)	-11.0 ± 0.2 (-48.0 – 13.1)	-3.6 ± 0.5 (-67.0 – 33.2)	-7.6 ± 0.4 (50.5 -28.9)

Effect of nest type and local climate on daily nest maximum temperature. Model comparisons showed substantial support for models containing nest type – treatment. The top two models included this term with the most parsimonious model having an Akaike weight of 0.85 (Table 5.4). The next model that excluded nest type – treatment was >20 ΔAICc units from the top model and with a weight <0.0001, supporting the importance of nest type - treatment in explaining variation in maximum nest temperature. Relative to exposed boxes, all other treatment groups were significantly cooler and had narrower daily temperature ranges. The greatest effect was observed for timber boxes with combined shade cloth and vegetation which were significantly cooler than the exposed box group (β = -4.80 ˚C, CI [-6.47 – -3.14 ˚C], Figure 5.10A-B; Appendix 5.2; Table A5.2). Vegetation shaded timber boxes showed a similarly significant effect (β = -4.29 ˚C, CI [-6.08 – -2.51 ˚C] Figure 5.10A-B; Appendix 5.2; Table A5.2). Artificially shaded boxes had weaker cooling effects (β = -2.42 ˚C, CI [-3.91 – -0.93 ˚C] Figure 5.10A-B; Appendix 5.2; Table A5.2). Exposed and shaded plastic tunnels were in general cooler than exposed boxes (β = -2.00 ˚C, CI [-3.58 – -0.41 ˚C]; β = -2.94 ˚C, CI [-4.74 – -1.75 ˚C] respectively, Figure 5.10A-B; Appendix 5.2; Table A5.2).

All local climate predictors were included in the top model (Table 5.4). As expected, ambient daily max temperature had a significant positive effect on nest temperature however this effect depended on whether or not ambient daily maximum exceeded 25 ˚C (Figure 4.9A-B). Nests reached maximums approximately 2.4 ˚C and 3.4 ˚C warmer than ambient on ‘warm’ and ‘cool’ days respectively (Figure 5.10A&C). Wind speed had a negative effect on maximum nest temperature for both onshore and offshore winds, with a significantly stronger cooling effect of wind speed being observed in onshore winds (-0.92 ˚C per 10km/hr and -0.65 ˚C per 10km/hr respectively; Figure 4.9C).

Maximum ambient relative humidity had a weak but significant negative effect on nest maximum temperature (β = -0.18 ˚C, CI [-0.21 – -0.14 ˚C], Figure 5.10D, Appendix 5.2; Table A5.2).

Table 5.4 Top models (ΔAICc < 5) for all subsets linear regression model set predicting mean daily maximum temperature of new artificial nest designs on Penguin Island based on combined nest type and shading treatment and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), and model weight (ω_i), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	ω_i	***k***	$R^2_{marg.}$
Intercept	*67256.62*	*11387.55*	*0.00*	*6*	*0*
Nest type-treatment + ambient temp max + temperature category+ ambient RH max + wind speed at 12pm + wind direction at 12pm + wind speed at 12pm * wind direction at 12pm + ambient temp max*temperature category	55869.07	0	0.85	18	0.50
Nest type-treatment + ambient temp max + temperature category+ ambient RH max + wind speed at 12pm + wind direction at 12pm + wind speed at 12pm * wind direction at 12pm + ambient temp max*temperature category + year	55872.57	3.50	0.15	20	0.50

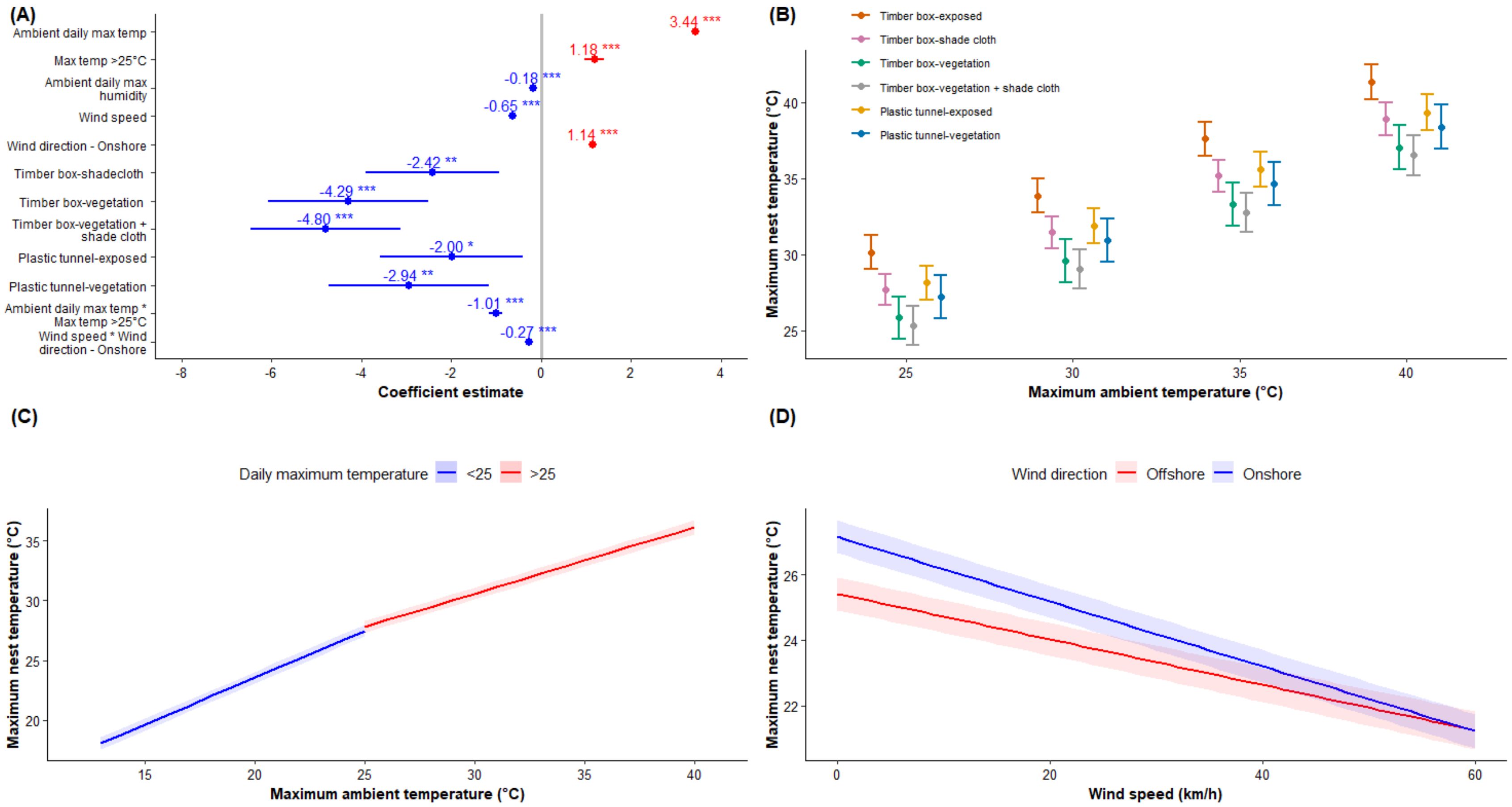

Figure 5.10: **(A)** Coefficient effects of top performing model for effect of nest type and shading treatment and local climatic conditions on nest maximum temperature. **(B)** Predictions from Linear Mixed Models of the effect of nest type and treatment on nest maximum temperature at different maximum ambient air temperatures (Mean ± 95%CI). **(C)** Predictions from Linear Mixed Models of the effect of maximum ambient air temperature on nest maximum temperature (Shaded area represent 95% CI). **(D)** Predictions from Linear Mixed Models of the interactive effect of wind speed and direction on nest maximum temperature (Shaded areas represent 95% CI).

Effect of nest type and local climate on daily nest minimum temperature. Model comparisons investigating predictors of minimum nest temperature revealed similar results to maximum temperature models, as expected. Both the nest type - treatment group and local climate were important predictors of nest temperature however there were observed differences in the magnitude of the effects.

The top eight models included nest type - treatment group with the two best fitting model having Akaike weights of 0.52 and 0.48 respectively (Table 5.5). The next model that excluded nest type - treatment was >33 ΔAICc units from the top model and with a weight <0.0001, suggesting that the nest type - treatment was important in explaining variation in minimum nest temperature. Relative to exposed boxes, other nest type - treatment groups were marginally but significantly warmer. Plastic tunnels shaded by vegetation showed the strongest insulative effects (β = 1.98 ˚C [1.30 – 2.65 ˚C], Figure 5.11A&B; Appendix 5.3; Table A5.3). Exposed plastic tunnels had a slightly lesser effect (β = 1.43 ˚C [0.83 – 2.02]; Figure 5.11A&B; Appendix 5.3; Table A5.3), while timber boxes with vegetation or combined shade cloth and vegetation had the weakest insulative effects (β = 0.74 ˚C [0.07 – 1.41 ˚C]; β = 0.80 ˚C [0.17 – 1.43 ˚C]; respectively (Figure 5.11A&B; Appendix 5.3; Table A5.3). The exception was artificially shaded boxes which had a slight negative effect (were cooler than exposed boxes) (β = -0.05 ˚C [-0.61 – 0.51], however this was not significant and confidence intervals overlapped zero suggesting artificially shaded boxes probably experienced similar minimum temperature to exposed boxes (Figure 5.11A-B; Appendix 5.3; Table A5.3).

All local climate predictors were included in the top model (Table 5.5). Effects of local climate were similar to what was observed in maximum temperature models but differed in the magnitude of the effect. Higher ambient temperatures lead to greater nest temperatures (β = 2.95 ˚C [2.92 – 2.98 ˚C], Figure 5.11A-C; Appendix 5.3; Table A5.3). The effect of wind speed was significantly dependent of wind direction (Figure 5.11D). Wind speed during an onshore wind had a cooling effect on minimum nest temperature (-0.12 ˚C per 10km/hr) whereas the effect of windspeed on nest minimum during offshore winds was negligible (-0.01 ˚C per 10km/hr). Relative humidity had a weak positive effect on nest temperature ($\beta = 0.26$ [0.24 – 0.27]; Figure 5.11A; Appendix 5.3; Table A5.3).

Model comparisons revealed that while the best performing model did not include year, a second model including this predictor showed equal support (difference in AIC values < 2) (Table 5.5). However, examination of model averaged coefficients (Appendix 5; Table A5.33) indicated some uncertainty in the importance of year as a predictor suggesting variation in nest temperature could be better explained by other factors.

Table 5.5: Top models (ΔAICc < 5) for all subsets linear regression model set predicting mean daily minimum temperature of new artificial nest designs on Penguin Island based on combined nest type and shading treatment and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), and model weight (ω_i), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	ω_i	***k***	$R^2_{marg.}$
Intercept	55007.97	*20251.90*	*0.00*	*6*	*0*
Nest type-treatment + ambient temp min + ambient RH max + wind speed at 6am + wind direction at 6am + wind speed 6am * wind direction 6am	34756.07	0	0.52	16	0.82
Nest type-treatment + ambient temp min + ambient RH max + wind speed at 6am + wind direction at 6am + wind speed 6am * wind direction 6am +year	34756.19	0.12	0.48	18	0.82

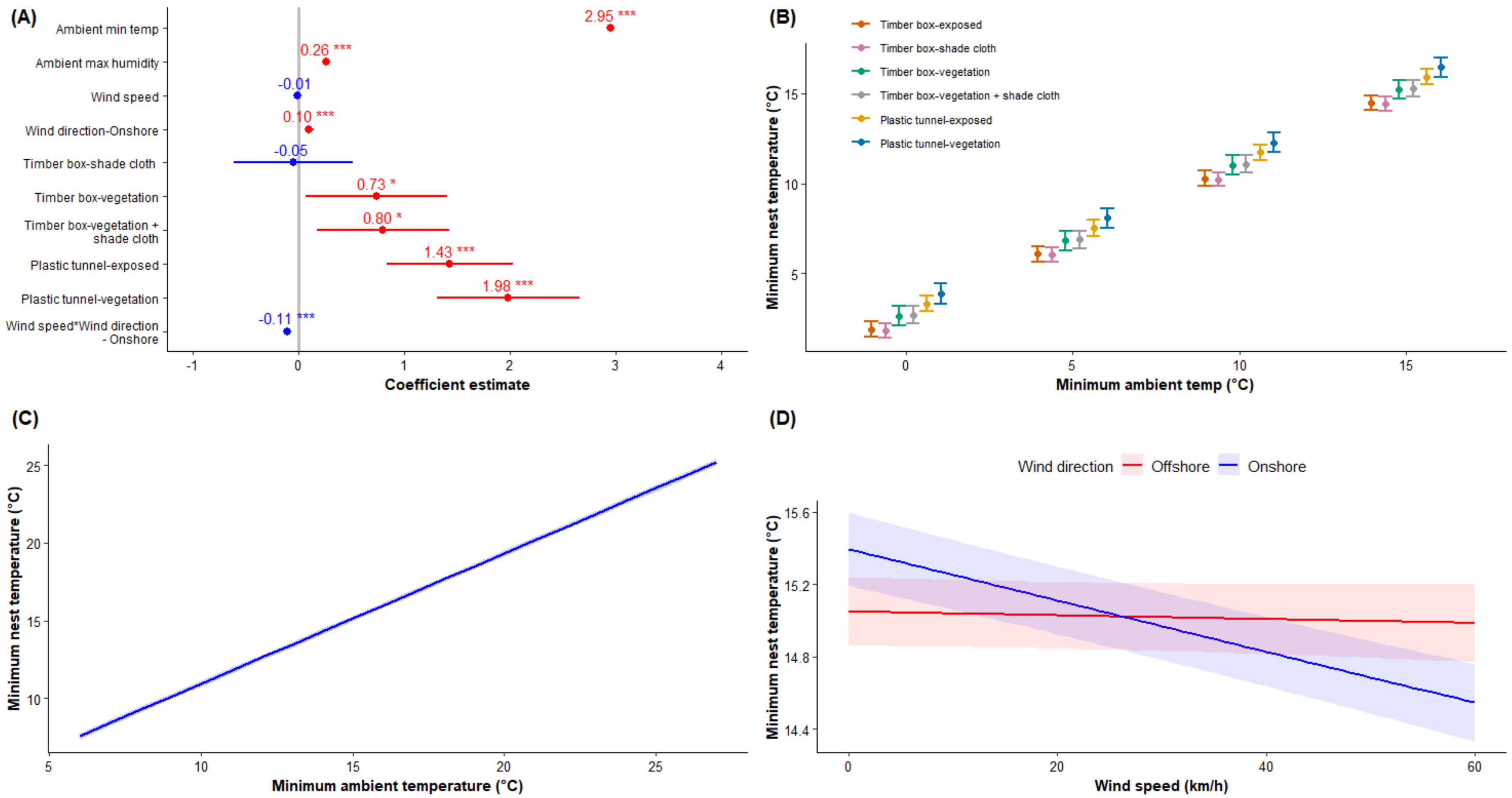

Figure 5.11: (A) Coefficient effects of top performing model for effect of nest type and shading treatment and local climatic conditions on nest minimum temperature. **(B)** Predictions from Linear Mixed Models of the effect of nest type and treatment on nest minimum temperature at different maximum ambient air temperatures (Mean ± 95%CI).**(C)** Predictions from Linear Mixed Models of the effect of maximum ambient air temperature on nest minimum temperature (Shaded area represent 95% CI). **(D)** Predictions from Linear Mixed Models of the interactive effect of wind speed and direction on nest minimum temperature (Shaded areas represent 95% CI).

Effect of nest type and local climate on nest exposure hours ≥30 ˚C and ≥35 ˚C. Treatment group was again well supported as an important predictor for explaining variation in nest exposure hours over both ≥30 ˚C and ≥35 ˚C. Nest type - treatment was included in each of the top 12 candidate models investigating exposure hours to temperatures ≥30 ˚C accounting for >99% of total Akaike weight; the most parsimonious model having a weight of 0.39 (Table 5.6). Model comparisons revealed similarly competitive results in the ≥35 ˚C model set with nest type - treatment present in the top seven models accounting for >93% of the total Akaike weight with the top model having a weight of 0.41 (Table 5.7). While models indicated nest type - treatment to be important, inspection of individual results revealed that only timber boxes with vegetation, timber boxes with combined vegetation and shade cloth and plastic tunnels shaded by vegetation had a significant effect.

Relative to exposed timber boxes, timber boxes with vegetation or combined vegetation and shade cloth spent fewer hours exposed to temperatures exceeding 30°C (β = -0.49 [-0.69 – -0.29], and β = -0.49 [-0.68 – -0.29], respectively; Figure 5.12A; Appendix 5.4; Table A5.4) and temperatures exceeding 35 ˚C (β = -0.58 [-0.88 – -0.27 ˚C] , and β = -0.38 [-0.69 – -0.07 ˚C], respectively; Figure 5.13A; Appendix 5.5; Table A5.5). Vegetation shaded plastic tunnels also spent less time exposed to > 30 °C than the exposed boxes (β = -0.19 [-0.40 – -0.01 ˚C]; Figure 5.12A; Appendix 5.4; Table A5.4) however there was less certainty on the effect of this treatment when temperatures exceeded 35 °C (Figure 5.13A; Appendix 5.5; Table A5.5). This was also true for the remaining treatment groups when temperatures exceed both 30°C and 35°C (Figure 5.12A; Figure 5.13A; Appendix 5.4; Table A5.4; Appendix 5.5; Table A5.5).

The top models for exposure ≥30 ˚C indicated that all local climate predictors were influential on the hours of nest exposure (Table 5.6). As anticipated, high ambient maximum temperature were associated with significantly longer exposure (β = 0.40 [0.38 – 0.42]; Figure 5.12A-C, Appendix 5.4; Table A5.4) while ambient relative humidity slightly reduced exposure hours (β = -0.03 [-0.05 – -0.01]; Figure 5.12A; Appendix 5.4; Table A5.4). Likewise, ambient maximum temperature had a positive effect on hours of exposure to nest temperatures exceeding 35 ˚C (β = 0.37 [0.32 – 0.41]; Figure 5.13A- C; Appendix 5.4; Table A5.4)

The role wind played on influencing nest temperature was more complex. Offshore winds enhanced the effect of wind speed on exposure hours over 30 ˚C increasing exposure hours, while the effect of windspeed during an onshore wind was negligible (Figure 5.12D). Wind speed and its interaction with wind direction was absent from top performing models examining exposure hours ≥35 ˚C suggesting the role of wind in influencing nest exposure hours was less important once nest temperatures exceeded 35°C (Table 5.7).

