

The Use of Artificial Perches in the Restoration of a Degraded  
Coastal Environment in Southern Australia



Victoria Elizabeth Anne McCarron

BSc (Hons)

A thesis submitted in fulfilment of the requirements for the degree of Doctor of  
Philosophy

School of Biological Sciences

The University of Adelaide

March 2021

# Contents

<b>Contents .....</b>	<b>2</b>
<b>List of figures.....</b>	<b>6</b>
<b>List of tables .....</b>	<b>10</b>
<b>Abstract.....</b>	<b>12</b>
<b>Declaration .....</b>	<b>14</b>
<b>Acknowledgements .....</b>	<b>15</b>
<b>Chapter 1. General introduction .....</b>	<b>16</b>
1.1 Land modification and the need for restoration .....	16
1.2 Restoration of degraded environments.....	16
1.3 The use of artificial perches for restoration .....	18
1.4 Aim and outline of thesis .....	20
<b>Chapter 2. Background ecology of the Younghusband Peninsula and the need for restoration.....</b>	<b>22</b>
2.1 Overview of the study region .....	22
2.2 Degradation and the need for artificial perches .....	23
2.3 The role of birds and plants in the restoration of Cantara.....	27
2.4 Recruitment barriers.....	34
2.5 Conclusion.....	35
<b>Chapter 3. The use of artificial perches by birds on the Younghusband Peninsula.....</b>	<b>36</b>
3.1 Introduction .....	36
3.2 Methods.....	37
3.2.1 Study location .....	37
3.2.2 Artificial perch implementation .....	38
3.2.3 Perch observations .....	39
3.2.4 Faecal analysis .....	40
3.2.5 Statistical analysis .....	41

3.3 Results .....	43
3.3.1 Direct observations of perch use .....	43
3.3.2 Remote camera observations of perch use .....	44
3.3.3 Perch complexity .....	50
3.3.4 Faecal analysis .....	50
3.4 Discussion .....	52
3.4.1 Use of artificial perches by seed-dispersing birds .....	52
3.4.2 Influence of visitation frequency on seed deposition .....	54
3.4.3 Changes in visitation during the peak fruiting seasons .....	55
3.4.4 Ecological services provided by perches .....	56
3.5 Conclusion.....	56
<b>Chapter 4. The effectiveness of artificial perches in overcoming dispersal limitations for fleshy-fruited plants on the Younghusband Peninsula.....</b>	<b>58</b>
4.1 Introduction .....	58
4.2 Methods.....	60
4.2.1 Study location .....	60
4.2.2 Artificial perch and seed trap implementation .....	60
4.2.3 Statistical analysis .....	64
4.3 Results .....	66
4.3.1 Seed rain characteristics .....	66
4.3.2 Annual and seasonal variation in seed deposition .....	73
4.4 Discussion .....	75
4.4.1 Seed dispersal limitation.....	75
4.4.2 Species deposition .....	77
4.4.3 Temporal variation in seed deposition .....	78
4.4.4 Implications for restoration .....	79
4.5 Conclusion.....	82

<b>Chapter 5. Seed germination and seedling survival on the Younghusband Peninsula</b>	<b>83</b>
5.1 Introduction .....	83
5.2 Methods.....	85
5.2.1 Study location .....	85
5.2.2 Experimental design .....	86
5.2.3 Seed germination in the glasshouse.....	86
5.2.4 Effect of introduced grasses on seedling emergence and establishment.....	87
5.2.5 Effect of herbivory on seedling survival .....	88
5.2.6 Statistical analysis .....	89
5.3 Results.....	92
5.3.1 Seed germination in the glasshouse.....	92
5.3.2 Effect of introduced grasses on seedling emergence and establishment.....	94
5.3.3 Effect of herbivory on seedling survival .....	95
5.4 Discussion .....	101
5.4.1 Seed germination in the glasshouse.....	101
5.4.2 Effect of introduced grasses on seedling emergence and establishment.....	102
5.4.3 Effect of herbivory on seedling survival .....	103
5.4.4 Likelihood of germination and recruitment beneath artificial perches .....	104
5.5 Conclusion.....	106
<b>Chapter 6. General discussion .....</b>	<b>107</b>
6.1 Summary of findings.....	107
6.2 Limitations with artificial perches and recommendations for future research.....	108
6.2.1 Overcoming post-dispersal barriers.....	108
6.2.2 Evaluation of bird and plant species before perch deployment.....	109
6.2.3 Considerations for practical implementation.....	112
6.2.4 Alternatives to artificial perches.....	114
6.3 Conclusion.....	116

<b>References.....</b>	<b>118</b>
<b>Appendices.....</b>	<b>137</b>
Appendix 1 .....	137
Appendix 2 .....	138
Appendix 3 .....	139

## List of figures

Figure 2.1. Younghusband Peninsula located in South Australia. Note the location of Cantara, which is the primary study site in the region.....	22
Figure 2.2. Degradation pathway in the Younghusband Peninsula, including the processes that have resulted in landscape degradation and the barriers that have prevented regeneration. ....	24
Figure 2.3. Map broadly outlining the different types of habitat present in the study area of Cantara. ....	25
Figure 2.4. Photos taken in the study site which a) demonstrates the extent of vegetation clearance within the southern paddocks and b) highlights the presence of dense remnant vegetation on the hind dunes surrounding the southern paddocks. ....	26
Figure 2.5. Fleshy-fruited species commonly consumed by frugivorous birds in the Younghusband Peninsula including a) <i>Leucopogon parviflorus</i> , b) <i>Myoporum insulare</i> , c) <i>Acacia sophorae</i> , d) <i>Rhagodia candolleana</i> , e) <i>Exocarpos syrticola</i> and f) <i>Lycium ferocissimum</i> . ....	29
Figure 2.6. The primary fruiting times of fleshy-fruited plants in the Younghusband Peninsula. ....	30
Figure 2.7. Fruiting availabilities of four fleshy-fruited species determined from plants sampled at five sites along the Coorong National Park. ....	31
Figure 2.8. Common frugivorous birds in the Younghusband Peninsula, including a) the silvereye <i>Zosterops lateralis</i> , b) the singing honeyeater <i>Lichenostomus virescens</i> and c) the spiny-cheeked honeyeater <i>Acanthagenys rufogularis</i> . ....	33
Figure 3.1. Aerial view of the southern paddocks associated with Cantara Homestead (top centre), where the artificial perches were erected. The locations of 12 simple perches (PS) and 2 complex perches (PC) are indicated with crosses. ....	38
Figure 3.2. Artificial perch designs erected in the Cantara paddocks which consisted of: a) simple perch and b) complex perch. ....	39
Figure 3.3. Daily perch visits (mean + SE) in summer (December 2016–February 2017) and autumn (March–April 2017) as determined for all birds, seed-dispersing birds (SDB), spiny-cheeked honeyeaters (SCH), Australian magpies (AM) and singing honeyeaters (SIH) at seven artificial perches (combined data from one complex perch and six simple perches). .	46
Figure 3.4. Visits of varying durations (as a percentage of total visits) to eight artificial perches (combined data from two complex and six simple perches) between summer and	