Table 5.6: Top models (ΔAICc < 5) for all subsets generalised linear regression model set predicting hours of exposure per day exceeding 30 ˚C of new artificial nest designs on Penguin Island based on combined nest type and shading treatment and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), and model weight (ω_i), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	**ω_i**	***k***	**$R^2_{marg.}$**
Intercept	*12607.01*	*1683.27*	*0.00*	*3*	*0*
Nest type-treatment + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm + wind speed 12pm * wind direction 12pm	10923.73	0	0.39	13	0.33
Nest type-treatment + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm + wind speed 12pm * wind direction 12pm + year	10924.62	0.88	0.25	15	0.34
Nest type-treatment + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm	10925.99	2.26	0.13	12	0.33
nest type-treatment + ambient temp max + ambient RH max + wind direction at 12pm	10926.38	2.65	0.10	11	0.33
Nest type-treatment + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm + year	10927.12	3.39	0.07	14	0.33
Nest type-treatment + ambient temp max + ambient RH max + wind direction at 12pm + year	10927.78	4.05	0.05	13	0.33

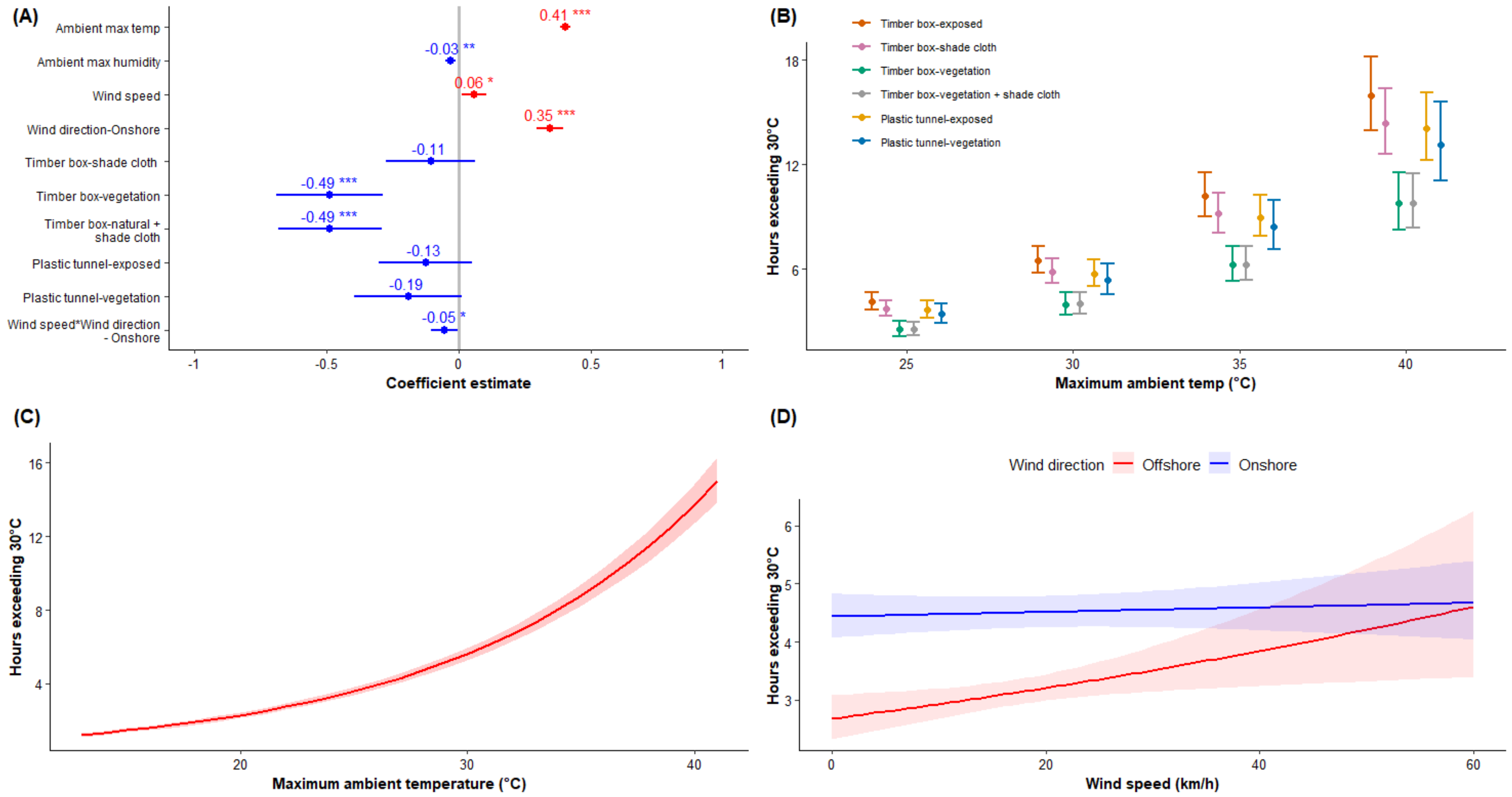

Figure 5.12. (A) Coefficient effects of top performing model for effect of nest type and shading treatment and local climatic conditions on hours of exposure to temperatures exceeding 30 ˚C. **(B)** Predictions from Generalised Linear Mixed Models of the effect of nest type and treatment on hours of exposure to temperatures exceeding 30 ˚C at different maximum ambient air temperatures (Mean ± 95%CI). **(C)** Predictions from Generalised Linear Mixed Models of the effect of maximum ambient air temperature on hours of exposure to temperatures exceeding 30 ˚C (Shaded area represent 95% CI). **(D)** Predictions from Generalised Linear Mixed Models of the interactive effect of wind speed and direction on hours of exposure to temperatures exceeding 30 ˚C (Shaded areas represent 95% CI).

Table 5.7: Top models (ΔAICc < 5) for all subsets generalised linear regression model set predicting hours of exposure per day exceeding 35 ˚C of new artificial nest designs on Penguin Island based on combined nest type and shading treatment and local climatic conditions. Akaike's Information Criterion corrected for small sample size (AICc), distance from the lowest AICc (ΔAICc), and model weight (ω_i), number of parameters (k) and marginal ($R^2_{marg.}$) pseudo R^2.

Model	**AICc**	**ΔAICc**	**ω_i**	**k**	**$R^2_{marg.}$**
Intercept	*3165.52*	*283.10*	*0.00*	*3*	*0*
Nest type-treatment + ambient temp max + wind direction at 12pm + year	2882.42	0	0.41	12	0.26
Nest type-treatment + ambient temp max + ambient RH max + wind direction at 12pm + year	2884.46	2.04	0.15	13	0.26
Nest type-treatment + ambient temp max + wind speed at 12pm + wind direction at 12pm + year	2884.47	2.05	0.15	13	0.26
Nest type-treatment + ambient temp max + wind speed at 12pm + wind direction at 12pm+ year + wind speed 12pm * wind direction 12pm	2885.18	2.77	0.10	14	0.26
Nest type-treatment + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm+ year	2886.52	4.10	0.05	14	0.26
Nest type-treatment + ambient temp max + ambient RH max + wind speed at 12pm + wind direction at 12pm+ year + wind speed 12pm * wind direction 12pm	2886.99	4.57	0.04	15	0.26

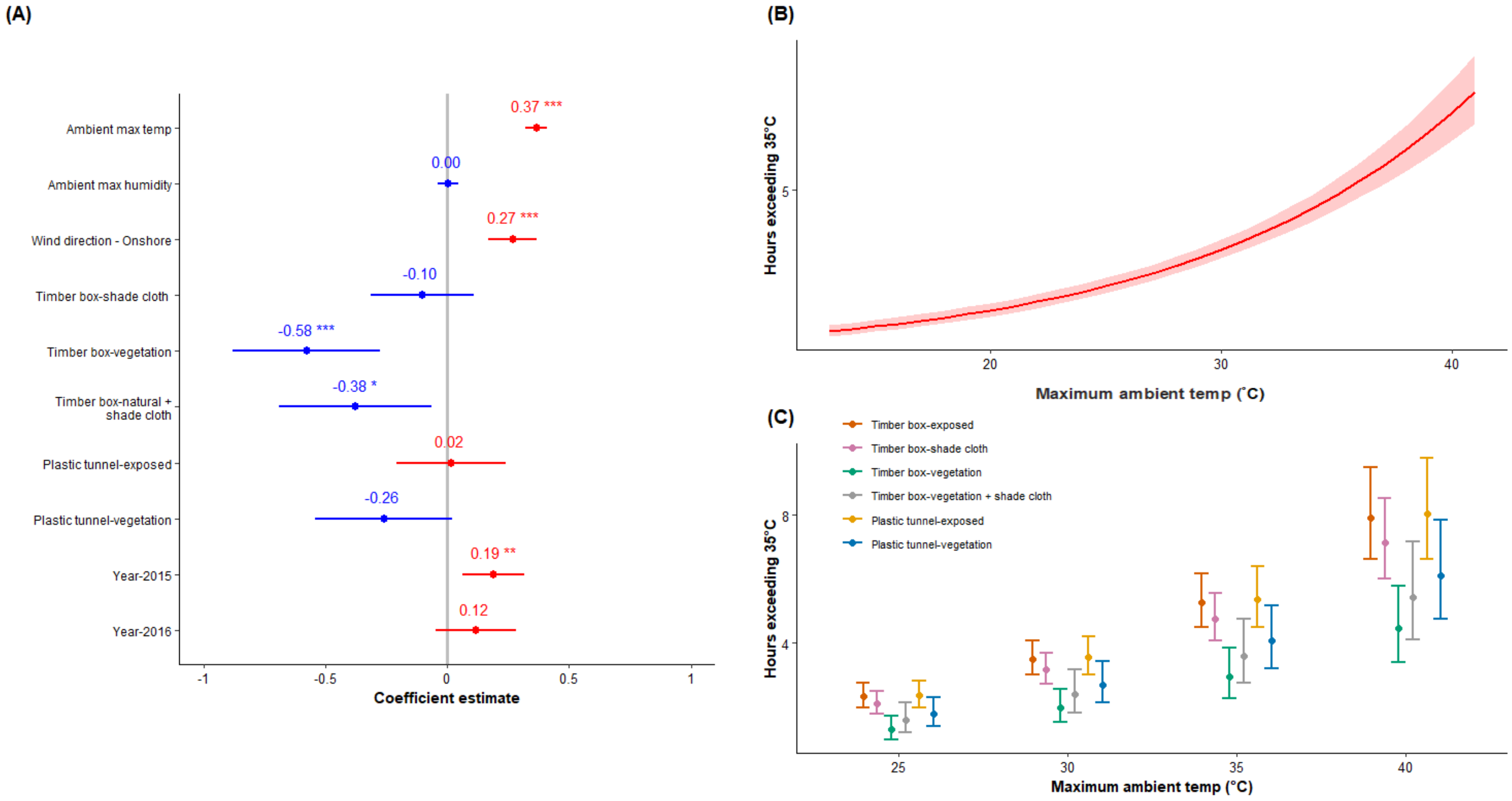

Figure 5.13: A) Coefficient effects of top performing model for effect of nest type and shading treatment and local climatic conditions on hours of exposure to temperatures exceeding 35 ˚C. **(B)** Predictions from Generalised Linear Mixed Models of the effect of maximum ambient air temperature on hours of exposure to temperatures exceeding 35 ˚C (Shaded area represent 95% CI). **(C)** Predictions from Generalised Linear Mixed Models of the effect of nest type and treatment on hours of exposure to temperatures exceeding 35 ˚C at different maximum ambient air temperatures (Mean ± 95%CI).

Comparison of nest temperature between natural nests and new artificial nest designs. As expected, exposed timber boxes were significantly warmer than natural nests and reached mean daily maximum temperatures around 2 – 3 ˚C higher than natural nest throughout the year (Figure 5.14). Exposed timber boxes exceeded upper thermoneutral limits more frequently than natural nests with the largest difference observed in the months of April, October and November (Figure 5.15). Artificially shaded timber boxes, exposed plastic tunnels and naturally shaded plastic tunnels exhibited similar thermal profiles to natural nests however exposed plastic tunnels had higher daily maximum temperatures during the cooler months (May – September), while artificially shaded timber boxes were warmer during the Spring (September – November) (Figure 5.14). In contrast, timber boxes that had shading vegetation were significantly cooler than natural nests (and other nest types) throughout the year, particularly during the summer months when boxes were ~2.5 - 3 ˚C cooler than natural nests (Figure5.14). The proportion of days per month where temperatures exceeded thermoneutral limits was also significantly lower with naturally shaded nests exhibiting a greater than 50% reduction in the number of days exceeding 30 ˚C with the biggest differences (<100%) observed in the Autumn and Spring (Figure 5.15A).

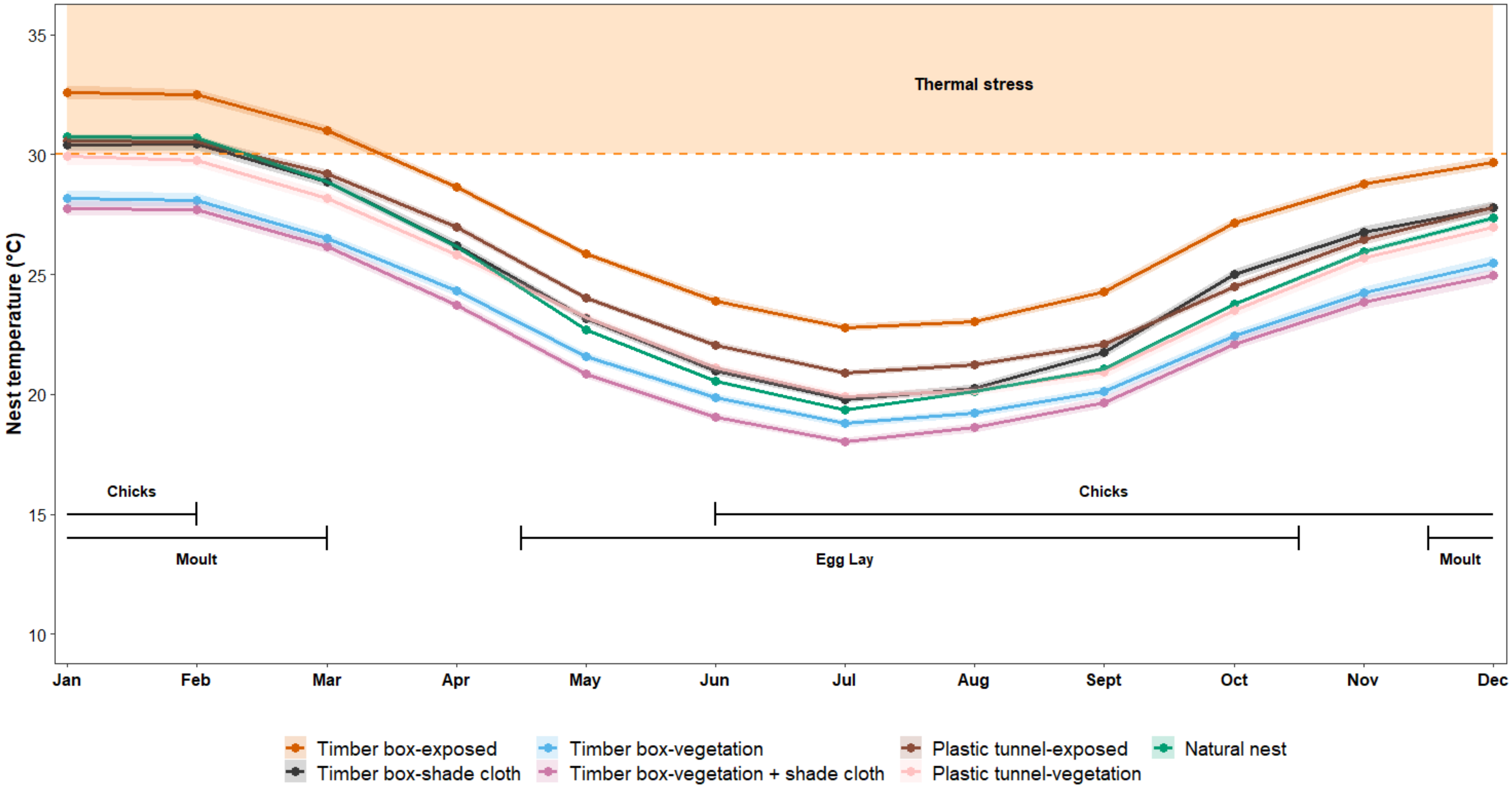

Figure 5.14: Model predicted mean daily maximum temperature per month for natural nests and different new artificial nests types (shaded area = 95% CI).

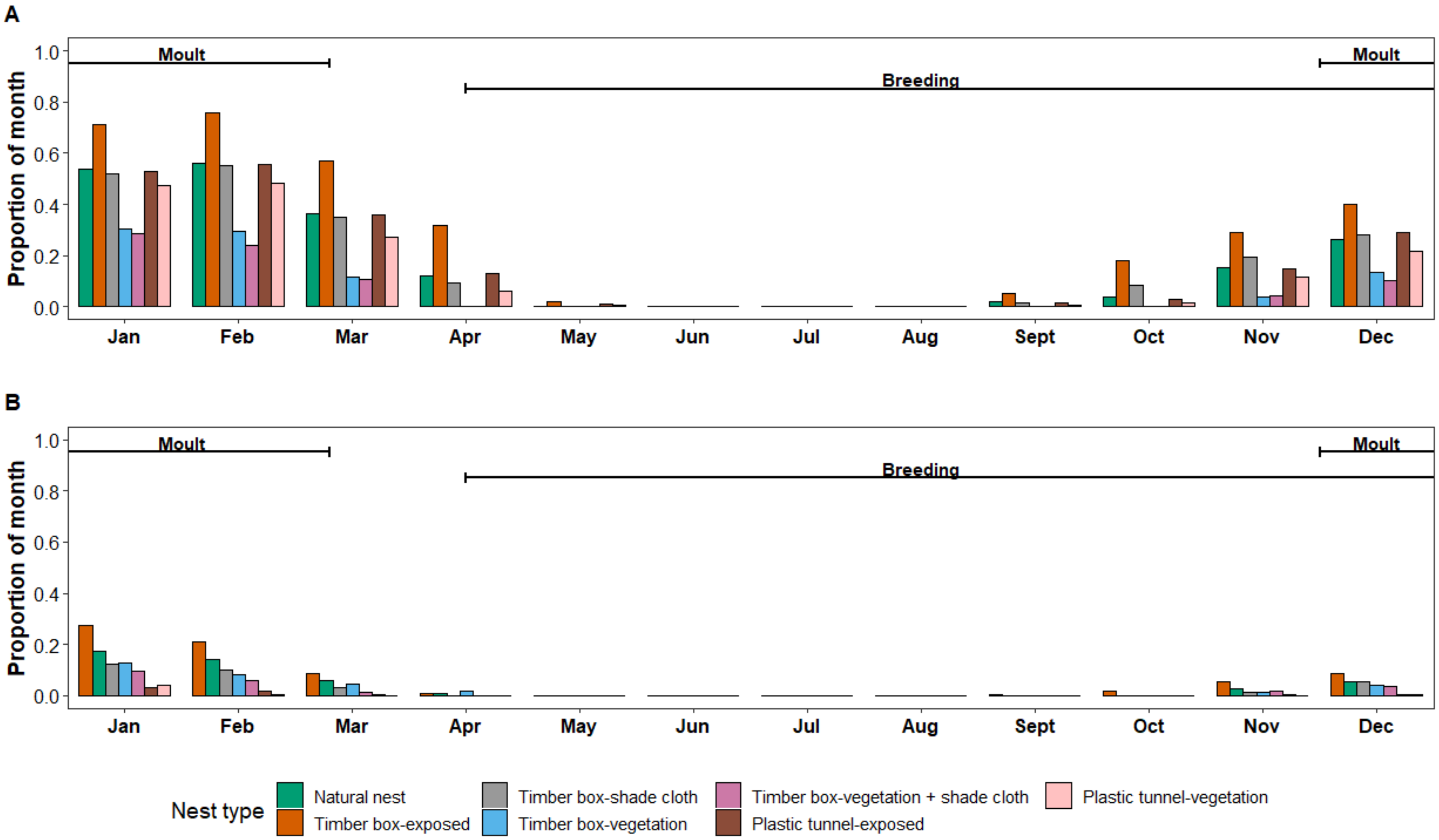

Figure 5.15: Model predicted mean proportion of days per month exceeding: A) 30 ˚C, and B) 35 ˚C for natural nests and different new artificial nest types

5.5 Discussion

After ambient temperature, nest box design and shading treatment were the strongest drivers of nest temperature. All nest types were generally hotter than the ambient conditions with some nests exceeding the daily ambient maximum by several degrees. While nest design and shading methods were effective at ameliorating nest temperature, shading vegetation had the greatest buffering effect, significantly lowering maximum nest temperature as well as the frequency of exposure to upper thermoneutral limits. Shaded timber boxes and buried plastic tunnels had thermal profiles either comparable or cooler than natural nests and substantially reduced the number of days nests exceeded thermoneutral limits. These findings highlight the importance of shading vegetation in moderating temperature in artificial nests and provide insight into the potential consequences of uninformed provisioning of artificial nests.

The length of time that exposed artificial nests maintained thermal extremes was particularly concerning and may have considerable biological consequences. Temperatures above 30 ˚C are considered stressful for little penguins and extended periods (more than two hours) exceeding 35 ˚C are likely to induce hyperthermia (Stahel and Nicol 1982; Horne 2010). Once reaching 30 ˚C or 35 ˚C, exposed artificial nests maintained temperatures above these thresholds on average four and five hours respectively. This far exceeds what might be considered safe for penguin occupants and in some cases may be fatal. This has been observed in other temperate penguin colonies, where extended periods of extreme temperature stress have resulted in chick and adult mortality (Dann 1992; Kemper *et al.* 2007).

5.5.1 Effect of nest design and shading on microclimate

Temperature. Compared to exposed timber boxes, all experimental nest types and treatments were successful at moderating nest temperatures. As expected, the most effective treatments were those positioned under shading vegetation which recorded cooler maximum and warmer minimum temperatures than their unshaded counterparts. Furthermore, nests shaded by vegetation were more effective at minimising the frequency and hours spent exposed to hyperthermic conditions. This illustrates the significance of vegetation cover as a natural insulator. Increased canopy cover limits solar insolation thus nest temperatures are reduced; an effect reported by several authors (Isaac *et al.* 2008; Rowland *et al.* 2017; Larson *et al.* 2018). In addition to shading, vegetation has additional cooling properties through increased evapotranspiration (Huang *et al.* 1987) which can also influence nest humidity. Vegetation can play an important role in determining microclimate inside bird nests (Klomp *et al.* 1991; Kim and Monaghan 2005a; Kim and Monaghan 2005b) thus should be an important factor when considering placement.

The multifaceted cooling properties of vegetation was further evidenced by the relatively higher temperatures recorded in boxes shaded by cloth only. The addition of shade cloth to timber boxes was less effective than vegetation at lowering daily maximum nest temperatures inside timber boxes. More importantly, it was significantly less effective at minimising exposure hours, thereby suggesting the artificial shading method described here is not a sufficient substitute for vegetation, particularly when ambient temperatures become elevated. On days where local temperature exceeded 30 ˚C, nest boxes with artificial shade treatment experienced thermal conditions likely to cause physical stress or hyperthermia in little penguins. While the frequency of days exceeding thermal limits was minimised, the capacity to dissipate heat once temperatures reached critical levels was inhibited. Still, it may be possible to achieve desired buffering capacity by increasing the shade provided by cloth or trialling other shading methods. Cassin's auklet (*Ptychoramphus aleuticus*) nest boxes shaded with timber were found to be cooler and less variable than unshaded boxes (Kelsey *et al.* 2016a). Similarly, wood duck (*Aix sponsa*) nests shaded with camouflage netting were also cooler, possibly improving hatching success (Olson 2017).

Improving nest microclimate through artificial methods alone warrants further investigation. While the effect of combining the shade cloth with vegetation was not significantly different to the effect of vegetation alone, it may be possible to enhance the insulative properties of vegetation by further increasing the artificial shade cover. The combination of the two shading treatments may give more protection from solar insolation than vegetation or shade cloth alone. Furthermore, the addition of shade cloth could also provide supplementary shade when vegetation cover recedes in the spring and summer months. The use of artificial shade as a complement to vegetation may be a valuable tool for mitigating negative effects associated with seasonal senescence of vegetation.

Compared to exposed timber boxes, buried plastic tunnels recorded cooler daily temperatures but had a noticeable time lag of three to four hours reaching daily maximum. This is likely due to the greater thermal inertia of the soil covering the tunnel. Consequently, this also meant that the plastic tunnels were less effective at dissipating heat and remained warmer than the ambient conditions well into the late afternoon and evening. Such a slow cooling trajectory likely was related to the lack of ventilation (boxes had ventilation holes whereas the ventilation of plastic tunnels was restricted to one opening at the front). While the buried plastic tunnels were on average cooler than exposed boxes, they exhibited high variability, frequently exceeding temperature thresholds and maintained critical temperatures for durations comparable to exposed boxes. Nonetheless, the buffering capacity of the plastic tunnels could potentially be enhanced and the variability moderated by increasing the depth to which the nests are buried. Fischer *et al.* (2018) demonstrated that procellariform nest boxes buried to a depth of 400 mm, were effective at retaining the stable environment and buffering capabilities expected in natural burrows. Similarly, a study investigating temperature inside artificial nests at varying depths used by burrowing owls (*Athene cunicularia*) found deeper nests were cooler but were sometimes below the lower critical temperature for the species increasing the thermoregulatory cost of incubating females (Nadeau *et al.* 2015). Thus, there is likely to be an optimum depth which is thermally suitable to a species. Replicating this kind of design merits further investigation for use in little penguin colonies, however, may pose logistical difficulties. The limestone and sandy substrates on Penguin Island make it inherently difficult to excavate large holes required to install subterranean structures. Furthermore, the extraction of penguins from the plastic tunnels for monitoring purposes was difficult and at times not possible without potentially damaging chicks and eggs. Nonetheless this type of design warrants further investigation and could have potential benefits in providing habitat in non-monitored areas or for moulting birds.

Humidity. Humidity was highly correlated to temperature, thus the observed variation between nest types was probably related to temperature differences. Even so, different materials differ in moisture holding properties and presumably have an influence on nest humidity. Additionally, vegetation was likely influencing humidity through transpiration (Huang *et al.* 1987). While the difference in humidity between nest type was negligible it is an important consideration as humidity can have negative effects on egg development (Grant 1982). The hygroscopic nature of artificial nests constructed of timber could have potential negative effects on breeding outcomes.

5.5.2 Effect of ambient conditions on temperature

As expected, nest temperature in all nest types and treatments increased with ambient temperature and maximum nest temperatures frequently exceeded maximum ambient temperatures. However, the degree to which nest temperature diverged from ambient was reduced on warmer days (>25 ˚C). This pattern may be due to the buffering properties of soil within the nest where soils warmer than the ambient air transfer heat to the air space within the nest box thereby limiting the cooling effect. Further, these conditions occur during the cool, wet season when soil moisture is higher thereby increasing the conductive nature of the soil. In contrast, when air temperature within the nest exceeded soil temperature, heat would be conducted to the now cooler soil reducing the rate at which the nest temperature rises. These buffering capacities of the soil contribute to a lagged change in nest box temperatures and with increasing differential between soil and air temperatures the effect is anticipated to diminish, particularly at high air temperatures and low relative humidity.

For altricial birds such as penguins, this pattern could prove beneficial during cooler parts of the year as warmer nests can reduce parental costs of incubation and enhance chick growth (Bryan and Bryant 1999; Dawson *et al.* 2005). However, despite the reduced rate of heating during the warmer months, nests failed to adequately buffer temperatures and conditions often exceeded thermoneutral limits (particularly in exposed timber boxes). Consequently, adults and chicks present in nests later in the season would have increased thermostatic demands, reducing energy allocation to reproduction and growth (Bryan and Bryant 1999; Pérez *et al.* 2008).

Humidity and wind conditions moderated nest temperature although the effect of humidity was negligible. The effect of wind was largely dependent on the interaction between wind speed and direction. Both onshore and offshore winds had a cooling effect on artificial nest temperature; however, onshore winds were not associated with reduced maximum temperatures as was expected and it was only during strong wind conditions (≥30 knots) that onshore winds began to have a significant cooling effect. This is possibly related to the positioning of the nests, most of which were located on the leeward side of the island, protecting them from westerly onshore winds. Increased wind speed is reported to reduce nest temperature (Ropert-Coudert *et al.* 2004; Heenan and Seymour 2012). However, as artificial nests are generally less permeable than natural nests, faster wind speeds are likely needed to have a similar cooling effect observed in natural nests.

Strong winds were less influential on the duration nests spent above upper thermoneutral limits. Strong offshore winds were associated with longer duration above 30 ˚C however the strength of onshore wind had no effect on duration over 30 ˚C and wind had no significant effect on the duration nests exceeded 35 ˚C. This has important implications as while strong onshore winds provide relief on hot days by lowering surface temperature on the island, these effects are not reaching artificial nests which remain at elevated temperatures even after surrounding conditions have cooled substantially. Nest entrance orientation and ventilation has the potential to influence nest microclimate due to the cooling effects of prevailing winds (Austin 1976; Ropert-Coudert *et al.* 2004; Long *et al.* 2009) Thus, artificial nests could benefit by having improved ventilation achieved structurally through changes in nest design (e.g., more ventilation holes) and by orientating entrances to the south west allowing for cooling onshore winds to reach nest boxes.

5.5.3 Management implications

With increasing temperatures, declining rainfall, and more frequent heat waves climate change is certain to decrease quality and availability of little penguin habitat and therefore increase reliance on artificial nesting structures. Exposed nesting structures create a substantial risk of further accelerating population decline via physiologically stressful thermal conditions. Here I have quantified the effects of design and shading, finding they are essential to providing appropriate thermal conditions. The capacity for artificial nests to shelter occupants from temperature extremes is critical in evaluating their suitability as a conservation tool; however, the effect that increasing surface temperature will have on microclimate characteristics within artificial nests is poorly understood (Catry *et al.* 2011; Griffiths *et al.* 2017). While there has been growing interest in the thermal suitability of artificial nests across multiple taxa (Ellis 1999; Isaac *et al.* 2008; Lei *et al.* 2014; Goldingay 2015; Nadeau *et al.* 2015; Griffiths *et al.* 2017; Maziarz *et al.* 2017; Rowland *et al.* 2017; Fischer *et al.* 2018), the application of mitigation strategies has received surprisingly little attention (but see Larson *et al.* 2018). My work fills an important gap, quantifying means by which to buffer occupants of artificial nests against stressful thermal conditions and will be invaluable in informing future conservation efforts (Catry *et al.* 2011).

Results from this study augment others that show many current artificial nest structures produce low quality environments not compatible with conditions suited to their target species (Ellis 1999; Isaac *et al.* 2008; Lei *et al.* 2014; Goldingay 2015; Nadeau *et al.* 2015; Griffiths *et al.* 2017; Maziarz *et al.* 2017; Rowland *et al.* 2017). Future management of this colony should ideally have a strong focus on maintaining and restoring quality vegetation that will facilitate natural nesting and provide sufficient cover over artificial nests. However, climate driven change in habitat quality and availability will mean managers may need to rely on artificial shading methods or alternate nest construction for ameliorating temperature extremes. The artificial shading method described and tested here is unlikely to be adequate in buffering artificial nests against predicted thermal extremes. However, increasing shade cloth would provide additional protection from effects of increased temperature and is recommended as a minimum for management of exposed artificial nests. Future work should continue to investigate alternate methods of insulating or shading artificial nests. For example the use of thicker timber (Calder *et al.* 1983), increasing ventilation and airflow (Ropert-Coudert *et al.* 2004) , the use of insulating soil (Nadeau *et al.* 2015; Fischer *et al.* 2018) or the application of thermal insulation materials such as polystyrene or aluminium foil batts (Larson *et al.* 2018), have been suggested as possible options for enhancing insulative properties of artificial nests; though a combination of these alternative methods is likely the best approach. Regardless, vegetation cover remains a critical component in nest temperature thus a more active management strategy such as targeted irrigation and/or using drought and heat tolerant plant species for shading artificial nests may be necessary for long term management of little penguin habitat.

For artificial nests to be a successful climate adaptation tool, they must be attractive to their target species while providing an environment that is the comparable, if not superior, to natural conditions. Ideally, they must also maintain suitable conditions into the future under predicted climate change scenarios. All nest type-shading treatments tested here were effective at buffering temperature relative to exposed timber boxes. However more importantly, shaded timber boxes and buried plastic tunnels had thermal profiles either comparable or cooler than natural nests and substantially reduced the number of days nests exceeded thermoneutral limits, highlighting their potential as climate adaptation strategy, at least in the short term. This does not negate the need for continued consideration of their limitations and the potential consequences an incompatible design may have on the occupants. Results from this study improve our understanding of microclimate of artificial nests and provides direction for future management of little penguins and other burrow nesting seabirds.

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CHAPTER 6

General Discussion

6.1 Introduction

Almost half of the world's seabird species are undergoing considerable decline with climate change a major contributing factor driving this trend (Chambers *et al.* 2011; Sydeman *et al.* 2012; Dias *et al.* 2019). The effect of climate variability in marine ecosystems on seabird population dynamics is well documented (Congdon *et al.* 2007; Grémillet and Boulinier 2009; Chambers *et al.* 2011; Chambers *et al.* 2013). However, comparatively few studies examine how changes in the terrestrial environment could be compounding climate change impacts on some species; all seabirds rely on land (islands, continental margins, ice shelves) for reproduction – a crucial bottleneck in their life cycle. Particularly vulnerable to synergistic marine and terrestrial climate pressures are those populations existing at the latitudinal margins of a species distribution (Hampe and Petit 2005; Grémillet and Boulinier 2009; Sydeman *et al.* 2012). Exposed to higher climatic variability relative to those at the range core, edge populations are becoming increasingly important for predicting and managing species' responses to expected climate change (Channell 1995; Hampe and Petit 2005; Lomolino and Pauls *et al.* 2013).

Much early research on species' distributional response to climate change, especially for vagile animals, is centered on the capacity to migrate poleward or up in elevation (Opdam and Wascher 2004). As change has accelerated and research has developed, it has become increasingly clear that species specific response will vary and many species will instead have to rely on *in situ* adaptation to persist (Davis *et al.* 2005; Vedder *et al.* 2013). Seabirds with their widely separated breeding locations, frequently on islands epitomize this issue. At the same time, environmental managers and decision makers have been faced with the challenge of identifying management interventions that assist population persistence and do not make matters worse (Greenwood *et al.* 2016). Exploring strategies to improve species' ability to adapt within their current range is gaining more attention but research and quantitative evaluation of measures have lagged (Hobday *et al.* 2015; Greenwood *et al.* 2016). Managing and adapting terrestrial habitat quantity and quality to enhance breeding success and adult survival is one compensatory measure that can be used to offset the effects of climate change on seabirds (Mawdsley *et al.* 2009; Chambers *et al.* 2011).

The broad objectives of this thesis were to describe and quantify use and microclimate of nesting habitat used by a vulnerable rear edge population of little penguins (*Eudyptula minor)*. It sought to identify implications of terrestrial climate change and evaluate the efficacy of artificial nests as an adaptive management option for this species. To achieve this, I characterised little penguin nesting habitat and quantified relationships between nest attributes, microclimate (temperature and humidity), nest use and reproductive success. I tested two artificial nest designs and shading treatments, assessing their capacity to provide microclimate conditions comparable to natural nest burrows. Here I provide an overall synthesis of the main findings of the research chapters (Chapters 3 -5). I discuss the management implications of climate change on nest habitat and microclimate. I discuss the efficacy of artificial nests as a climate adaptation tool and implications for management and suggest management actions that could be made to maintain and improve both the natural and artificial breeding habitat on Penguin Island. Finally, I outline directions for future research.

6.2 Quantifying nest habitat use

Management practices aimed at restoring and supplementing habitat involve a diverse range of actions and are often challenging (Hale *et al.* 2019). Effective management can fail when a mismatch occurs between human perception of good habitat and what are functional habitats for animals, leading to unintended ecological traps, where species preferentially occupy habitats that reduce fitness (Severns 2011; Hale *et al.* 2015). A critical first step in achieving habitat management objectives and avoiding ecological traps, is the identification of what habitat features are preferred and how these features might influence reproductive output or survival of target species (Jones 2001). Perhaps more importantly, it is essential to gather population specific habitat selection information as conservation measures based on data gathered from a species' central populations may be inappropriate and, in some cases, counterproductive for peripheral populations (Hampe and Petit 2005). Furthermore, contrasts in the habitats of peripheral and core populations could provide insight into future changes in species distributions and adaptation under climate change (Valladares *et al.* 2014).

Penguin Island's little penguin colony represents a rear edge population at the north-western limit of this species range. Most previous studies examining little penguin breeding habitat has been centred on core populations in south-eastern Australian and New Zealand (Weerheim *et al.* 2003; Braidwood *et al.* 2011; Schumann *et al.* 2013; Sutherland *et al*. 2014; Marker 2016). The differences in breeding phenology, nesting substrate and climate observed at this north-western population warrants the need for quantification of both natural and artificial habitats at this location and will provide important contrasts to other portions of the species range. Such information is critical for informed management of edge populations. In Chapter 3, I quantified the characteristics of both natural and artificial nests and investigated the influence of nest characteristics on (a) probability of nest use, and (b) probability of nest success. I found that little penguins did not select nest sites randomly, but instead based nest site selection on topographical, vegetation and nest site attributes. Penguins nesting in natural sites selected taller thicker vegetation located nearer to penguin landfall sites. In contrast, natural features played less of a role in the selection of nest boxes and use was predominately driven by the structure of the box (longer boxes had a greater probability of use). Neither landscape nor nest site attributes influenced the overall success of nests and the annual success was comparable between nest types.

Landscape position and topographical attributes are common parameters investigated within studies of nesting habitat in other little penguin colonies (Weerheim *et al.* 2003; Braidwood *et al.* 2011; Schumann *et al.* 2013; Marker 2016) with the underlying premise that easy access to nest sites assists in the reduction of energy demands (Pinshow *et al.* 1977). The preference of Penguin Island little penguins for nesting near to landfall sites suggests that location on the island is a major factor driving selection at this colony as well. In contrast, there was no preference of landscape attributes evident in the selection of artificial nests, although this is likely due to the non-random manner in which artificial nests have historically been placed (Klomp *et al.* 1991) making topograpahical comparisons problematic. The preference of little penguins for nesting in close proximity to landfall areas combined with the observed fidelity of little penguins to landfall sites (Wienecke *et al.* 1995; Weerheim *et al.* 2003) highlights the critical need for preservation of these habitats. Accordingly, landing sites and surrounding areas must be a priority consideration in the future management and conservation planning for this species.