autumn (December 2016–May 2017) as determined by remote cameras. Perching durations were depicted for four seed-dispersing species that frequently visited the perches, including a) spiny-cheeked honeyeater, b) singing honeyeater, c) Australian magpie and d) Australian raven.....	47
Figure 3.5. Diurnal patterns to visitation for eight artificial perches (combined data from two complex and six simple perches) between summer and autumn (December 2016–May 2017) as determined by remote cameras. Relative frequency of visits across the day were depicted for a) all bird species and b–e) bird species that most frequently visited the perches.....	48
Figure 3.6. Bird behaviours observed on the artificial perches including: a) welcome swallows basking, b) Australian kestrel with prey, c) Australian raven antagonising an Australian magpie and d) an Australian magpie defaecating. ....	49
Figure 3.7. Frequency of occurrence (%) of the seeds of five fleshy-fruited plant species in faecal samples containing seed produced by three bird species across five sites in the Younghusband Peninsula in a) January 2015 and b) January 2016. ....	52
Figure 4.1. Aerial view of the experimental design deployed in the southern paddocks of Cantara, where 12 artificial perches of simple design were erected. A 1 × 1 m seed trap was placed beneath each perch. Twenty-five 1 × 1 m seed traps were also placed in open areas of the paddocks. The location of each perch is indicated with a cross, whereas the location of each seed trap in the open is indicated with a square. ....	61
Figure 4.2. An artificial perch located in the southern paddocks of Cantara with a 1 × 1 m seed trap placed beneath it and remnant dune vegetation evident in background (a) and seed traps made from superfine 0.25 mm fibreglass mesh were used to capture defaecated seeds (b).....	62
Figure 4.3. Aerial view of the experimental design deployed in the southern paddocks of Cantara and adjacent dunes, where seed traps were placed under ten adult plants from four shrub species, both in the paddocks and in the remnant dune vegetation. The location of each shrub in the dunes is indicated with a triangle, whereas the location of each shrub in the paddocks is indicated with a circle. ....	63
Figure 4.4. The abundance of seed (a) and species richness of seed (b) deposited in seed traps (both mean/m <sup>2</sup> /year + SE) beneath artificial perches ( <i>n</i> = 12), paddock shrubs ( <i>n</i> = 4 species, 10 shrubs per species; averaged mean), dune shrubs ( <i>n</i> = 4 species, 10 shrubs per species; averaged mean) and in the open paddock ( <i>n</i> = 25) during a 12-month period, between September 2015 and August 2016.....	66

Figure 4.5. Two-dimensional non-metric multidimensional scaling ordination visualising differences in the compositions of seed (based on species abundance) that were collected in traps set under the artificial perches ( $n = 12$ ), four species of paddock shrub ( $n = 10$ shrubs per species) and in the open paddock ( $n = 25$ ) during a 12-month period, between September 2015 and August 2016. ....	68
Figure 4.6. Seeds commonly deposited beneath the 12 artificial perches in the paddocks of Cantara, according to a) species (mean seed/m <sup>2</sup> /year + SE) and b) life form (mean percentage of seed/m <sup>2</sup> /year + SE, seed categorised according to origin). ....	69
Figure 4.7a–d. Quantities of seed (mean seed/m <sup>2</sup> /year + SE) from different plant species that were commonly collected in traps set under four shrubs species ( $n = 10$ shrubs per species) in the paddocks of Cantara. ....	70
Figure 4.8a–d. Quantities of seed (mean seed/m <sup>2</sup> /year + SE) from different plant species that were commonly collected in traps set under four shrubs species ( $n = 10$ shrubs per species) located in the dunes surrounding Cantara. ....	71
Figure 4.9. Seasonal variation in the seeds collected in traps set under the 12 artificial perches over 7 seasons between 2015 and 2017, including in the a) abundance and species richness of seed deposited (mean seed/m <sup>2</sup> /season + SE), b) dry biomass of seed deposited (mean mg/m <sup>2</sup> /season + SE) and c) abundances of commonly deposited species (mean seed/m <sup>2</sup> /season ± SE). ....	74
Figure 4.10. Seed trap located beneath an artificial perch that is abundant with seed from the introduced species <i>Lycium ferocissimum</i> . The trap contains 1 month of deposited seed, captured in April 2016 (i.e. mid-autumn), during the peak deposition of <i>L. ferocissimum</i> . ...	75
Figure 5.1. Aerial view of the southern paddocks associated with Cantara Homestead (top centre), including the locations of six 25 × 25 m fenced plots (solid perimeter) and six 25 × 25 m open plots (dashed perimeter) where field experiments were conducted. ....	87
Figure 5.2. Cumulative germination proportion (1-Kaplan-Meier estimates) for seeds of a) <i>Acacia sophorae</i> , b) <i>Rhagodia candolleana</i> , c) <i>Leucopogon parviflorus</i> and d) <i>Myoporum insulare</i> that were passed through the gut ( $n = 100$ seeds) or were extracted from fruit ( $n = 50$ seeds). <i>Exocarpos syrticola</i> was excluded as this species did not germinate in either treatment. ....	92
Figure 5.3. The number of seedlings (mean ± SE) recorded in subplots with introduced grasses and subplots cleared of introduced grasses ( $n = 4$ subplots per treatment) at Cantara for a) <i>Acacia sophorae</i> and b) <i>Rhagodia candolleana</i> . ....	94



Figure 5.4. For seedlings of *Acacia sophorae* that were open to mammal herbivory ( $n = 100$ ), a–c) the condition of seedlings from different height classes after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals, and d–f) initial seedling height versus change in seedling height after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals. ....97

Figure 5.5. For seedlings of *Myoporum insulare* that were open to mammal herbivory ( $n = 100$ ), a–c) the condition of seedlings from different height classes after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals, and d–f) initial seedling height versus change in seedling height after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals. ....98

Figure 5.6. For seedlings of *Rhagodia candolleana* that were open to mammal herbivory ( $n = 100$ ), a–c) the condition of seedlings from different height classes after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals, and d–f) initial seedling height versus change in seedling height after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals. ....99

Figure 5.7. For seedlings of three species that were excluded from mammal herbivory, a–c) the condition of seedlings from different height classes after 7 weeks for ungrazed seedlings and seedlings grazed by insects or snails, and d–f) initial seedling height versus change in seedling height after 7 weeks for ungrazed seedlings and seedlings grazed by insects or snails. Seedlings ( $n = 100$  seedlings per species) were deployed in the paddocks of Cantara in late August 2016. ....100