In addition to island position, vegetation attributes played a key role in the selection of natural nest sites. Vegetation is proposed to have various functions with the two most common being concealment from predators and protection from solar insolation (Colombelli-Négrel 2019; Stokes and Boersma 1998; Goodenough *et al.* 2009). For artificial nests however, vegetation attributes were not found to be important and use was predominantly related to the structural design of the box. Although penguins utilised all three nest types available, there was an apparent preference for longer boxes which may be due to this structure more closely replicating a well-covered nest cavity. The readiness of little penguins to occupy artificial nest boxes is well documented and a variety of designs have been used successfully in the management of little penguin colonies across Australia and New Zealand (Houston 1999; Perriman and Steen 2000; Johannesen *et al.* 2002; Sutherland *et al.* 2014; Marker 2016). This suggests that in most cases, artificial nest boxes are effectively providing the visual cues sought by little penguins prospecting for a nest site. However, the use of artificial habitat does not necessarily indicate habitat quality and the fundamental differences between a natural and artificial nest means that the microclimate provided by artificial nest boxes is unlikely to represent the conditions of a natural nest. This was supported by results presented in Chapter 4 that revealed nest boxes were ineffective at replicating microclimate conditions of natural nests, were significantly warmer, and have the potential to become an ecological trap, jeopardising their effectiveness as a management tool (Catry *et al.* 2011). Despite this, nest success between nest types were comparable suggesting that differences in nest temperature observed between the nest types is currently not having a direct impact of the overall breeding outcome of nests. Nonetheless, warmer temperatures in nest boxes could have sublethal effects through increasing thermostatic demands, influencing fledgling weight thus reducing juvenile survival and subsequent recruitment into the population (Dann and Norman 2006; Catry *et al.* 2011).

The preference of little penguins on Penguin Island for nesting in close proximity to shore line, combined with the low elevation profile of most little penguin nest sites potentially exposes this colony to climate change impacts associated with rising sea level and increased frequency and intensity of storms. Furthermore, warmer and drier terrestrial conditions associated with climate change (Bates *et al.* 2008; Andrys *et al.* 2017) are likely to reduce both the quality and availability of important nesting vegetation. The resulting reduction in available habitat plus high natal philopatry observed in little penguins (limiting their dispersal capacity) may lead to an increased reliance on artificial nests at this colony.

In addition to climate change implications, this study highlighted the potential conflict within management objectives between the need to maintain both the ecological and social values of Penguin Island. Landscape features selected by little penguins for nesting (flat or gently sloping ground near to landfall sites on the leeward side of the island) are also the ideal sites for the placement of visitor and management infrastructure such as buildings, walkways and visitor use areas. A review of current management strategies may be necessary to ensure consideration of preferred nesting habitat when planning for future infrastructure.

Findings from Chapter 3 filled an important knowledge gap in understanding the nesting habitat requirements of little penguins on Penguin Island. Management programs interested in restoring and supplementing little penguin nesting habitat should be targeted at:

(1) Retaining and expanding areas of high vegetation cover near to known landfall sites on flat or gently sloping ground.

(2) Revegetating and conserving established bushes of preferred plant species.

(3) Concentrating management of nest habitat on the leeward side of Penguin Island.

(4) Considering design and location when placing artificial nests in the field.

(5) Considering nesting habitat preferences when planning infrastructure work.

6.3 Nest microclimate

Nest microclimate is critically important to egg and chick development; nest temperature and humidity have been linked to a number of reproductive parameters including clutch size, embryonic development, chick growth and survival (Wiebe 2001; Larson *et al.*

2015; Bobek *et al.* 2018) thus playing an important role in reproductive success and ultimately population stability. Prior to developing and testing any management-based adaptation strategies that involve nesting habitat, it is firstly important to obtain quantifiable microclimate data for nests and understand the mechanisms that drive thermal properties. In Chapter 4, I quantified microclimate of artificial nest boxes and natural nest burrows and investigated how local climate conditions and nest characteristics influence nest microclimate, focussing on the daily maximum temperature and exposure to the upper thermoneutral limits of little penguins. This study revealed that nest boxes were ineffective at replicating microclimate conditions of natural nests. Nest boxes experienced significantly higher daily maximum temperature and longer duration exposed to temperatures exceeding upper thermoneutral limits. Thermal properties of nests were strongly influenced by local climate conditions, specifically ambient temperature. However, fine scale biotic and abiotic nest characteristics have important buffering properties influencing the maximum daily temperature and hours of exposure to upper thermoneutral limits.

Ambient temperature was a strong predictor of nest temperature however the capacity for current natural and artificial nest types on Penguin Island to moderate increases in ambient temperature were significantly limited. This is worrisome given that the warming and drying trend observed over recent decades in southwestern Australia is predicted to continue (Bates *et al.* 2008; Andrys *et al.* 2017). Therefore, understanding how climate change will modify the microclimate of nests is critical to the development of appropriate conservation strategies. Using nest temperature models developed here, I generated predictions of nest temperature based on a 2 ˚C rise in ambient temperature. I found both nest types will become limited in their capacity to provide optimal nesting environment exposing penguins to negative thermal conditions during multiple stages of their annual life cycle. The number of days annually where natural and nest box conditions exceed thermally stressful conditions (≥30 ˚C) is predicted to increase by approximately 37% and 56% and the number of days exceeding hyperthermic conditions (≥35 ˚C) predicted to increase by approximately 41% and 49% respectively.

The ability to delay or advance breeding is one way seabirds cope with ocean climate variability (Reed *et al.* 2009). However, this relies on the conditions within the nesting environment during incubation and chick rearing remaining thermally neutral. The warmer temperature observed in nest boxes could already be limiting the extent to which penguins can adjust their breeding, potentially leading to an asynchrony between food availability and optimal nesting conditions and a shorter nesting window (Figure 6.1A). A warming of 2 ˚C presented a concerning scenario whereby the thermally neutral window was shortened in both nest boxes and natural nests substantially reducing the optimal breeding period for both nest types (Figure 6.1B). If the current temperature trajectory continues unabated this will have major implications for the resilience and longevity of the population on Penguin Island.

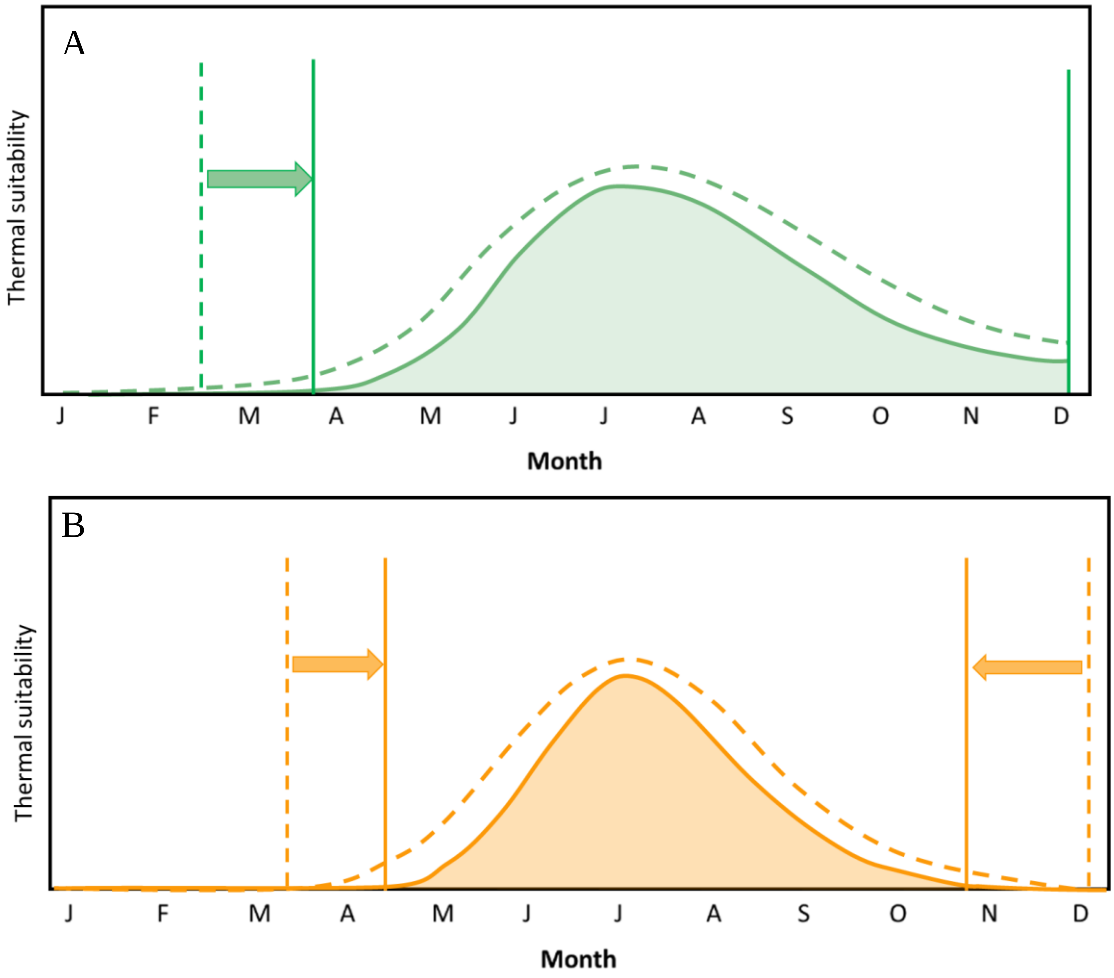

Figure 6.1: Potential shortening of thermal window suitable for nesting (dashed lines represent current thermal window solid filled lines represent thermal window under a 2˚C climate warming scenario for **(A)** natural nests and **(B)** nest boxes. Arrows represent shortening of thermal window.

While nest temperature is predominantly influenced by ambient temperature, there is potential for these effects to be buffered by local environmental heterogeneity (Hampe and Petit 2005). Results here demonstrated the important buffering properties of vegetation. This supports findings in Chapter 3 highlighting the critical importance of conserving and increasing cover of vegetation in both natural and artificial penguin nesting habitats. This is particularly pertinent for management of nest boxes given the inclination of little penguins to occupy any artificial cavity that replicates a burrow-like environment irrespective of vegetation cover (Chapter 3). The mismatch between the attractiveness and quality observed for artificial nests means penguins are being inadvertently encouraged to nest in suboptimal environments. Ensuring the quality of artificial nests remains coupled with their attractiveness through adequate vegetation cover is imperative to avoid nest boxes becoming an ecological trap.

All seabirds must rely on terrestrial habitats during their breeding phase. Penguins are unique among seabirds in that they utilise terrestrial habitats for two critical life events: breeding and moulting. However, most studies on climate change effects on little penguins have focused on the indirect effects of changes in food availability on the phenology, reproductive output and survival at sea (Numata *et al.* 2000; Perriman *et al.* 2000; Cullen *et al.* 2009; Cannell *et al.* 2012; Sidhu *et al.* 2012). Here I have highlighted the importance of capturing data spanning the entire annual cycle and demonstrated that natural habitat presently available to little penguins may not be adequate throughout all stages of their annual cycle. Increases in temperature are likely to significantly challenge the thermoregulatory abilities of this species during their moult and increased frequency of hot days predicted with climate change could result in increased mortality (Cannell *et al.* 2016).

To sustain their moult little penguins use 15% more energy than they would under normal rest conditions (Gales *et al.* 1988). As air temperature rises, hyperventilation can further enhance energy demands (Baudinette *et al.* 1986). Little penguins are unable to forage during moult, consequently using excess energy could increase the risk of starvation. This presents another potential management conflict between balancing both ecological and social values on Penguin Island. Popularity of the 12 hectare island as a tourist destination has grown over recent decades with peak daily visitation in excess of 1000 visitors occurring regularly during the summer months (Smith 2014; Smith 2019). On Penguin Island, heat stressed little penguins have been observed retreating to the water to cool down. However, this has only been observed when there is no perceived threat such as the presence of humans (E Clitheroe, pers. obs.). Thus, during the summer months when visitation is high, the risk of mortality from hyperthermia is exacerbated. High adult survival is crucial to population stability (Dann 1992) and even small decreases from elevated stress likely have disproportionate impacts on persistence likelihood.

Findings from Chapter 4 provided critical insight into how predicted changes in terrestrial climate may compound marine climate change impacts on this colony, providing a more complete understanding of the climate limitations of edge populations. This chapter revealed that the current and future thermal environment of little penguin terrestrial habitat frequently exceed little penguin upper thermal limits. Exceedance of physiological limits has been shown to induce stress with negative demographic consequences. Intervention to improve nesting habitat and better quantify consequences is urgently needed given recent estimates of a declining population. Short term management strategies might focus on:

(1) Retaining and expanding areas of high vegetation cover and ensuring artificial nest boxes are not exposed to direct solar insolation.

(2) Removal of artificial nests that present dangerous thermal conditions.

(3) Modification of artificial nests through increasing vegetation cover.

(4) Implementing management strategies that minimise mortality of adult penguins during moult such as:

    a) Provision of cooling aids.

    b) Limiting visitor access on high risk days.

6.4 Artificial nests as a climate adaptation tool

Results from Chapter 4 indicated that while natural nesting habitat on Penguin Island currently provides a nesting environment within thermoneutral limits, conditions during the moulting phase are often suboptimal. Increasing temperature and decreasing rainfall predicted with climate change means high quality nesting and moulting habitat will likely become limited, increasing reliance on artificial nests at this colony. Additionally, the period whereby nesting conditions are considered optimal is predicted to shorten potentially causing a significant asynchrony between food availability and optimal nesting conditions. Furthermore, artificial nests currently used by little penguins on Penguin Island potentially present an ecological trap for penguin occupants as they are readily used by little penguins but fail to meet the microclimate conditions of natural nest sites. Nonetheless, artificial nesting habitat that provides a thermoneutral environment may be a valuable tool for management of this vulnerable colony of little penguins.

For artificial nests to be a successful climate adaptation tool, they must be attractive to their target species while providing an environment that is the comparable, if not superior, to natural conditions. Further, they must maintain suitable conditions into the future under predicted climate change scenarios. In Chapter 5, I experimentally evaluated the effectiveness of two nest designs and shading methods in buffering artificial nest temperature. All nest type-shading treatments tested were effective at buffering temperature relative to exposed timber boxes. Shaded timber boxes and buried plastic tunnels had thermal profiles either comparable or cooler than natural nests and substantially reduced the number of days nests exceeded thermoneutral limits, highlighting their potential as climate adaptation strategy.

In the absence of shading vegetation, the artificial shading of nest boxes could be an effective means for reducing nest temperatures and is an option for short term management of exposed artificial nest boxes. However, shading vegetation provides an environment that is significantly cooler and may be beneficial in not only providing a safe thermal environment for the duration of the breeding season, but could also provide more optimal moulting habitat than what might be naturally available, particularly as conditions become warmer and drier.

The introduction of precautionary management actions is critical to boost population resilience to global climate change, increasing the prospect of autonomous adaptation (Chambers *et al.* 2011; Trathan *et al.* 2015). However, the difficultly of achieving such changes in marine habitats means that interventions may be limited to terrestrial habitats at the local scale (Chambers *et al.* 2011). Without the implementation of land based management actions, it is unlikely that a population will be able to cope with multiple climate and non-climate anthropogenic pressures. Artificial nests that provide suboptimal or physically stressful thermal conditions, such as those currently provided on Penguin Island, have the potential to place undue pressure on the little penguin population thus reducing adaptive capacity. On the other hand, well designed, appropriately shaded nest boxes may be a viable management strategy to reduce nest temperature and mitigate negative effects of increased global temperature thus boosting the resilience to climate change and non-climate change effects.

Results from this study demonstrate an achievable and effective approach to mitigating climate change effects through the careful design and placement of artificial nest boxes. However, caution must be taken as results from Chapter 4 and 5 revealed the risks associated with using poorly managed artificial nests in warm climates particularly for thermally sensitive species. The capacity of artificial nests to exhibit a wide thermal range emphasises the critical need for continued monitoring and management to ensure they remain safe and effective (Hobday *et al.* 2015). To maintain the efficacy of artificial boxes I recommend:

(1) Continuous monitoring of box condition and extent of cover.

(2) Promote vegetation growth around and over nest boxes.

(3) Artificially shading boxes where necessary in the short term while encouraging vegetation growth.

(4) Regular monitoring of nest box temperature to ensure any shifts towards more unfavourable thermal conditions are anticipated and mitigated.

6.5 Directions for future research

This thesis has presented novel data on nest habitat selection and microclimate of little penguins nesting in a disjunct rear edge population, highlighting the implications of terrestrial climate change effects on seabird populations at range edges and demonstrated the potential of well designed artificial nests as a means to effectively buffer the negative effects of climate change for thermally sensitive and burrow nesting species. However, it identifies several key areas requiring further research in order to expand our understanding of the ecology and conservation of little penguins.

In Chapter 3, little penguin nesting habitat on Penguin Island was characterised however, the nesting preferences for this species will likely vary across their range thus climate change impacts on their nesting habitat are also likely to differ. Conservation measures based on data from one colony may not be applicable for management of other populations. The adaptive capacity of a species to climate change will vary depending on location (Chambers *et al.* 2011), thus it is important to extend our understanding of nesting preferences to encompass little penguin populations throughout their range, particularly at range edges. Knowledge on the intraspecific variation in little penguin nesting habitat could be useful to examine trade offs between competing selection pressures and inform management priorities for different colonies across Australia and New Zealand.

Chapter 4 provided a concerning insight into the current and future nest habitat conditions of little penguin nests. The documented thermal tolerance of little penguins and physiological effects of being exposed to temperatures exceeding those limits (Stahel and Nicol 1982; Horne 2010) suggests little penguins have a limited capacity to cope with such changes in air temperature. However, there is limited knowledge on the reproductive and subsequent population level effects of increasing nest temperatures. Further investigation into links between variation in nest temperature and reproductive success, considered in unison with marine climate change effects, is essential to fully understand how this population may be affected by climate change.

Chapter 5 presented an effective adaptive management approach that could assist in in mitigating climate change pressures on this populations. However, work should continue to investigate ways in which to improve natural and artificial nest climates through alternative methods of shading or insulation. Additionally, while I have tested one compensatory measure for climate change adaptation, there are a number of other land based management options that should be considered in order to buffer anticipated changes in climate and boost resilience including management of non-climate threats or ex-situ conservation or translocation (Chambers *et al.* 2011).

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Appendices

Appendix 3.1 Breeding use and success of natural nest sites in relation to nest physical, vegetation and location attributes for penguins nesting on Penguin Island, Western Australia.

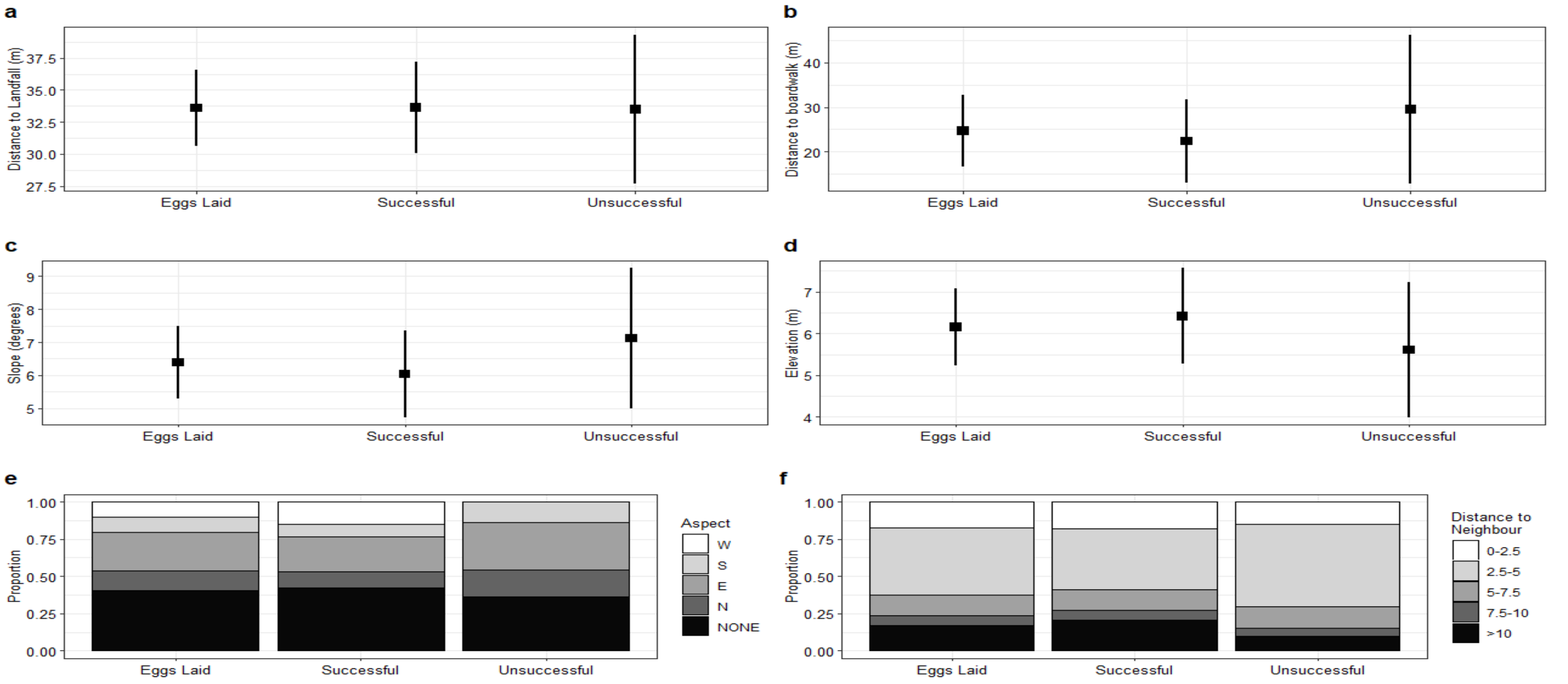

Figure A3.1 Breeding use and success of natural little penguin nests in relation to mean (95% confidence interval) or frequency of **a)** distance to landfall (m), **b)** distance to boardwalk (m); **c)** slope (degrees); **d)** elevation (meters above sea level), **e)** aspect (compass direction) and, **f)** Distance to nearest neighbour (m). Successful nests = chicks fledged; unsuccessful nests = no chicks fledged.

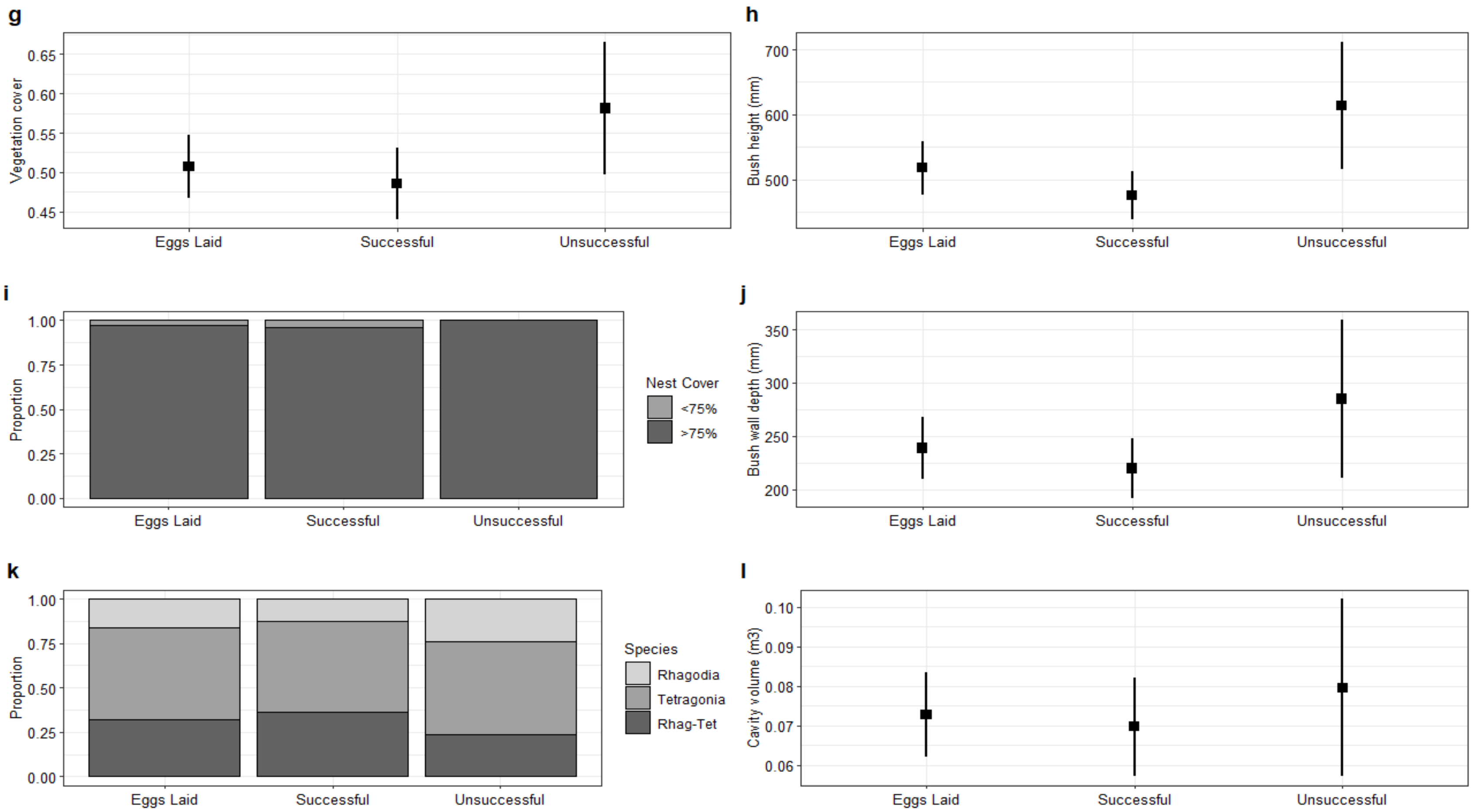

Figure A3.1 continued: Breeding use and success of natural little penguin nests in relation to mean (95% confidence interval) or frequency of **g)** vegetation cover (%) , **h)** bush height (mm), **i)** Nest cover (%), **j)** bush wall depth (mm), **k)**Species composition, and **l)** cavity volume(m3). Successful nests = chicks fledged; unsuccessful nests = no chicks fledged.

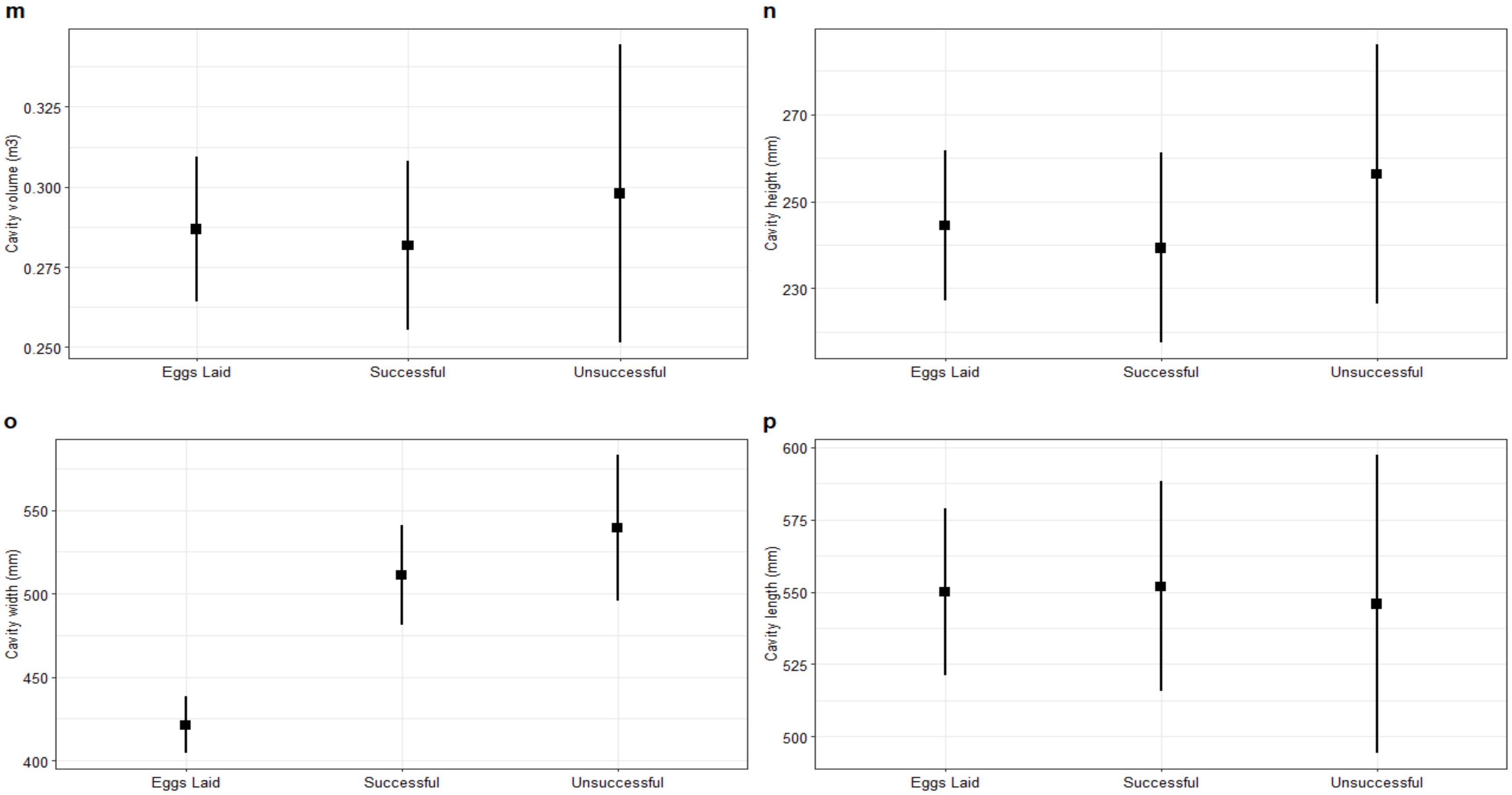

Figure A3.1 continued: Breeding use and success of natural little penguin nests in relation to mean (95% confidence interval) or frequency of **m)** Cavity area (m2) , **n)** cavity height (mm), **o)** Cavity width (mm) , and **p)** cavity length (mm). Successful nests = chicks fledged; unsuccessful nests = no chicks fledged.

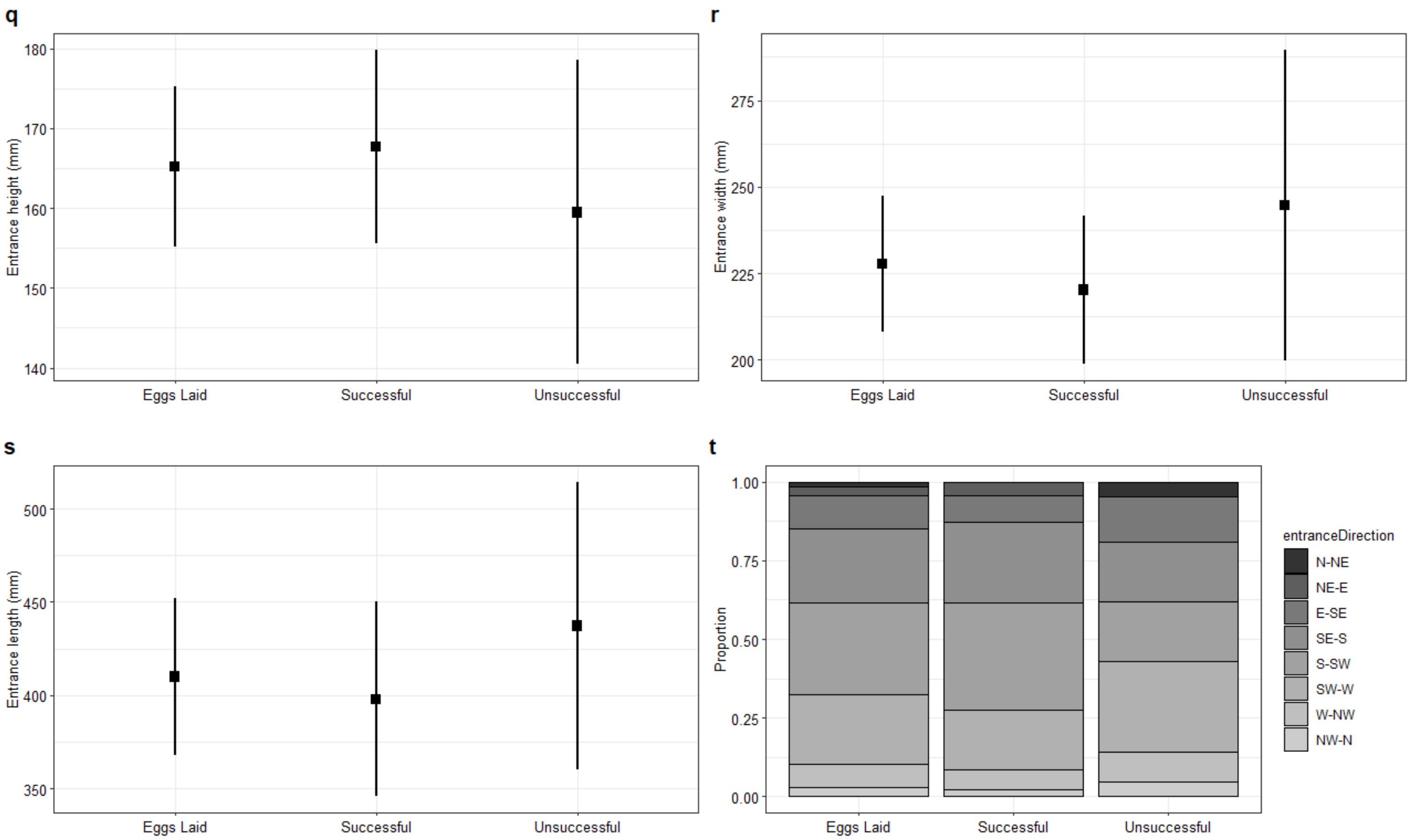

Figure A3.1 continued: Breeding use and success of natural little penguin nests in relation to mean (95% confidence interval) or frequency of **q)** Entrance height (mm) , **r)** entrance width (mm), **s)** entrance length (mm) and **t)** entrance direction (mm). Successful nests = chicks fledged; unsuccessful nests = no chicks fledged.

Appendix 3.2 Breeding use and success of artificial nest sites in relation to nest physical, vegetation and location attributes for penguins nesting on Penguin Island, Western Australia.

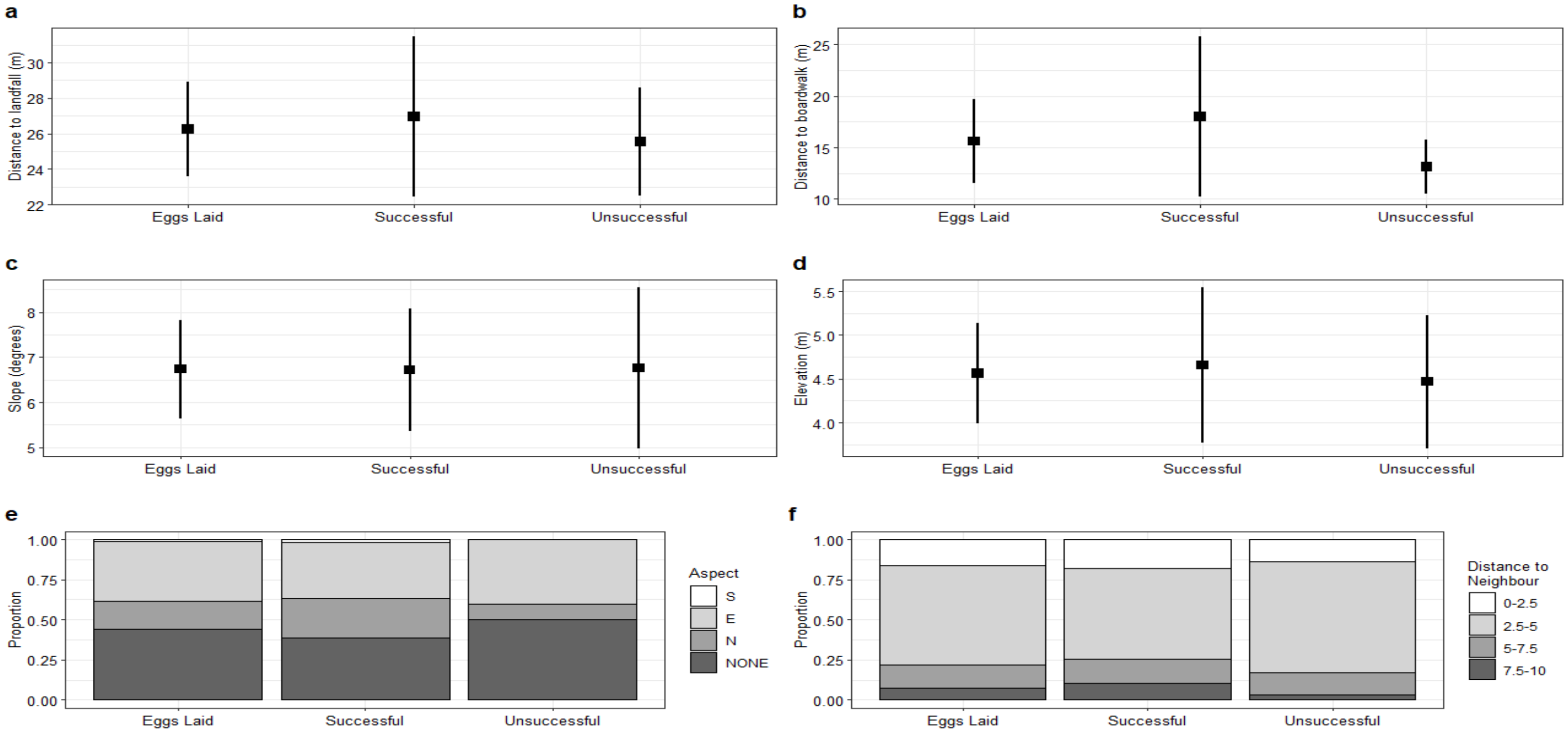

Figure A3.2: Breeding use and success of artificial little penguin nests in relation to mean (95% confidence interval) or frequency of **a)** distance to landfall (m), **b)** distance to boardwalk (m), **c)** slope (degrees), **d)** elevation (meters above sea level), **e)** aspect (compass direction), f) Distance to nearest neighbour (m). Successful nests = chicks fledged; unsuccessful nests = chicks no chicks fledged.