## List of tables

Table 2.1. The family, life form and fruit type of fleshy-fruited species dispersed by frugivorous birds in the Younghusband Peninsula. ....	28
Table 2.2. Seed-dispersing birds of the Younghusband Peninsula and the fruits they potentially disperse, as determined from local data sources (1–3) and non-local data sources (4–12): 1) personal observation (scat collection); 2) Forde (1986); 3) local bird censuses (Paton, unpubl. data); 4) Gosper (1999); 5) Attiwill (1970); 6) Rose (1999); 7) Mellor (1931); 8) Lea and Gray (1935a); 9) Noble and Adair (2014); 10) Lea and Gray (1935b); 11) Stansbury (1996) and 12) Dunstan <i>et al.</i> (2013). ....	32
Table 3.1. Bird visitation to the artificial bird perches summarised from 102 hours of direct observation between mid-spring and early summer (October–December 2015) and 6 months of remote camera observation recorded between summer and autumn (December 2016–May 2017). ....	45
Table 3.2. Number of captures (retraps in parentheses) and number of faeces collected from three bird species captured across five sites in the Younghusband Peninsula in January 2015 and January 2016. ....	50
Table 3.3. Contribution of five fleshy-fruited species to the total number of seeds passed (with percentage of contribution to total in parenthesis) by three bird species captured across five sites in the Younghusband Peninsula in January 2015 and January 2016. ....	51
Table 4.1. Species of seed present in seed traps beneath the artificial perches (AP; $n = 12$ ), paddock shrubs ( $n = 4$ shrub species, 10 shrubs per species), dune shrubs ( $n = 4$ shrub species, 10 shrubs per species) and in seed traps set in the open paddock (OP; $n = 25$ ) during a 12-month period, between September 2015 and August 2016. ....	67
Table 4.2 Similarity percentage (SIMPER) analysis, showing the species that contributed the most (up to 50%) to the average Bray-Curtis dissimilarity between paddock shrubs and dune shrubs in their compositions of seed rain, based on a) the abundance of species in the seed rain and b) the identity of species in the seed rain (i.e. species presence/absence). ....	72
Table 5.1. Cox proportional hazards semi-parametric models for a) <i>Acacia sophorae</i> , b) <i>Myoporum insulare</i> and c) <i>Rhagodia candolleana</i> seedling survival. The model shows the effect of herbivory treatment and initial seedling height on seedling survival time (i.e. the dependent variable). ....	95

Table 5.2. The percentage of a) *Acacia sophorae* and b) *Myoporum insulare* and c) *Rhagodia candolleana* seedlings at each census that were damaged or dead under two grazing treatments: excluded from mammal herbivory and open to mammal herbivory.....96

## Abstract

Artificial perches are a restoration tool used to accelerate the regeneration of degraded environments. They work by encouraging frugivorous birds to rest and defaecate seed in sites that lack vegetation. If these seeds can germinate and establish, then this may result in plant recruitment. This method was trialled for the first time in a degraded temperate coastal environment, which was located on the Youngusband Peninsula, South Australia. The potential effectiveness of artificial perches as a restoration tool was investigated by observing the frequency of perch use by seed-dispersing birds, by measuring seed deposition under perches and by determining the likelihood of subsequent plant recruitment under perches.

The artificial perches were able to attract seed-dispersing birds. This was determined through direct observations and the use of remote cameras. In total, 24 bird species visited the perches, 9 of which were known to disperse seed. These seed-dispersers were not obligate frugivores but rather consumed fruit as part of their varied diets. During the peak fruiting period of summer and autumn, the spiny-cheeked honeyeater (*Acanthagenys rufogularis*) and the singing honeyeater (*Lichenostomus virescens*) were the species that most frequently visited the perches. These birds were important visitors, as they frequently consumed fruit and dispersed seed from a variety of plant species.

The artificial perches effectively facilitated the dispersal of seed to the degraded site. Over 12 months, the quantities of seed collected beneath the perches were significantly greater than the quantities of seed that arrived in open areas of the degraded site ( $2161.2 \pm 578.5$  seeds/m<sup>2</sup> compared to  $0.32 \pm 0.18$  seeds/m<sup>2</sup> [mean  $\pm$  SE]). Most of this seed was deposited in summer and autumn, during the main period of fruit availability. On average, native plants accounted for 57.4% of the seeds received at the perches. To the benefit of restoration, the perches received the seeds from many native species (up to 13 species), including from the abundant and hardy shrubs *Rhagodia candolleana*, *Myoporum insulare* and *Acacia sophorae*. To the detriment of restoration, 42.4% of the seed deposited beneath the perches on average originated from the introduced shrub *Lycium ferocissimum*, which was likely due to its presence in the degraded site. This result indicated that perches have the potential to facilitate the spread of introduced fleshy-fruited species in degraded areas.

While the artificial perches facilitated the deposition of many seeds, very few of these seeds were likely to recruit due to post-dispersal barriers. Recruitment potential was investigated

for fleshy-fruited shrub species whose seeds were commonly deposited at the perches. Glasshouse and field experiments indicated that the establishment of these species was limited by recruitment barriers including poor germination and herbivory from grazing mammals. Recruitment may have also been limited by competition with introduced grasses. These factors combined would likely limit the recruitment of most species in the degraded areas of the Younghusband Peninsula. These findings suggest that if artificial perches are to be deployed to promote regeneration in the Younghusband Peninsula, then additional treatments will be required to help seedlings overcome post-dispersal recruitment barriers.

## **Declaration**

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

I give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

I acknowledge the support I have received for my research through the provision of an Australian Government Research Training Program Scholarship.

**Signature:**

**Date:** 31/03/2021

## Acknowledgements

This thesis would not have been possible without the help of many people. First, I would like to thank my supervisors Associate Professor David Paton and Dr John Goodfellow. Dave, thank you for your guidance and considerable feedback on the thesis, and for your help in the field. John, thank you for your positivity and for providing comments on my thesis.

I am grateful to the many people who assisted me with field work, as this thesis would not have been possible without them. These outstanding people endured the blasting cold winds of the Southern Ocean in winter, hidden snakes in spring, and overwhelmingly hot summers — thankfully, autumn was mostly pleasant. Thank you to Hayley Merigot for the many trips you made down to Cantara, including the days spent watching perches in the blistering sun. Thank you to Colin Bailey and Tommy Bradley for the backbreaking work they put in to construct my exclusion plots. Thank you to those who made a trip down to help, including Tom Shaw, Grace Hodder, Naomi Tucker, Cathy Rowe, and Mike and Chris McCarron. I hope you can all forgive me for making you collect copious amounts of bird excrement.

Thanks goes to those I shared an office with, including Hayley, Grace, Tom, Casey, Kim, Hannah, James, Peri and Claire. I feel privileged to have spent the past few years with people who have the same passion for the environment as I do. Your feedback, support and humour during the writing process were also invaluable. Thanks also goes to my family and friends for their continued interest and ongoing encouragement throughout this project.

Site access and use was provided by the Department of Environment and Water and the Ngarrindjeri people. This project was supported by the Holsworth Wildlife Research Endowment from the Equity Trustees Charitable Foundation, the Lirabenda Endowment Fund from the Field Naturalists Society of South Australia and by a research award from the Friends of Private Bushland. These generous funds made this project possible and are gratefully acknowledged.

All photos used in this thesis were taken by the author (Victoria McCarron). Maps throughout this thesis were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license.

This thesis is dedicated to my nana, Anna Agius. She was known for her love of animals, including birds. I am proud to have shared this passion with her.

# Chapter 1. General introduction

## 1.1 Land modification and the need for restoration

More than 60% of Earth's terrestrial surface has been transformed by humans through land-use activities, such as agricultural practices, resource extraction and infrastructure development (Hurt et al. 2006; Choi 2017). This land modification has supposedly been necessary to support expanding human populations but has led to a growing trend of overexploitation, degradation and eventual land abandonment (Ramankutty and Foley 1999). All modification practices leave a legacy on the landscape. Altered plant biomass, hydrology and soil structure modify ecosystem processes and these changes can endure for hundreds, or even thousands of years after the practices have ceased (Foster et al. 2003). When degradation is extensive and intensive, the threshold for self-repair is passed and some form of restoration becomes necessary (Cramer et al. 2008). Of course, restoration is not often prioritised or carried out, especially when natural resource management funds are limited (Aronson et al. 2006). Rather, these funds are spent on conservation efforts, including the acquisition and preservation of intact habitats (Possingham et al. 2015). Such efforts, however, are no longer viable when few areas of intact habitat remain, or when the remaining habitat is unable to support its biota (Hobbs and Harris 2001). Conservation in this situation can be achieved through restoration, as it can improve or expand the remaining intact habitats (Young 2000). Evidently, restoration is now essential to biodiversity conservation in many parts of the world, including Australia, South Africa, North America and some parts of Europe (Aronson et al. 2006; Suding 2011).