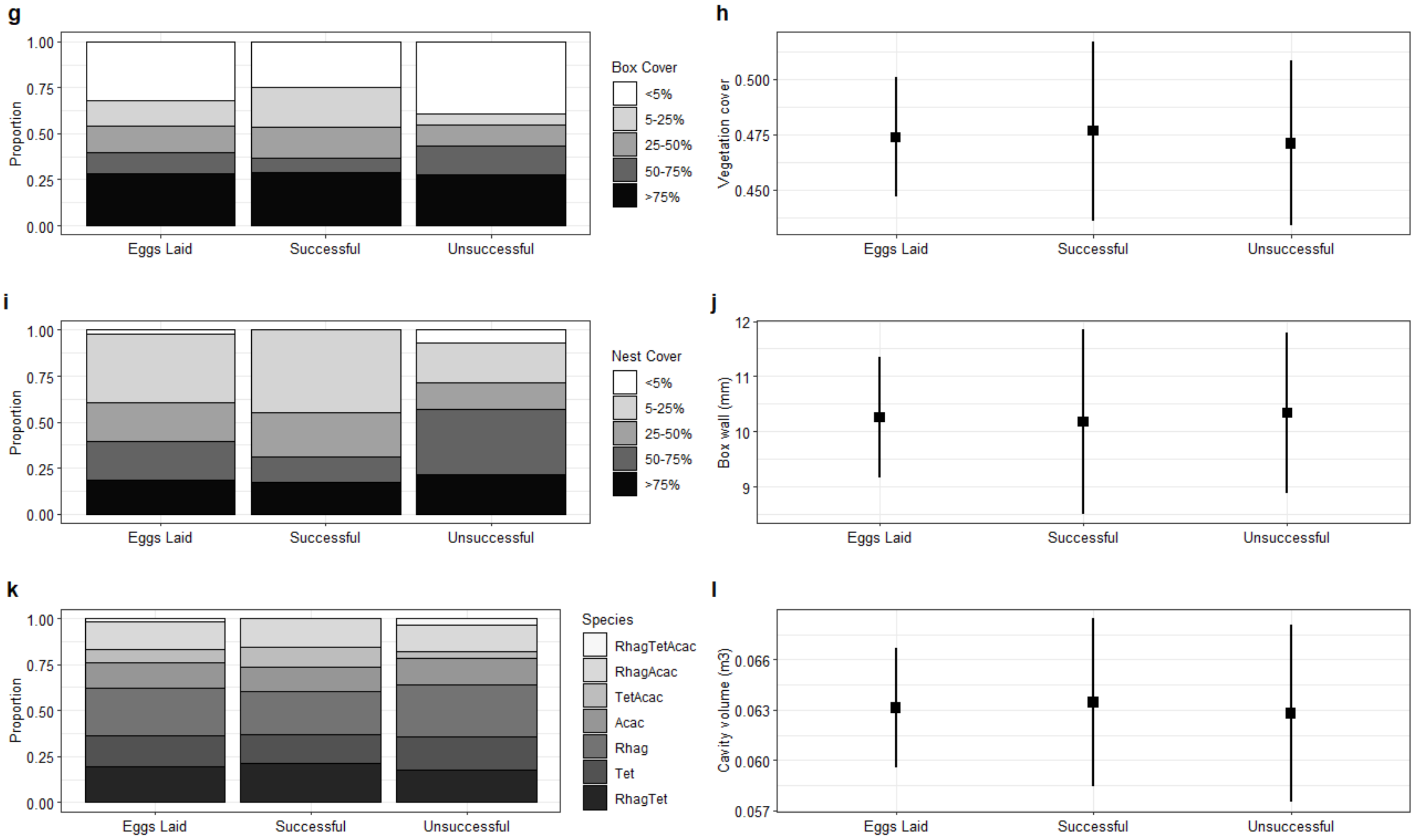

Figure A3.2 continued: Breeding use and success of artificial little penguin nests in relation to mean (95% confidence interval) or frequency of **g)** box cover (%) , **h)** vegetation cover(%), **i)** nest cover (%), **j)** box wall depth (mm), **k)** Species composition, and **l)** cavity volume (m3). Successful nests = chicks fledged; unsuccessful nests = no chicks fledged

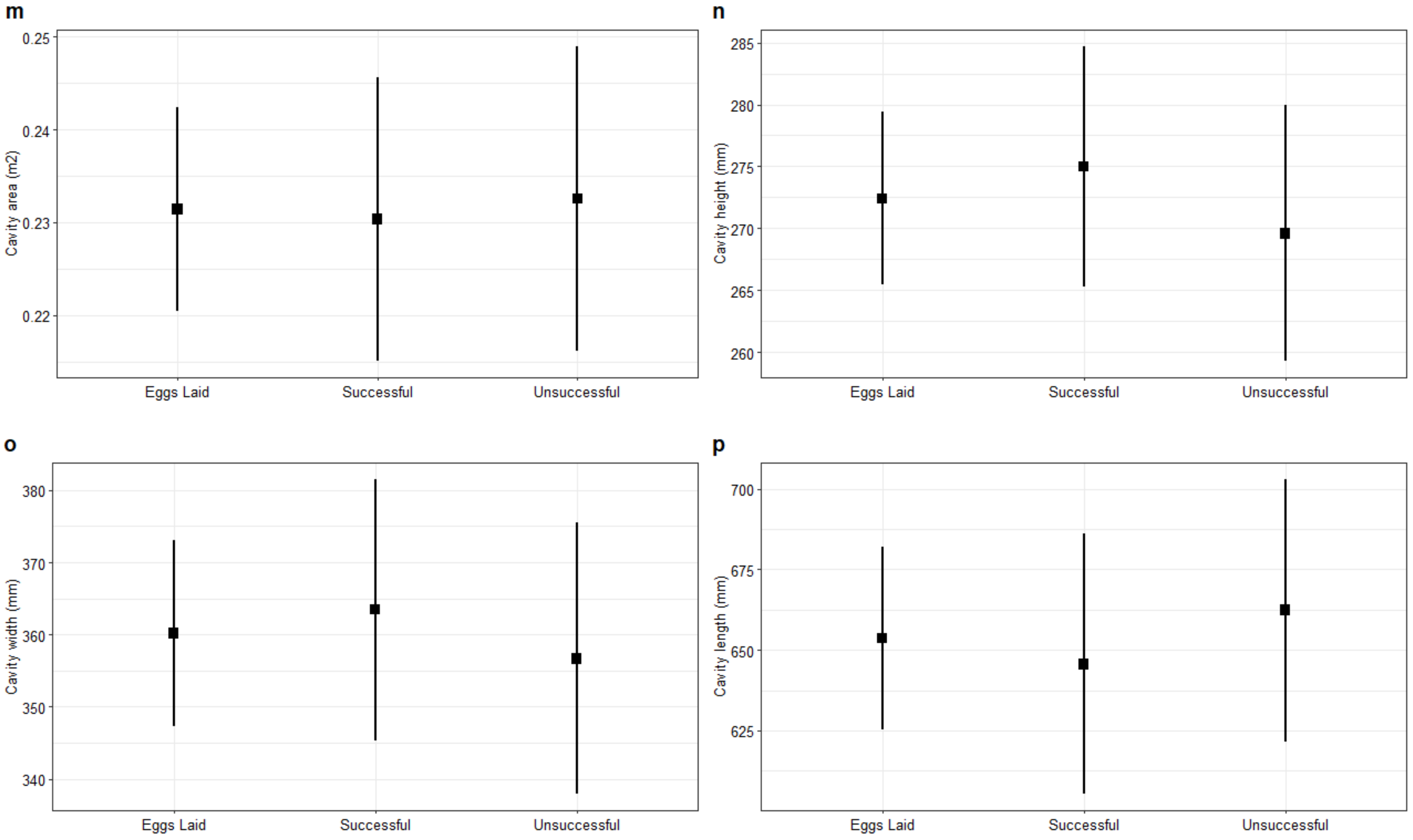

Figure A3.2 continued: Breeding use and success of artificial little penguin nests in relation to mean (95% confidence interval) or frequency of **m)** Cavity area (m^2) , **n)** cavity height (mm), **o)** Cavity width (mm) , and **p)** cavity length (mm). Successful nests = chicks fledged; unsuccessful nests = no chicks fledged.

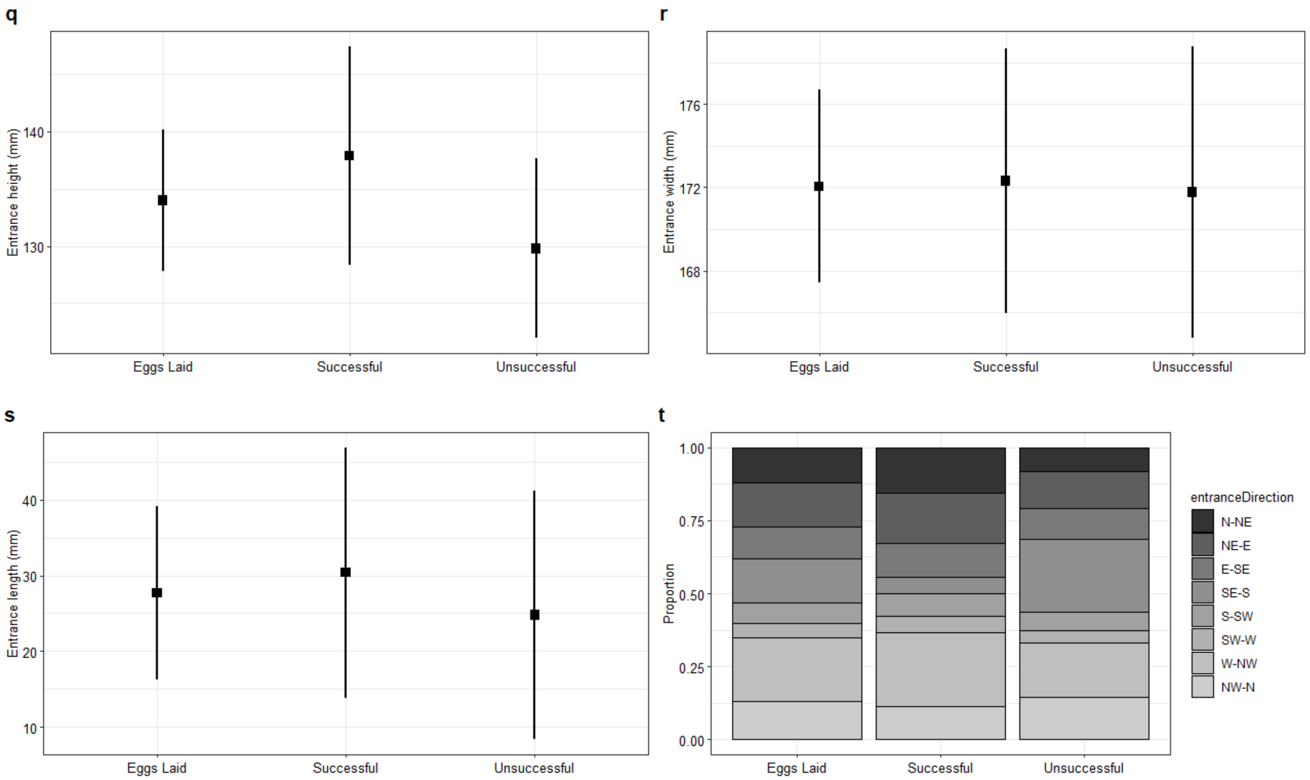

Figure A3.2 continued: Breeding use and success of artificial little penguin nests in relation to mean (95% confidence interval) or frequency of **q)** entrance height (mm) , **r)** entrance width (mm), **s)** entrance length (mm), and **t)** entrance direction (mm). Successful nests = chicks fledged; unsuccessful nests = no chicks fledged.

Appendix 4.1:

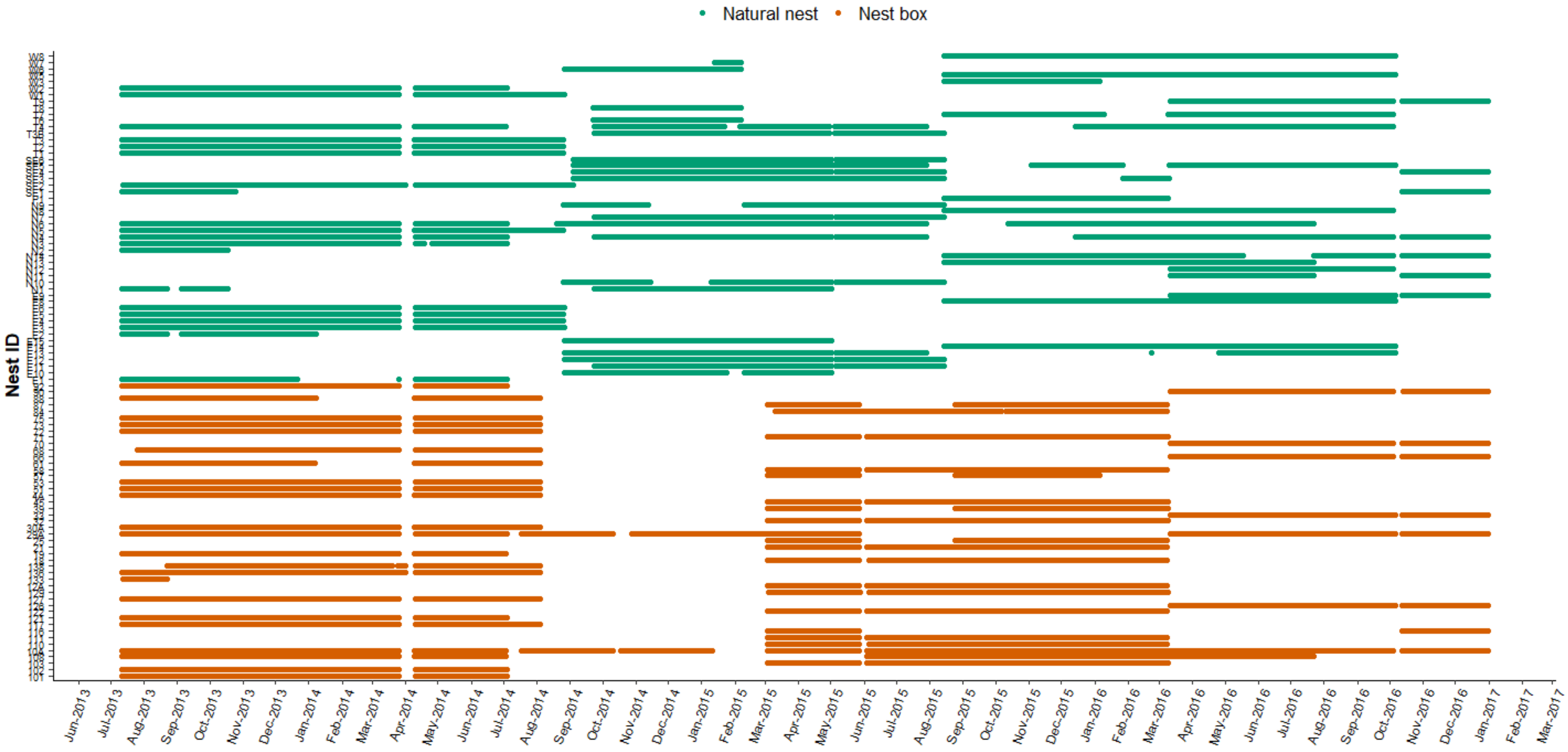

Figure A4.1: Dates of continuous temperature and relative humidity observations of each sample nest indicating occurrence of data losses

Appendix 4.2

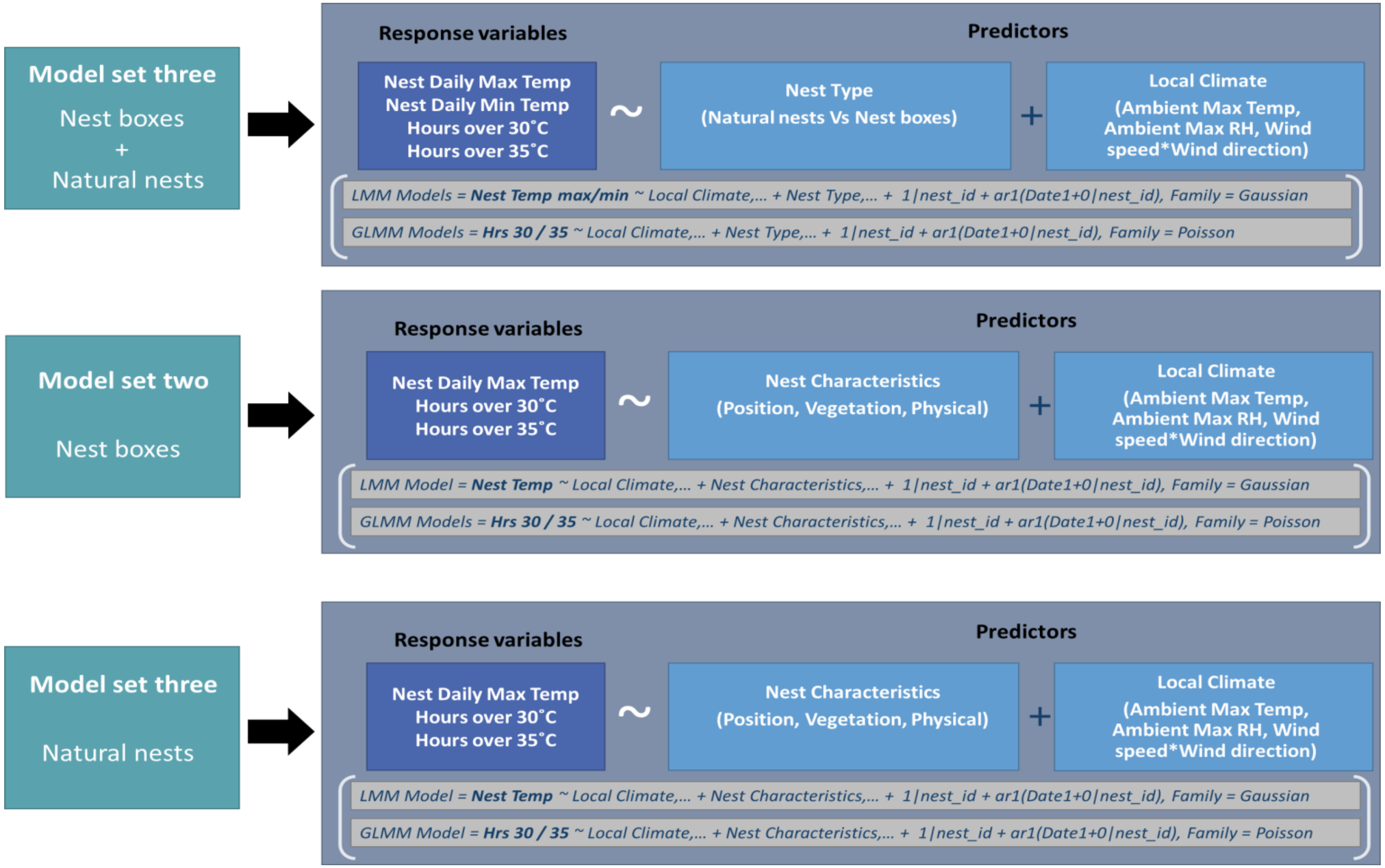

Figure A4.2: Modelling framework used to predict nest temperature of natural nests and artificial nest boxes of little penguins nesting on Penguin Island, Western Australia.