## 1.2 Restoration of degraded environments

In general, the first step in ecological restoration focuses on the removal of the disturbances that are causing degradation (e.g. fire, grazing, irrigation), so the system can begin to passively restore itself (Palmer et al. 2016). For example, the removal of livestock can allow for the passive recovery of vegetation (Batchelor et al. 2015), small vertebrates (Haby and Brandle 2018) and biological soil crusts (Read et al. 2011). In another example, the cessation of fire suppression activities can allow fire regimes to approach historical standards (McIver and Starr 2001). Passive restoration can effectively restore ecosystems, most particularly in areas where the disturbance has been light or short-lived (Holl and Aide 2011; Bechara et al. 2016). Passive restoration, however, is often also slow, especially when there are limitations in the drivers of recovery (e.g. propagule supply, disperser availability;



Rey Benayas *et al.* 2008; Zahawi *et al.* 2014). An active approach to restoration may be preferred under these circumstances. This approach includes interventions such as vegetation planting, direct seeding, weeding, burning, and thinning — all of which are used to produce a desired pattern, structure or composition in the landscape (Rey Benayas *et al.* 2008; Bechara *et al.* 2016). Active restoration projects are becoming increasingly popular, although, these projects are often expensive and require considerable time, maintenance and labour (Holl and Aide 2011). These requirements can restrict the scale of restoration and limit associated outcomes (Shono *et al.* 2007). For example, a recent review of revegetation literature in Australia estimated establishment costs for manual tubestock plantings to range from \$1763 to \$6396/ha and direct seeding costs to range from \$597 to \$2519/ha (Summers *et al.* 2015). While direct seeding is less expensive, restoration attempts using this method are generally less successful due to poor germination, high mortality and intense weed competition (Ceccon *et al.* 2015; Palma and Laurance 2015).

Restoration techniques that aim to stimulate natural regeneration could reduce the need for expensive and labour-intensive methods. These techniques work by removing or manipulating restoration barriers in a low-intensity and cost-effective manner (Shono *et al.* 2007). For example, competition from herbaceous vegetation can be reduced through herbicide application, cutting and even low-intensity grazing, which in turn can stimulate native plant regeneration (Shoo and Catterall 2013). In another example, fire can be used to help trigger seed germination and reduce competition from fire sensitive species (Pyke *et al.* 2010). Currently, most natural regeneration techniques aim to increase establishment, growth and survival of plants (Shoo and Catterall 2013). In contrast, few of the techniques aim to increase the arrival of propagules, even though limited propagule supply is often a barrier to regeneration in disturbed ecosystems (Holl *et al.* 2000; Zimmerman *et al.* 2000; Standish *et al.* 2007). This barrier is often observed in cleared and degraded habitats (i.e. habitats of reduced quality) where animals are relied upon to carry out seed dispersal. Seed dispersal is limited as the animal dispersers have little incentive to enter degraded environments, especially when they lack food resources, perching sites and structurally complex vegetation (Wunderle 1997; Duncan and Chapman 2002). Natural regeneration techniques that overcome dispersal limitations include soil and seed bank translocations, as well as more novel techniques such as artificial shelters and perches, which facilitate the movement of seed-dispersing animals into disturbed or degraded areas (McClanahan and Wolfe 1993; Reis *et al.* 2010).

### **1.3 The use of artificial perches for restoration**

From the range of available natural regeneration methods, artificial perches in particular have received considerable attention from researchers (Guidetti *et al.* 2016). This restoration method works by encouraging seed-dispersing birds to rest while moving across the degraded landscape. While perched, the birds may defaecate seeds of fruits they have consumed, which may then lead to the recruitment of pioneer plants. These pioneer plants may then facilitate the recruitment of other plants, allowing regeneration to occur (Reis *et al.* 2010). One of the main advantages of this restoration method is that the composition of seeds deposited and recruited beneath the artificial perches can resemble that of the nearby remnant vegetation, as it is able to act as a primary source of seed (Bechara *et al.* 2016; Guidetti *et al.* 2016). Perches may also provide beneficial ecosystem services beyond the facilitation of seed dispersal. They can attract raptors, which may use the perches to hunt for exotic pests, such as invasive mice or snails (Kay *et al.* 1994; Pias *et al.* 2012). Perches can also increase the movement of pollinating birds across the landscape and thus assist with plant genetic outbreeding (Liu *et al.* 2013). Of course, there are also disadvantages with this restoration method. The seed deposited beneath an artificial perch is not always able to recruit, particularly when there are recruitment barriers present (e.g. seed and seedling predation, competition with introduced species; Holl *et al.* 2000). Artificial perches are also often deployed in small numbers and over small scales, limiting the area that could potentially be restored over the short-term (Bechara *et al.* 2016).

Artificial perches have been implemented in a variety of designs, including crossbars (Holl 1998), branch piles (Castillo-Escrivà *et al.* 2019), dead branches (Elgar *et al.* 2014) and dead trees (McClanahan and Wolfe 1993). Several researchers have compared the effectiveness of various perch designs and found that structurally complex perches were generally more attractive to birds than simple perches (McDonnell and Stiles 1983; Holl 1998; Athiê and Dias 2016). Past research has also tested whether the distance of the perch from remnant vegetation had an influence on seed deposition, as some birds may avoid venturing far into degraded habitats (Wunderle 1997). Two studies found that seed deposition decreased as perch distance increased (McClanahan and Wolfe 1993; Wilson and Aebischer 1995), whereas other studies observed no effect at all, as the birds that dispersed seed to the perches were willing to move far into the degraded area (Vicente *et al.* 2010; La Mantia *et al.* 2019).

Artificial perches have been deployed to aid natural recruitment and recovery in a variety of degraded habitats, including former pastures, agricultural lands, plantations, closed landfills, reclaimed mining sites and cleared forests (Holl 1998; Scott *et al.* 2000; Zanini and Ganade 2005; Pillatt *et al.* 2010; Vicente *et al.* 2010; Graham and Page 2012). Many of these studies were located in tropical and subtropical forests, which makes sense given the dominance of fleshy-fruited plant species and frugivorous birds in these environments (Howe and Smallwood 1982; Guidetti *et al.* 2016). Comparatively, fewer studies evaluating the use of artificial perches have been undertaken in temperate and semi-arid environments (e.g. Heelemann *et al.* 2012; La Mantia *et al.* 2019; Martínez-López *et al.* 2019). In these systems frugivory is less common (Willson *et al.* 1989).