Appendix 4.3

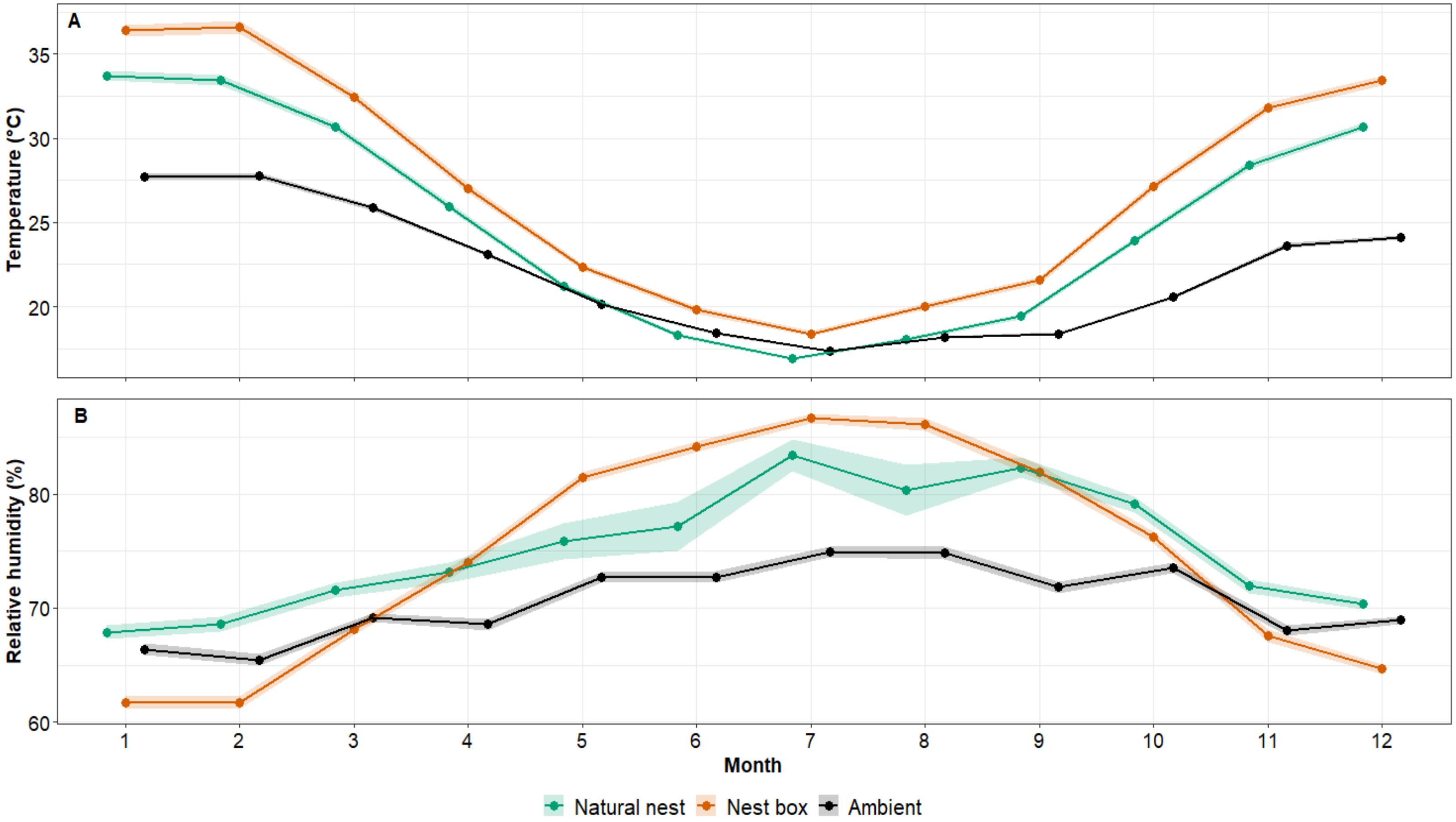

Figure A4.3: Mean monthly max temperature (A) and Mean humidity (B) of natural nests and nest boxes on Penguin Island and ambient conditions at Garden Island.

Appendix 4.4

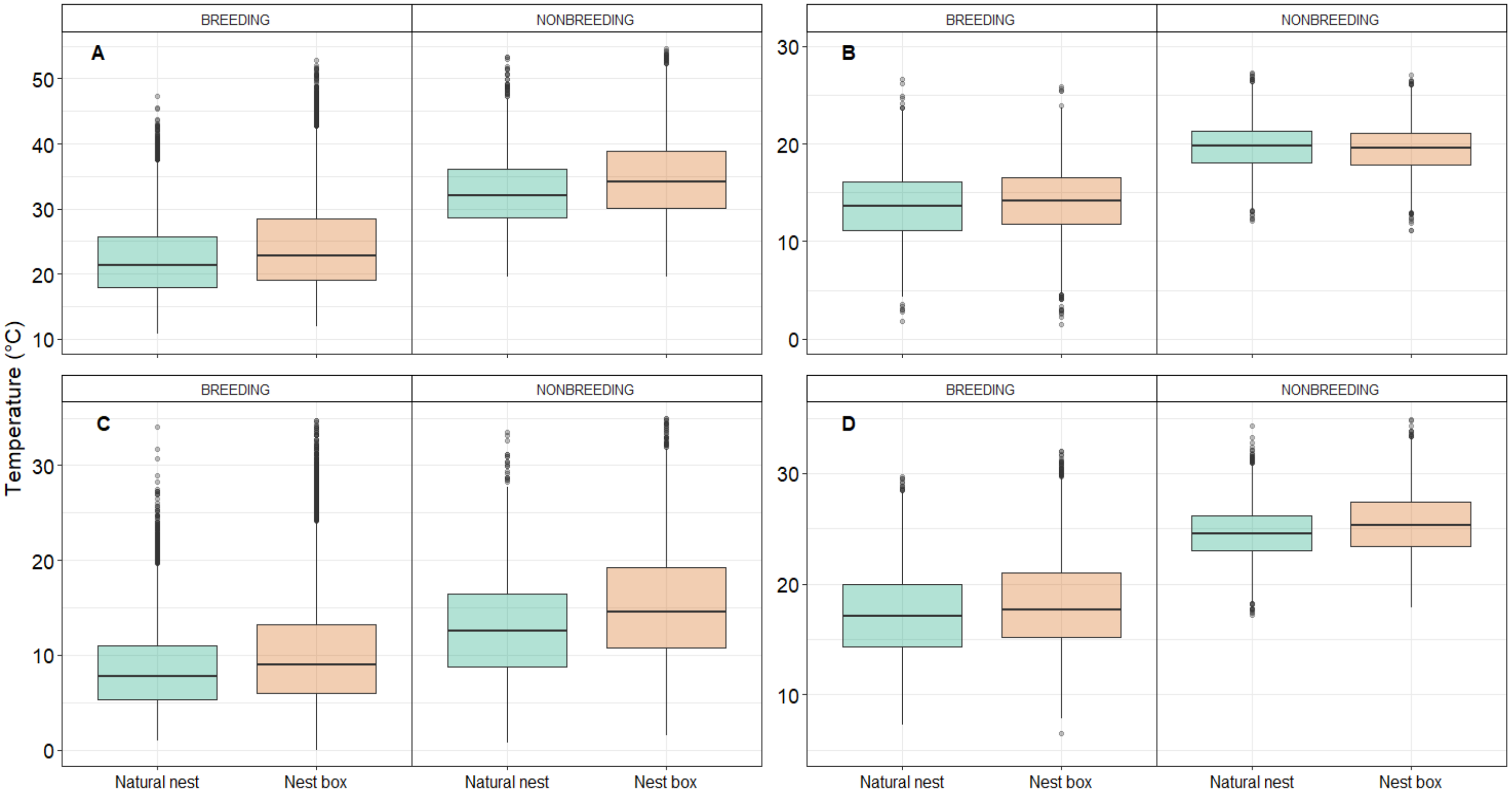

Figure A4.4: Box plots of mean daily temperature observations for natural nests and nest boxes during the breeding (April – December) and non-breeding seasons (December - March. (A) Daily maximum; (B) daily minimum; (C) daily range; (D) daily mean

Appendix 4.5

Table A4.5: Model-averaged estimates across full and conditional model sets for of effect on daily maximum nest temperature

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Nest type								
Natural nest	*Reference*							
Nest box	**2.04**	**0.48**	**4.29**	**<0.001**	**2.04**	**0.48**	**4.29**	**<0.001**
Ambient daily max Temperature	**4.20**	**0.03**	**125.40**	**<0.001**	**4.20**	**0.03**	**125.40**	**<0.001**
Temperature Category								
Max temp <25 ˚C	*Reference*							
Max temp >25 ˚C	**1.02**	**0.06**	**17.85**	**<0.001**	**1.02**	**0.06**	**17.85**	**<0.001**
Ambient daily max humidity	**-0.19**	**0.01**	**15.82**	**<0.001**	**-0.19**	**0.01**	**15.82**	**<0.001**
Wind Speed	**-0.75**	**0.02**	**34.98**	**<0.001**	**-0.75**	**0.02**	**34.98**	**<0.001**
Wind direction								
Offshore	*Reference*							
Onshore	**1.06**	**0.03**	**37.32**	**<0.001**	**1.06**	**0.03**	**37.32**	**<0.001**
Ambient daily max temp * Temp Cat								
*Ambient daily max temp * Max temp <25 ˚C*	*Reference*							

*Ambient daily max temp * Max temp >25 ˚C*	**-1.22**	**0.05**	**26.10**	**<0.001**	**-1.22**	**0.05**	**26.10**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	**-0.13**	**0.03**	**5.29**	**<0.001**	**-0.13**	**0.03**	**5.29**	**<0.001**
Year								
2013	*Reference*							
2014	-0.01	0.13	0.06	0.95	-0.02	0.23	0.10	0.92
2015	0.17	0.31	0.55	0.58	0.52	0.34	1.53	0.13
2016	0.08	0.25	0.32	0.75	0.24	0.39	0.63	0.53

Appendix 4.6

Table A4.6: Model-averaged estimates across full and conditional model sets for of effect on daily minimum nest temperature

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Nest type								
Natural nest	*Reference*							
Nest box	0.23	0.17	1.34	0.18	0.30	0.14	2.14	0.03
Ambient daily min temperature	3.16	0.01	354.55	**<0.001**	3.16	0.01	354.55	**<0.001**
Ambient daily max humidity	0.23	0.01	43.92	**<0.001**	0.23	0.01	43.92	**<0.001**
Wind Speed	-0.06	0.01	8.90	**<0.001**	-0.06	0.01	8.90	**<0.001**
Wind direction								
Offshore	*Reference*							
Onshore	-0.16	0.01	11.69	**<0.001**	-0.16	0.01	11.69	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	-0.10	0.01	9.44	**<0.001**	-0.10	0.01	9.44	**<0.001**
Year								

2013	*Reference*							
2014	0.07	0.08	0.94	0.35	0.07	0.08	0.94	0.35
2015	-0.07	0.11	0.70	0.48	-0.07	0.11	0.70	0.48
2016	0.45	0.12	3.70	**<0.001**	0.45	0.12	3.70	**<0.001**

Appendix 4.7

Table A4.7: Model-averaged estimates across full and conditional model sets for of effect on exposure hours ≥30 ˚C

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|*z*|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|*z*|)**
Nest type								
Natural nest	*Reference*							
Nest box	0.18	0.06	3.05	**<0.01**	0.18	0.05	3.32	**<0.001**
Ambient daily max temp	0.38	0.01	68.50	**<0.001**	0.38	0.01	68.50	**<0.001**
Ambient daily max humidity	-0.02	0.01	4.05	**<0.001**	-0.02	0.01	4.07	**<0.001**
Wind Speed	0.00	0.01	0.33	0.74	-0.01	0.01	0.50	0.62
Wind direction								
Offshore	*Reference*							
Onshore	0.30	0.01	22.38	**<0.001**	0.30	0.01	22.38	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	0.01	0.01	0.49	0.62	0.02	0.01	1.56	0.12
Year								

2013	*Reference*							
2014	0.02	0.01	1.20	0.23	0.02	0.01	1.20	0.23
2015	0.00	0.02	0.03	0.98	0.00	0.02	0.03	0.98
2016	0.10	0.02	4.15	<**0.001**	0.10	0.02	4.15	<**0.001**

Appendix 4.8

Table A4.8: Model-averaged estimates across full and conditional model sets for of effect on exposure hours ≥35 ˚C

Predictor	Full model set				Conditional model set			
	Estimate	**Adjusted SE**	***z value***	**Pr(>|*z*|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|*z*|)**
Nest type treatment								
Natural nest	*Reference*							
Nest box	**0.28**	**0.07**	**4.14**	**<0.001**	**0.28**	**0.07**	**4.18**	**<0.001**
Ambient daily max temp	**0.38**	**0.01**	**35.95**	**<0.001**	**0.38**	**0.01**	**35.95**	**<0.001**
Ambient daily max humidity	0.00	0.01	0.28	0.78	-0.01	0.01	0.57	0.57
Wind Speed	-0.02	0.01	1.18	0.24	-0.02	0.01	1.25	0.21
Wind direction								
Offshore	*Reference*							
Onshore	**0.24**	**0.02**	**11.89**	**<0.001**	**0.24**	**0.02**	**11.89**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	-0.01	0.02	0.44	0.66	-0.02	0.02	0.94	0.35

Year								
2013	*Reference*							
2014	0.01	0.02	0.56	0.58	0.02	0.03	0.75	0.45
2015	0.01	0.03	0.35	0.73	0.02	0.04	0.44	0.66
2016	0.05	0.05	1.04	0.30	**0.08**	**0.04**	**1.93**	**0.05**

Appendix 4.9

Table A4.9: Model-averaged estimates across full and conditional model sets for of effect on Daily Maximum temperature natural nests

Predictor	Full model set				Conditional model set			
	Estimate	**Adjusted SE**	***z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Vegetation								
Bush Wall	-0.34	0.33	1.03	0.30	-0.51	0.28	1.84	0.07
Species								
Rhagodia	*Reference*							
Rhagodia -Tetragonia	-0.26	0.57	0.45	0.65	-0.89	0.74	1.20	0.23
Tetragonia	-0.13	0.46	0.28	0.78	-0.44	0.78	0.57	0.57
Exposure								
Slope	***1.02***	***0.53***	***1.94***	***0.05***	***1.08***	***0.47***	***2.29***	***0.02***
Aspect								
None	*Reference*							
North	-0.41	0.86	0.48	0.63	-0.82	1.06	0.77	0.44
South	-0.97	1.26	0.77	0.44	-1.92	1.15	1.66	0.10
Climate								
Ambient daily max Temperature	**4.27**	**0.05**	**79.84**	**<0.001**	**4.27**	**0.05**	**79.84**	**<0.001**
Temp Category								
Max temp <25 ˚C	*Reference*							

Max temp >25 ˚C	**1.30**	**0.09**	**14.83**	**<0.001**	**1.30**	**0.09**	**14.83**	**<0.001**
Ambient daily max humidity	**-0.22**	**0.02**	**11.95**	**<0.001**	**-0.22**	**0.02**	**11.95**	**<0.001**
Wind Speed	**-0.62**	**0.03**	**19.79**	**<0.001**	**-0.62**	**0.03**	**19.79**	**<0.001**
Wind direction								
Offshore	*Reference*							
Onshore	**1.20**	**0.04**	**27.50**	**<0.00.1**	**1.20**	**0.04**	**27.50**	**<0.00.1**
Ambient daily max temp * Temp Cat								
*Ambient daily max temp * Max temp <25 ˚C*	*Reference*							
*Ambient daily max temp * Max temp >25 ˚C*	**-1.37**	**0.07**	**18.56**	**<0.001**	**-1.37**	**0.07**	**18.56**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	**-0.22**	**0.04**	**5.76**	**<0.001**	**-0.22**	**0.04**	**5.76**	**<0.001**
Year								
2014	*Reference*							
2015	0.26	0.34	0.75	0.45	0.37	0.36	1.03	0.30
2016	-0.30	0.43	0.70	0.48	-0.43	0.45	0.95	0.34

Appendix 4.10

Table A4.10: Model-averaged estimates across full and conditional model sets for of effect on hours of exposure ≥30 ˚C in nests.

Predictor	Full model set				Conditional model set			
	Estimate	**Adjusted SE**	***z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Vegetation								
Bush Wall	***-0.13***	***0.03***	***4.86***	***<0.001***	***-0.13***	***0.03***	***4.86***	***<0.001***
Species								
Rhagodia	*Reference*							
Rhagodia -Tetragonia	-0.01	0.02	0.27	0.79	-0.04	0.05	0.83	0.40
Tetragonia	-0.01	0.02	0.23	0.82	-0.03	0.05	0.67	0.50
Exposure								
Slope	0.02	0.03	0.56	0.58	0.04	0.04	1.14	0.25
Aspect								
None	*Reference*							
North	0.01	0.04	0.19	0.85	0.05	0.09	0.55	0.58
South	0.00	0.04	0.12	0.91	0.03	0.10	0.31	0.76
Climate								
Ambient daily max temperature	**0.42**	**0.01**	**44.49**	**<0.001**	**0.42**	**0.01**	**44.49**	**<0.001**
Ambient daily max humidity	**-0.02**	**0.01**	**2.35**	**0.02**	**-0.03**	**0.01**	**2.83**	**<0.01**
Wind Speed	0.00	0.01	0.36	0.72	0.01	0.01	0.58	0.56

Wind direction								
Offshore	*Reference*							
Onshore	**0.30**	**0.02**	**13.41**	**<0.001**	**0.30**	**0.02**	**13.41**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - onshore*	*Reference*							
*Wind speed * Wind direction - onshore*	0.00	0.01	0.10	0.92	0.01	0.02	0.29	0.77
Year								
2014	*Reference*							
2015	**0.12**	**0.03**	**4.08**	**<0.001**	**0.12**	**0.03**	**4.08**	**<0.001**
2016	**0.20**	**0.03**	**6.16**	**<0.001**	**0.20**	**0.03**	**6.16**	**<0.001**

Appendix 4.11

Table A4.11: Model-averaged estimates across full and conditional model sets for of effect on hours of exposure ≥35 ˚C in natural nests.

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|*z*|)**	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|*z*|)**
Vegetation								
Bush Wall	**-0.10**	**0.05**	**1.92**	**0.05**	**-0.11**	**0.04**	**2.61**	**<0.01**
Species								
Rhagodia	*Reference*							
Rhagodia -Tetragonia	0.00	0.05	0.04	0.97	0.00	0.08	0.06	0.96
Tetragonia	0.06	0.09	0.67	0.51	0.13	0.09	1.46	0.14
Exposure								
Slope	0.03	0.05	0.58	0.56	0.06	0.05	1.15	0.25
Aspect								
None	*Reference*							
North	-0.01	0.06	0.15	0.88	-0.06	0.14	0.41	0.68
South	-0.01	0.06	0.12	0.90	-0.05	0.15	0.33	0.74
Climate								
Ambient daily max temperature	0.42	0.02	21.96	<**0.001**	0.42	0.02	21.96	<**0.001**
Ambient daily max humidity	0.00	0.01	0.16	0.87	-0.01	0.02	0.31	0.76
Wind Speed	0.00	0.02	0.06	0.96	0.00	0.03	0.08	0.94

Wind direction								
Offshore	*Reference*							
Onshore	**0.24**	**0.04**	**6.31**	**<0.001**	**0.24**	**0.04**	**6.31**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	-0.01	0.03	0.43	0.67	-0.05	0.04	1.26	0.21
Year								
2014	*Reference*							
2015	**0.14**	**0.07**	**1.95**	**0.05**	**0.14**	**0.07**	**2.00**	**0.05**
2016	**0.23**	**0.07**	**3.31**	**<0.001**	**0.24**	**0.07**	**3.55**	**<0.001**

Appendix 4.12

Table A4.12: Model-averaged estimates across full and conditional model sets for of effect on Daily Maximum temperature nest boxes.