The increased seed rain associated with the deployment of artificial perches has been well studied (Guidetti *et al.* 2016), however, there are still aspects of this method that need to be considered. For example, despite birds playing an important role in the seed dispersal process, only a small proportion of the former studies identified their perch visitors and observed perch use (e.g. Shiels and Walker 2003; Vicente *et al.* 2010; Graham and Page 2012). Many former studies have also neglected to monitor post-dispersal seedling recruitment, which is critical for determining the effectiveness of the restoration method (Elgar *et al.* 2014; Guidetti *et al.* 2016). This lack of monitoring is concerning, particularly as several researchers have promoted the utility of the artificial perches for restoration without knowing the potential for seedling recruitment (e.g. Athiê and Dias 2016; Ferreira and de Melo 2016; Oliveira *et al.* 2018; La Mantia *et al.* 2019). Conservation groups and practitioners may be enticed to adopt the restoration method before there has been sufficient field validation and thus risk wasting limited resources on methods that ultimately fail (Reid and Holl 2013).

Lastly, while artificial perches have been explored in many different environments, they are yet to be tested in coastal ecosystems. This is an oversight, especially as these ecosystems can support a diversity of prominent fleshy-fruited plants and frugivorous birds, which are required for the restoration method to work. This includes temperate coastal dunefields in South Africa (Castley *et al.* 2001), tropical coastal forests in southern India (David *et al.* 2015), temperate forests in New Zealand (Williams and Karl 1996), and many parts of the Australian coastline, ranging from southern Queensland to Western Australia (Smith 1973; Barson and Calder 1981; Kirkpatrick and Harris 1999; Oppermann 1999). Many of these coastal ecosystems have also been extensively cleared for human development, or degraded

in various ways, such as through grazing by stock and introduced herbivores like rabbits (Valiela 2006). Artificial perches could be used to promote seed rain and enhance vegetative regeneration in some of these degraded coastal environments. One particular system that is suited for this undertaking is the Youngusband Peninsula located in South Australia. Fleshy-fruited plants and frugivorous birds are prominent in the vegetation present on the more intact sand dunes of this Peninsula (Paton 2010) but there are also many cleared and degraded areas that are in need of restoration (Butcher and Rogers 2013).

#### **1.4 Aim and outline of thesis**

The primary aim of this thesis was to investigate the ability of artificial perches to overcome seed dispersal limitations and promote the vegetative restoration of a degraded temperate coastal environment, located on the Youngusband Peninsula. This aim was addressed through a comprehensive and systematic approach, which set out to determine the ability of the perches to attract seed-dispersing birds and facilitate seed dispersal but also sought to explore the potential for subsequent plant recruitment beneath the perches. This approach is structured in the thesis as follows.

Chapter 2 investigated the ecological context of the Youngusband Peninsula and used this information to consider how artificial perches could potentially perform in this environment. This chapter provided a summary of the land use and degradation; examined the local seed-dispersing birds and fleshy-fruited plants present, as well the relationships between these species; and reviewed the potential site-related barriers that could prevent recruitment.

Chapter 3 determined the range of bird species that visited the perches and particularly focused on those which were potential seed dispersers. This chapter considered how the behaviour and fruit consumption of the seed-dispersing birds influenced the restoration process. This chapter also investigated the influence of perch complexity on bird attraction and tested whether patterns of visitation were seasonal.

Chapter 4 examined the ability of the perches to facilitate the dispersal of seed into the degraded site. Seed deposition was measured over 21 months at the perches, which included measures of seed abundance and species richness. To determine the effectiveness of the dispersal facilitation, seed deposition was also measured over 12 months in open areas, at isolated vegetation in the degraded site, as well as at remnant vegetation in the surrounding dunes.

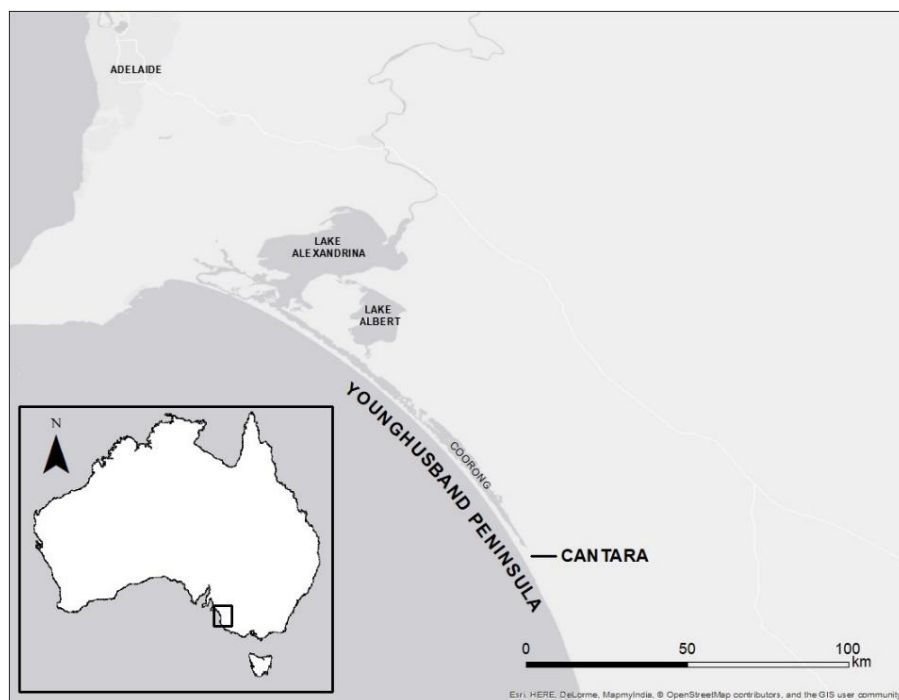
Chapter 5 investigated the significance of post-dispersal recruitment barriers and discussed the likelihood of recruitment at the perches. The recruitment barriers investigated in this chapter consisted of poor seed germination, competition with introduced species and seedling herbivory.

Lastly, Chapter 6 summarises the thesis findings and discusses the potential of artificial perches as a restoration method.

## Chapter 2. Background ecology of the Younghusband Peninsula and the need for restoration

### 2.1 Overview of the study region

The Younghusband Peninsula is located on the south-eastern coast of South Australia (Fig. 2.1). The climate in the region has been described as Mediterranean and is characterised by notable summer droughts. Average annual rainfall for the region is 521.8 mm per year (measured at Salt Creek's Pitlochry Outstation, 36.28° S, 139.84° E), with precipitation greatest in winter (June to August; Australian Bureau of Meteorology 2021).



**Figure 2.1.** Younghusband Peninsula located in South Australia. Note the location of Cantara, which is the primary study site in the region.

The Younghusband Peninsula is a narrow beach-dune barrier that separates the Coorong, a hypersaline lagoonal ecosystem, from the Southern Ocean. The Peninsula is only 1 to 2 km wide and extends from the River Murray Mouth for some 190 km towards the south-east (Bourman *et al.* 2018). The Younghusband Peninsula is comprised of a transgressive dune system, which is characterised by a strong zonation in coastal vegetation. The foredunes are stabilised by sand-binding grasses, which allow for the colonisation of other species including rushes, creeping succulents and occasional shrubs (Paton 2010). Further inland resides stabilised dunes that are more or less under a continuous cover of coastal shrubland

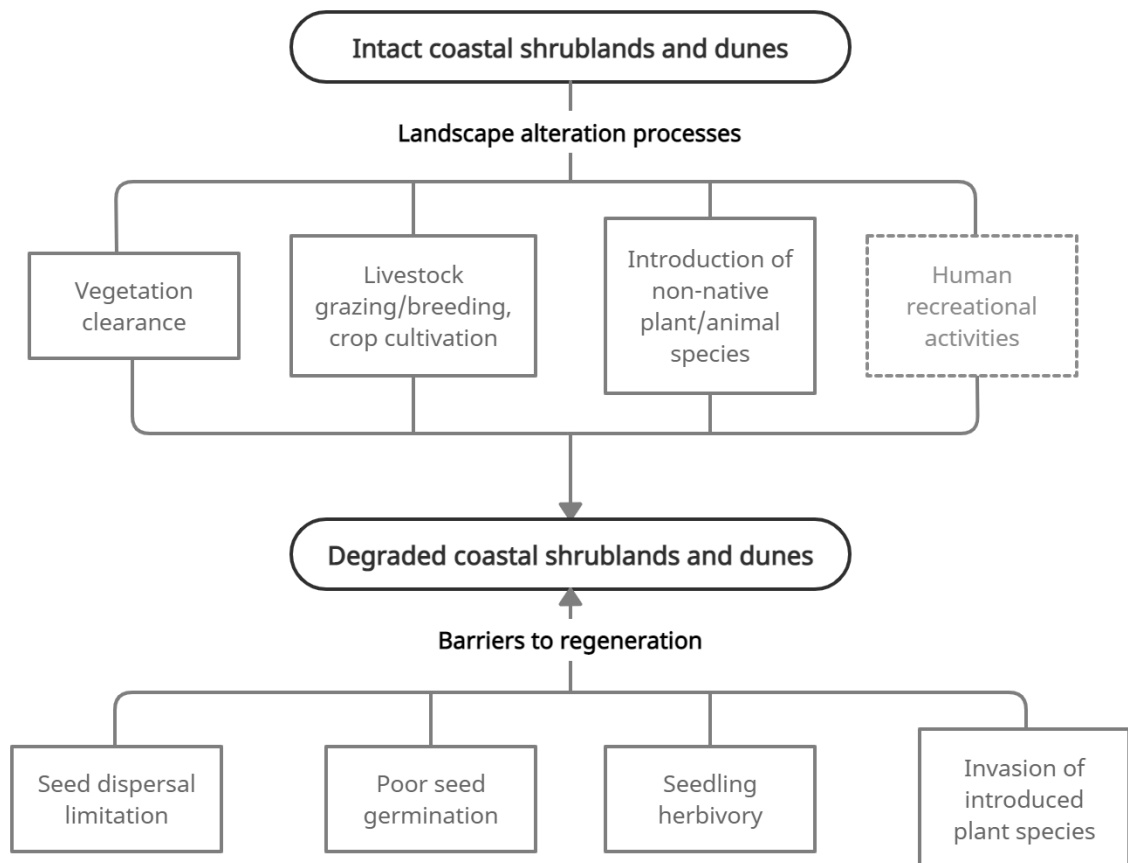
(Mowling and Taylor 1977; Gilbertson 1981). These shrublands are dominated by a range of fleshy-fruited species (Table 2.1) and the seeds of these plants are dispersed by a variety of fruit-consuming birds, which includes many perching birds, as well as the large-bodied and flightless emu (*Dromaius novaehollandiae*) (Forde 1986). Recent estimates indicate that approximately 60% of the Youngusband Peninsula is covered in remnant vegetation, with the remainder being either bare sand or abandoned pasture (Butcher and Rogers 2013).

## **2.2 Degradation and the need for artificial perches**

The Youngusband Peninsula has a long history of land degradation, which was initiated during the 1840s and 1850s, when the land was first settled (Rudduck 1982). Pastoral leases were issued, which allowed for grazing, stock breeding and crop cultivation. These pastoral activities led to the clearance of native vegetation and the introduction of a wide range of environmental weeds from Europe and Africa (Fig. 2.2; Paton 2010; Butcher and Rogers 2013). This included non-native grasses, such as barley (*Hordeum* spp) and oats (*Avena* spp), which were grown on some parts of the Peninsula as animal feed (Rudduck 1982). Other introduced grasses that are currently abundant in the region include *Vulpia* spp, *Ehrharta calycina*, *Bromus diandrus* and *Lagurus ovatus* (Milne 2015). The loss of native vegetation on the Youngusband Peninsula was hastened by the introduction of the European rabbit (*Oryctolagus cuniculus*), which arrived during the 1860s and was a major pest by 1882 (Fig. 2.2; Rudduck 1982; Butcher and Rogers 2013). By the 1960s, most pastoral activities had ceased as they had become unviable economically, and by 1976, much of the Youngusband Peninsula had been proclaimed as National Park (Rudduck 1982). In recent decades, degradation in the Peninsula has been the result of human recreational activities, including the use of off-road vehicles (Fig. 2.2; Gilbertson 1977; Paton 2010).

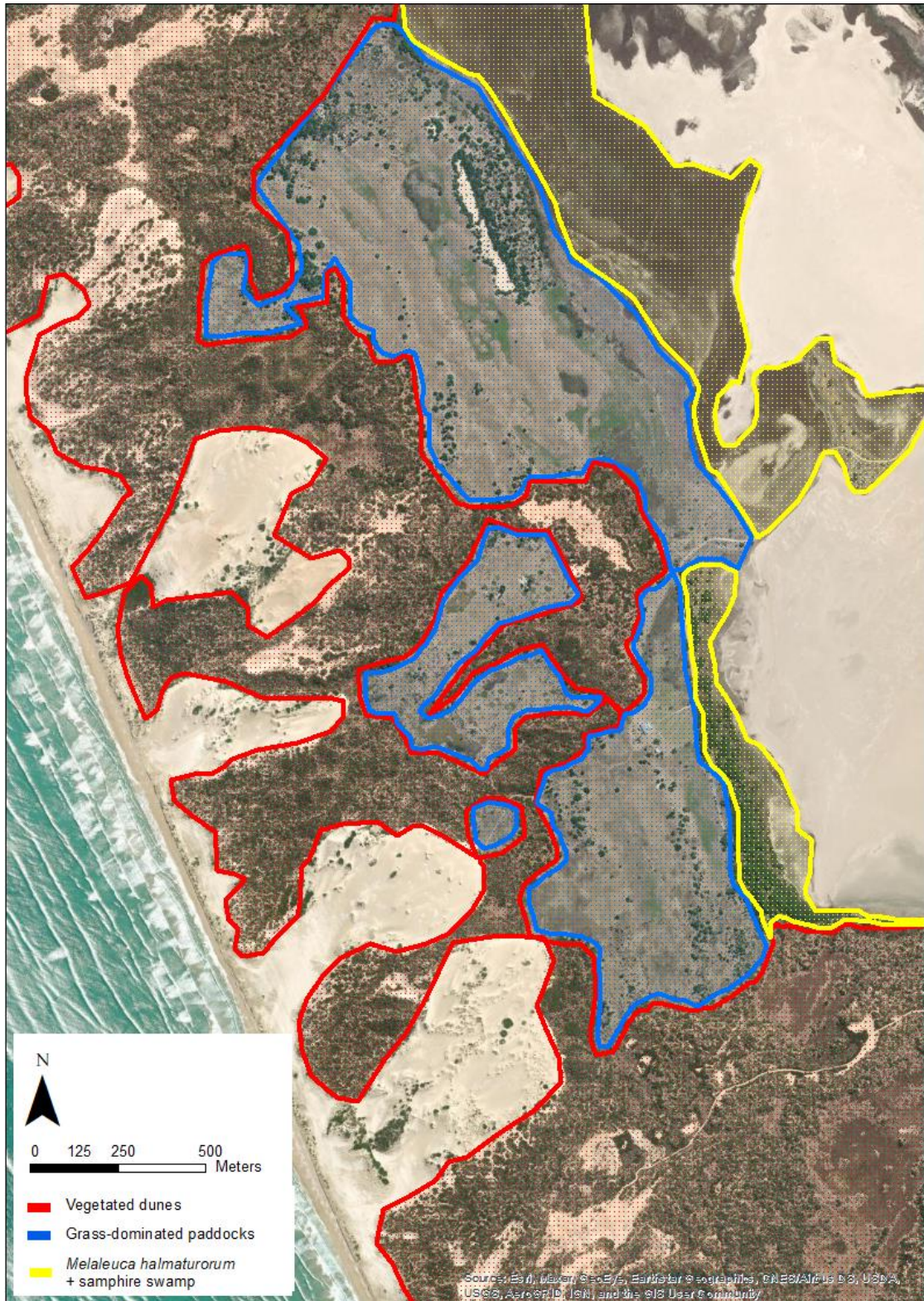
The vegetation on the Youngusband Peninsula has recovered somewhat following the removal of stock, restriction of off-road vehicle use and the introduction of several rabbit controls, which included the myxomatosis virus in 1952 and the rabbit haemorrhagic disease in 1996 (Paton 2010; Moulton *et al.* 2018). Despite these controls, some of the more heavily altered parts of the Youngusband Peninsula have been slow to recover. This includes Cantara, which is an abandoned property that has remained in a state of degradation. Cantara is in the southern part of the Youngusband Peninsula and resides on the eastern side of the dunal system, approximately 800 m inland from the Southern Ocean (36°20'S,