Predictor	Full model set				Conditional model set			
	Estimate	**Adjusted SE**	***z value***	**Pr(>|*z*|)**	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|*z*|)**
Vegetation								
Vegetation Cover	-0.81	0.51	1.60	0.11	**-0.93**	**0.43**	**2.18**	**0.03**
Box Cover								
Low	*Reference*							
Partial	-0.07	0.33	0.22	0.83	-0.37	0.68	0.55	0.59
Full	-0.17	0.52	0.33	0.74	-0.90	0.88	1.03	0.31
Vents								
Absent	*Reference*							
Present	-0.88	1.01	0.88	0.38	-1.49	0.90	1.66	0.10
Exposure								
Slope	-1.49	0.90	1.66	0.10	0.47	0.68	0.70	0.48
Aspect								
None	*Reference*							
North	0.72	1.12	0.64	0.52	1.63	1.16	1.41	0.16
South	1.01	1.48	0.68	0.49	2.29	1.42	1.61	0.11
Climate								

Ambient daily max Temperature	**4.37**	**0.06**	**76.53**	**<0.001**	**4.37**	**0.06**	**76.53**	**<0.001**
Temp Category								
Max temp <25 ˚C	*Reference*							
Max temp >25 ˚C	**1.15**	**0.09**	**12.84**	**<0.001**	**1.15**	**0.09**	**12.84**	**<0.001**
Ambient daily max humidity	**-0.21**	**0.02**	**10.31**	**<0.001**	**-0.21**	**0.02**	**10.31**	**<0.001**
Wind Speed	**-0.80**	**0.03**	**24.15**	**<0.001**	**-0.80**	**0.03**	**24.15**	**<0.001**
Wind direction								
Offshore	*Reference*							
Onshore	**1.02**	**0.05**	**22.04**	**<0.001**	**1.02**	**0.05**	**22.04**	**<0.001**
Ambient daily max temp * Temp Cat								
*Ambient daily max temp * Max temp <25 ˚C*	*Reference*							
*Ambient daily max temp * Max temp >25 ˚C*	**-1.22**	**0.08**	**15.75**	**<0.001**	**-1.22**	**0.08**	**15.75**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - onshore*	*Reference*							
*Wind speed * Wind direction - onshore*	**-0.23**	**0.04**	**5.57**	**<0.001**	**-0.23**	**0.04**	**5.57**	**<0.001**
Year								
2014	*Reference*							
2015	0.59	0.84	0.71	0.48	1.33	0.77	1.72	0.09
2016	0.74	1.03	0.72	0.47	1.66	0.92	1.80	0.07

Appendix 4.13

Table A4.13: Model-averaged estimates across full and conditional model sets for of effect on hours of exposure ≥30 ˚C in nest boxes.

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|*z*|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|*z*|)**
Vegetation								
Vegetation Cover	**-0.12**	**0.03**	**4.65**	**<0.001**	**-0.12**	**0.03**	**4.66**	**<0.001**
Box Cover								
Low	*Reference*							
Partial	0.01	0.02	0.42	0.68	0.03	0.03	0.83	0.41
Full	-0.02	0.04	0.45	0.66	-0.05	0.06	0.92	0.36
Vents								
Absent	*Reference*							
Present	-0.12	0.08	1.53	0.13	**-0.15**	**0.06**	**2.34**	**0.02**
Exposure								
Slope	-0.04	0.06	0.65	0.51	-0.07	0.06	1.13	0.26
Aspect								
None	*Reference*							
North	0.19	0.11	1.71	0.09	**0.20**	**0.10**	**1.94**	**0.05**
South	**0.31**	**0.15**	**2.09**	**0.04**	**0.33**	**0.13**	**2.51**	**0.01**

Climate								
Ambient daily max Temperature	**0.37**	**0.01**	**44.58**	**<0.001**	**0.37**	**0.01**	**44.58**	**<0.001**
Ambient daily max humidity	**-0.03**	**0.01**	**3.16**	**<0.01**	**-0.03**	**0.01**	**3.34**	**<0.001**
Wind Speed	-0.02	0.02	0.76	0.45	-0.02	0.02	1.20	0.23
Wind direction								
Offshore	*Reference*							
Onshore	**0.32**	**0.02**	**15.24**	**<0.001**	**0.32**	**0.02**	**15.24**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	0.02	0.02	0.81	0.42	**0.04**	**0.02**	**2.12**	**0.03**
Year								
2014	*Reference*							
2015	-0.06	0.04	1.43	0.15	-0.06	0.04	1.43	0.15
2016	**0.12**	**0.05**	**2.44**	**0.01**	**0.12**	**0.05**	**2.44**	**0.01**

Appendix 4.14

Table A4.14: Model-averaged estimates across full and conditional model sets for of effect on hours of exposure ≥35 ˚C in nest boxes.

	Full model set				Conditional model set			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Vegetation								
Vegetation Cover	**-0.11**	**0.05**	**2.36**	**0.02**	**-0.12**	**0.04**	**2.90**	**<0.01**
Box Cover								
Low	*Reference*							
Partial	0.01	0.03	0.21	0.83	0.03	0.05	0.51	0.61
Full	-0.02	0.06	0.29	0.77	-0.07	0.10	0.75	0.45
Vents								
Absent	*Reference*							
Present	-0.21	0.12	1.80	0.07	**-0.24**	**0.10**	**2.53**	**0.01**
Exposure								
Slope	-0.04	0.08	0.48	0.63	-0.08	0.10	0.81	0.42
Aspect								
None	*Reference*							
North	0.14	0.16	0.87	0.38	0.20	0.16	1.26	0.21
South	0.28	0.24	1.14	0.26	**0.39**	**0.20**	**2.00**	**0.05**

Climate								
Ambient daily max Temperature	**0.38**	**0.01**	**26.48**	**<0.001**	**0.38**	**0.01**	**26.48**	**<0.001**
Ambient daily max humidity	0.00	0.01	0.43	0.67	-0.01	0.01	0.89	0.37
Wind Speed	-0.02	0.02	1.33	0.18	-0.03	0.02	1.52	0.13
Wind direction								
Offshore	*Reference*							
Onshore	**0.27**	**0.03**	**9.53**	**<0.001**	**0.27**	**0.03**	**9.53**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - offshore*	*Reference*							
*Wind speed * Wind direction - onshore*	0.00	0.02	0.25	0.80	-0.01	0.03	0.54	0.59
Year								
2014	*Reference*							
2015	-0.02	0.07	0.35	0.73	-0.02	0.07	0.35	0.73
2016	0.11	0.09	1.30	0.19	0.12	0.09	1.33	0.19

Appendix 5.1

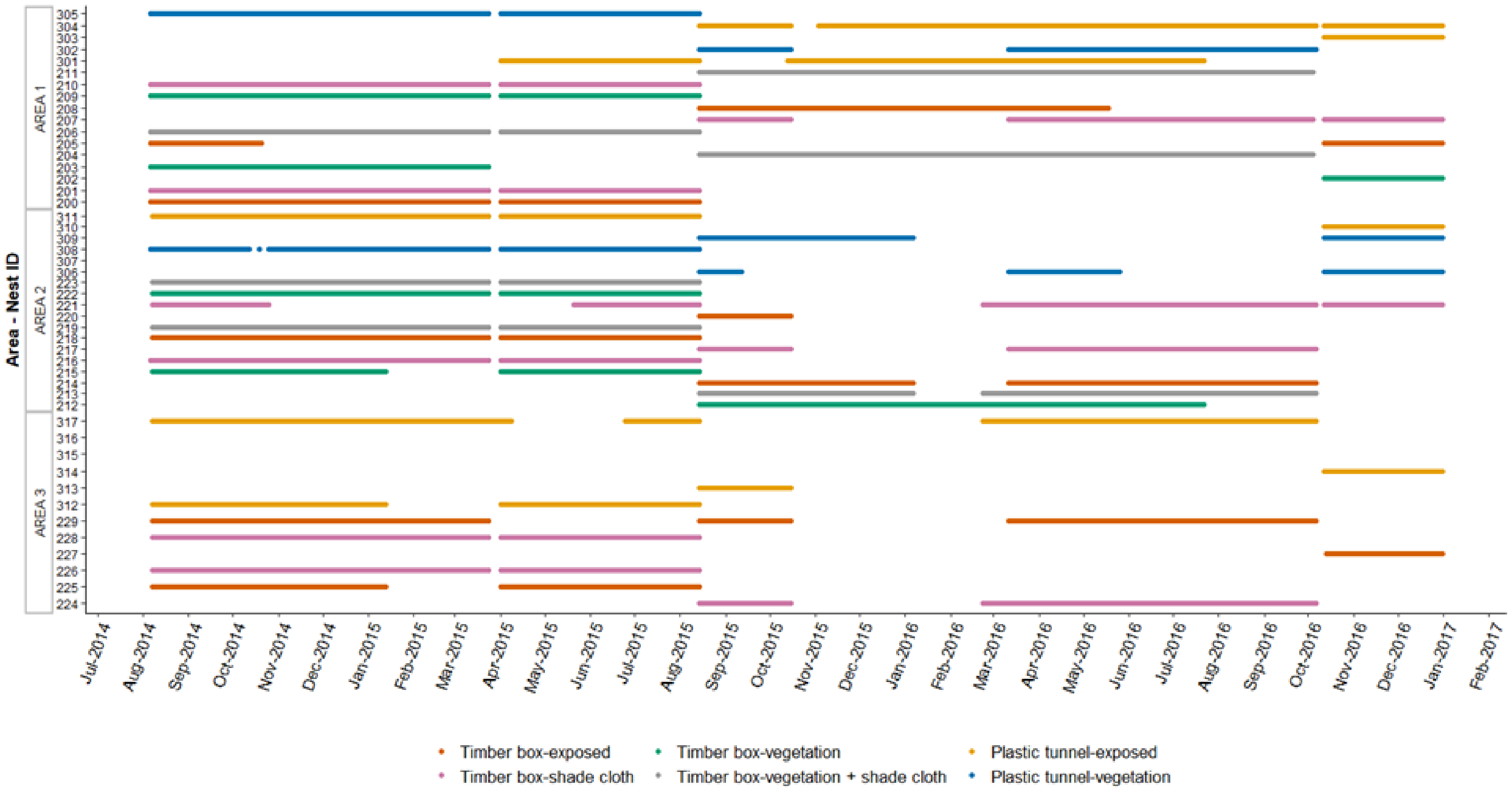

Figure A5.1: Dates of continuous temperature and relative humidity observations of each sample nest across three locations and six treatment types indicating occurrence of data losses.

Appendix 5.2

Table A5.2: Model-averaged estimates across full and conditional model sets for of effect on Daily Maximum nets temperature

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Nest type treatment								
Timber box – exposed	***Reference***							
Timber box – shade cloth	**-2.42**	**0.76**	**3.18**	**<0.01**	**-2.42**	**0.76**	**3.10**	**<0.01**
Timber box - vegetation	**-4.29**	**0.91**	**4.71**	**<0.001**	**-4.29**	**0.91**	**4.71**	**<0.001**
Timber box – vegetation + shade cloth	**-4.80**	**0.84**	**5.65**	**<0.001**	**-4.80**	**0.84**	**5.65**	**<0.001**
Plastic tunnel - exposed	**-2.00**	**0.81**	**2.47**	**0.01**	**-2.00**	**0.81**	**2.47**	**0.01**
Plastic tunnel - vegetation	**-2.94**	**0.92**	**3.22**	**<0.01**	**-2.94**	**0.91**	**3.22**	**<0.01**
Ambient daily max temp	**3.44**	**0.05**	**72.94**	**<0.001**	**3.44**	**0.05**	**72.94**	**<0.001**
Temp Category								
Max temp <25 ˚C	***Reference***							
Max temp >25 ˚C	**1.18**	**0.11**	**11.00**	**<0.001**	**1.18**	**0.11**	**11.00**	**<0.001**
Ambient daily max humidity	**-0.18**	**0.02**	**9.27**	**<0.001**	**-0.18**	**0.02**	**9.27**	**<0.001**
Wind Speed	**-0.65**	**0.03**	**19.82**	**<0.001**	**-0.65**	**0.03**	**19.82**	**<0.001**
Wind direction								
Offshore	***Reference***							
Onshore	**1.13**	**0.05**	**25.21**	**<0.001**	**1.13**	**0.05**	**25.21**	**<0.001**
Ambient daily max temp * Temp Cat								
*Ambient daily max temp * Max temp <25 ˚C*	***Reference***							
*Ambient daily max temp * Max temp >25 ˚C*	**-1.01**	**0.07**	**13.79**	**<0.001**	**-1.01**	**0.07**	**13.79**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction - onshore*	***Reference***							

*Wind speed * Wind direction - onshore*	**-0.27**	**0.04**	**6.82**	**<0.001**	**-0.27**	**0.04**	**6.82**	**<0.001**
Year								
2014	***Reference***							
2015	-0.03	0.13	0.22	0.82	-0.20	0.29	0.70	0.49
2016	-0.02	0.17	0.10	0.92	-0.12	0.44	0.27	0.79

Appendix 5.3

Table A5.3: Model-averaged estimates across full and conditional model sets for of effect on Daily minimum nets temperature

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Nest type treatment								
Timber box – exposed	***reference***							
Timber box – shade cloth	-0.05	0.29	0.19	0.85	-0.05	0.29	0.19	0.85
Timber box - *vegetation*	**0.74**	**0.34**	**2.15**	**0.03**	**0.74**	**0.34**	**2.15**	**0.03**
Timber box – vegetation + shade cloth	**0.80**	**0.32**	**2.49**	**0.01**	**0.80**	**0.32**	**2.49**	**0.01**
Plastic tunnel - *exposed*	**1.42**	**0.30**	**4.68**	**<0.001**	**1.42**	**0.30**	**4.68**	**<0.001**
Plastic tunnel - *vegetation*	**1.98**	**0.34**	**5.74**	**<0.001**	**1.98**	**0.34**	**5.74**	**<0.001**
Ambient daily min temp	**2.95**	**0.01**	**197.21**	**<0.001**	**2.95**	**0.01**	**197.21**	**<0.001**
Ambient daily max humidity	**0.26**	**0.01**	**29.07**	**<0.001**	**0.26**	**0.01**	**29.07**	**<0.001**
Wind Speed	-0.01	0.01	0.77	0.44	-0.01	0.01	0.77	0.44
Wind direction								
Offshore	***reference***							
Onshore	**0.10**	**0.02**	**4.31**	**<0.001**	**0.10**	**0.02**	**4.31**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction – offshore*	***reference***							
*Wind speed * Wind direction* - *onshore*	**-0.11**	**0.02**	**6.51**	**<0.001**	**-0.11**	**0.02**	**6.51**	**<0.001**
Year								
2014	***reference***							
2015	-0.09	0.02	0.72	0.47	-0.18	0.11	1.55	0.12
2016	0.01	0.12	0.10	0.98	0.03	0.17	0.15	0.88

Appendix 5.4

Table A5.4: Model-averaged estimates across full and conditional model sets for of effect on exposure hours ≥30 ˚C.

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|z|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|z|)**
Nest type treatment								
Timber box – exposed	***reference***							
Timber box – shade cloth	-0.10	0.09	1.21	0.23	-0.10	0.09	1.21	0.23
Timber box - vegetation	**-0.49**	**0.10**	**4.74**	**<0.001**	**-0.49**	**0.10**	**4.74**	**<0.001**
Timber box – vegetation + shade cloth	**-0.49**	**0.10**	**4.88**	**<0.001**	**-0.49**	**0.10**	**4.88**	**<0.001**
Plastic tunnel - exposed	-0.13	0.09	1.41	0.16	-0.13	0.09	1.41	0.16
Plastic tunnel - vegetation	-0.19	0.10	1.86	0.06	-0.19	0.10	1.86	0.06
Ambient daily max temp	**0.40**	**0.01**	**38.98**	**<0.001**	**0.40**	**0.01**	**38.98**	**<0.001**
Ambient daily max humidity	**-0.03**	**0.01**	**2.96**	**<0.01**	**-0.03**	**0.01**	**3.21**	**<0.01**
Wind Speed	0.04	0.03	1.33	0.18	0.05	0.03	1.76	0.08
Wind direction								
Offshore	***reference***							
Onshore	**0.35**	**0.03**	**13.30**	**<0.001**	**0.35**	**0.03**	**13.30**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction – offshore*	***reference***							
*Wind speed * Wind direction - onshore*	-0.04	0.03	1.06	0.29	**0.05**	**0.03**	**2.10**	**0.04**
Year								
2014	***reference***							
2015	0.02	0.03	0.63	0.53	0.05	0.03	1.73	0.08
2016	0.02	0.03	0.54	0.59	0.05	0.04	1.20	0.23

Appendix 5.5

Table A5.5: Model-averaged estimates across full and conditional model sets for of effect on exposure hours ≥35 ˚

	Full model set				**Conditional model set**			
Predictor	**Estimate**	**Adjusted SE**	***z value***	**Pr(>|*z*|)**	**Estimate**	**Adjusted SE**	***Z value***	**Pr(>|*z*|)**
Nest type treatment								
Timber box – exposed	***reference***							
Timber box – shade cloth	-0.10	0.11	0.92	0.36	-0.10	0.11	0.94	0.35
Timber box - *vegetation*	**-0.56**	**0.18**	**3.16**	**<0.01**	**-0.58**	**0.15**	**3.74**	**<0.001**
Timber box – vegetation + shade cloth	**-0.37**	**0.17**	**2.19**	**0.03**	**-0.38**	**0.16**	**2.37**	**0.02**
Plastic tunnel - *exposed*	0.01	0.11	0.13	0.90	0.01	0.11	0.13	0.90
Plastic tunnel - *vegetation*	-0.25	0.15	1.72	0.09	-0.26	0.14	1.81	0.07
Ambient daily max temp	**0.37**	**0.02**	**15.80**	**<0.001**	**0.37**	**0.02**	**15.80**	**<0.001**
Ambient daily max humidity	-0.00	0.01	0.11	0.91	-0.00	0.02	0.22	0.83
Wind Speed	0.01	0.03	0.31	0.75	0.02	0.04	0.55	0.58
Wind direction								
Offshore	***reference***							
Onshore	**0.27**	**0.05**	**5.73**	**<0.001**	**0.27**	**0.05**	**5.73**	**<0.001**
Wind speed * Wind direction								
*Wind speed * Wind direction* - *offshore*	***reference***							
*Wind speed * Wind direction* - *onshore*	-0.01	0.03	0.33	0.74	-0.06	0.05	1.21	0.23
Year								
2014	***reference***							
2015	**0.18**	**0.08**	**2.22**	**0.03**	**0.19**	**0.07**	**2.87**	**<0.01**
2016	0.10	0.09	1.25	0.21	0.12	0.08	1.38	0.17