139°44'E; Fig. 2.1, Fig. 2.3). This site was used as a horse-breeding station in the mid to late nineteenth century, stocking up to 1500 horses and in addition some cattle (Paton 1977). The number of horses declined to 350 by 1907 following the impacts of rabbit grazing, as they denuded the dunes of vegetation (Rudduck 1982). The land also stocked 2800 sheep from the early 1950s, although this had ceased by 1972 when the property was purchased by the National Parks and Wildlife Service (Rudduck 1982).



**Figure 2.2.** Degradation pathway in the Younghusband Peninsula, including the processes that have resulted in landscape degradation and the barriers that have prevented regeneration. The solid boxes show the alteration processes and regeneration barriers relevant to the study site of Cantara.





**Figure 2.3.** Map broadly outlining the different types of habitat present in the study area of Cantara. Eastwards of the paddocks reside *Melaleuca halmaturorum* + samphire swamp, as well as an ephemeral lake (Lake Cantara). Dunes stabilised with native vegetation occur westwards of the paddocks. Beyond this resides non-vegetated mobile dunes and the Southern Ocean.



**Figure 2.4.** Photos taken in the study site which a) demonstrates the extent of vegetation clearance within the southern paddocks and b) highlights the presence of dense remnant vegetation on the hind dunes surrounding the southern paddocks.

Almost 50 years have now passed since Cantara was destocked, and the land has not recovered during this time. The cleared and formerly grazed paddocks are readily observable in the landscape (Fig. 2.3, Fig. 2.4a) and they currently cover an area of approximately 125 ha. The land is largely devoid of native vegetation. Instead, introduced grasses and herbs are dominant. The slow regeneration at Cantara is likely in part due to poor seed dispersal into the abandoned paddocks (Fig. 2.2). The northern, western and southern sides of the former paddocks of Cantara are surrounded by the landward slopes of dunes which are covered with fleshy-fruited plant species (Fig. 2.3, Fig. 2.4b). The seeds

from these plants, however, are unable to disperse into and throughout Cantara as it lacks the vegetation required to attract seed-dispersing birds. Artificial perches could be used to overcome this seed dispersal limitation, as they would encourage seed-dispersing birds to move into the paddocks and would provide them with a place to rest and deposit seed. Seeds deposited beneath the artificial perches would then need to recruit to allow regeneration to occur. The following sections consider the suitability of the restoration method in facilitating the vegetative recovery of the area and considers how the local ecology may influence the restoration process.

### **2.3 The role of birds and plants in the restoration of Cantara**

Vegetative restoration through the use of artificial perches at Cantara will depend upon the local birds and plants, as the plants provide the seed for regeneration and the birds provide the service of dispersal. In terms of plants, there are at least 18 fleshy-fruited species present in the remnant vegetation of the Youngusband Peninsula that can provide seed for regeneration (Table 2.1). Most of the plant species are shrubs while a few are herbs or climbers. Many of these fleshy-fruited plant species can be found on the stabilised dune slopes that surround Cantara, which suggests that these areas could act as primary sources of seed. This suite of species should be suitable for promoting revegetation in the relatively lower-lying paddocks, as many of the fleshy-fruited species which occur on the dune slopes can also be found in lower-lying areas of the landscape (Mowling and Taylor 1977; Paton 2010).

Many of fleshy-fruited species present in the remnant vegetation surrounding the paddocks are expected to be dispersed to the perches, although some of these species are unlikely to establish during the initial stages of regeneration. For example, species such as *Amyema melaleucae*, *Exocarpos syrticola* and *Cassytha pubescens* are parasitic or semi-parasitic and require host plants to establish (Forde 1986; Reid and Yan 2000; Paton 2010). The dispersal of some fleshy-fruited species, such as *Lycium ferocissimum* and *Asparagus asparagoides* would be to the detriment of restoration, as they are both highly invasive species that originate from southern Africa (Alcock and Symon 1977). Species more inclined to initiate revegetation processes likely include native shrubs such as *Acacia sophorae*, *Myoporum insulare* and *Rhagodia candolleana*, as they are hardy species which have the ability to colonise coastal habitats, including those that have been disturbed by European settlement (Chladil and Kirkpatrick 1989; Kirkpatrick and Harris 1999; Heyligers 2006; Robinson *et*

al. 2008; Heyligers 2009; Liney 2011; Kelsall 2015). While these plant species appear to be useful in initiating regeneration, the vegetation community that these plant species may potentially restore is unlikely to resemble that which occurred prior to European settlement. This is because the rabbits introduced by Europeans have seemingly altered the structure and compositions of vegetation on the Youngusband Peninsula, from an open shrubland or grassland with *Casuarina* tree species to a continuous dense shrubland (Gilbertson 1981). Despite this, the regeneration that could potentially occur in the abandoned paddocks will be important for not only restoring the biodiversity of native plant species in the landscape but for also restoring habitat connectivity and function.

**Table 2.1.** The family, life form and fruit type of fleshy-fruited species dispersed by frugivorous birds in the Youngusband Peninsula. \* = introduced species. Plant information obtained from the Flora of South Australia (Department for Environment, Water and Natural Resources 2007), the South Australian Seed Conservation Centre (2020) and pers. obs. Widths (mm) are indicative of the shortest dimensions that occur in the fruit and seeds of the plant species. The term ‘seed’ also referred to the woody stones of *Leucopogon parviflorus* and *Myoporum insulare*, which potentially contain multiple seeds.

Species	Family	Life form	Fruit type	Fruit width (mm)	Seed width (mm)
<i>Acacia sophorae</i>	Fabaceae	shrub	fleshy aril	2–2.5	2.5–3
<i>Alyxia buxifolia</i>	Apocynaceae	shrub	drupe	8–10	4–5
<i>Amyema melaleucae</i>	Loranthaceae	mistletoe	drupe	6–8	4–5
<i>Asparagus asparagoides</i> *	Asparagaceae	climber	berry	6–10	2–4
<i>Billardiera cymosa</i>	Pittosporaceae	climber	drupe	6–7	2–3
<i>Cassytha pubescens</i>	Lauraceae	climber	drupe	6–8	4–5
<i>Dianella revoluta</i>	Hemerocallidaceae	herb	berry	6–8	1.5–12
<i>Enchylaena tomentosa</i>	Chenopodiaceae	shrub	fruiting perianth	5	1.5–2
<i>Exocarpos syrticola</i>	Santalaceae	shrub	fleshy pedicel	2.5–3.5	3
<i>Leucopogon parviflorus</i>	Ericaceae	shrub	drupe	3–5	2–3
<i>Lycium ferocissimum</i> *	Solanaceae	shrub	berry	5–8	0.5–1
<i>Muehlenbeckia gunnii</i>	Polygonaceae	climber	fruiting perianth	2.5–3	2.5
<i>Myoporum insulare</i>	Scrophulariaceae	shrub	drupe	6–8	3.5–4
<i>Rhagodia candolleana</i>	Chenopodiaceae	shrub	drupe	1.8–2	0.8–1
<i>Scaevola calendulacea</i>	Goodeniaceae	herb	drupe	7–10	2.5–3
<i>Tetragonia implexicoma</i>	Aizoaceae	climber	drupe	5	3–4
<i>Threlkeldia diffusa</i>	Chenopodiaceae	shrub	fruiting perianth	2	1.4–1.8

Evidently, some plant species would be more useful than others in the initial stages of regeneration, however, the species that ultimately arrive at the perches is determined by the bird species that visit the perches and the fruits that they chose to consume. The selection of fruit by birds is influenced by numerous traits, such as fruit arrangement, accessibility,

colour, size and nutritional content (Herrera 1984; Jordano 1987; Willson *et al.* 1990; Stanley and Lill 2001; Izhaki 2002). The plants of the Youngusband Peninsula show considerable diversity in these fruit traits (Table 2.1, Fig. 2.5a–f). Many of the fruits present as drupes (e.g. *Billardiera cymosa*), although some occur in the form of berries (e.g. *L. ferocissimum*), fruiting perianths (e.g. *Enchylaena tomentosa*) or fleshy pedicels (e.g. *E. syrticola*). In terms of arrangement, species such as *Leucopogon parviflorus* and *M. insulare* arrange their fruit along the branch (Fig. 2.5a, b), whereas *R. candolleana* produces dense fruit aggregates on the end of branches (Fig. 2.5d). In contrast, *A. sophorae* has pods, which contain 4–10 seeds (Fig. 2.5c). Each seed is attached to the pod by a fleshy aril, which acts as a food reward for a seed-dispersing bird.



**Figure 2.5.** Fleshy-fruited species commonly consumed by frugivorous birds in the Youngusband Peninsula including a) *Leucopogon parviflorus*, b) *Myoporum insulare*, c) *Acacia sophorae*, d) *Rhagodia candolleana*, e) *Exocarpos syrticola* and f) *Lycium ferocissimum*.

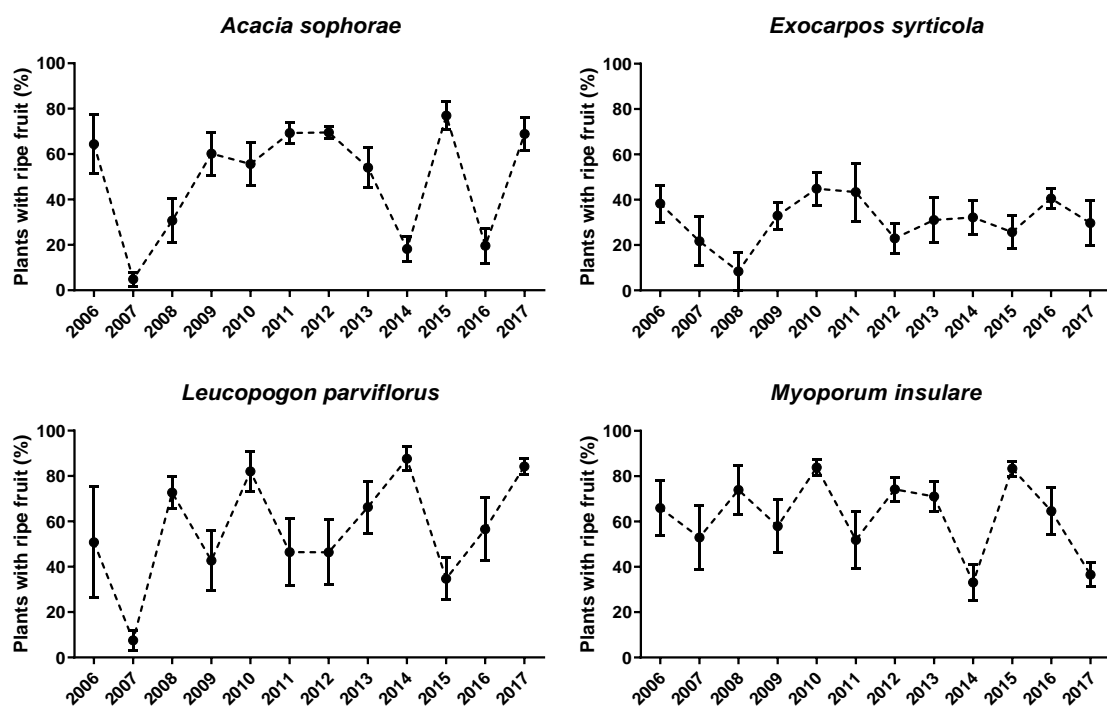
The fleshy fruits produced by plants on the Younghusband Peninsula also show variation in seasonal availability (Fig. 2.6), which has important implications for the timing of seed arrival at the perches. Notably, the plant species in the region predominantly fruit in summer (December–February) and autumn (March–April). Perches could be expected to be most effective at facilitating seed dispersal during these seasons and less so in winter (June–August) and spring (September–November), when few species produce fruit. Most of the plant species produce fruit over short periods, although some species can produce small amounts of fruit intermittently throughout the year, including *L. ferocissimum*, *E. tomentosa* and *R. candolleana* (Forde 1986).

Plant species	J	F	M	A	M	J	J	A	S	O	N	D
<i>Muehlenbeckia gunnii</i>									■	■	■	■
<i>Asparagus asparagoides</i> *										■	■	■
<i>Tetragonia implexicoma</i>										■	■	■
<i>Threlkeldia diffusa</i>	■	■									■	■
<i>Dianella revoluta</i>	■	■	■								■	■
<i>Acacia sophorae</i>	■	■	■									■
<i>Leucopogon parviflorus</i>	■	■	■	■								■
<i>Exocarpos syrticola</i>	■	■	■	■								■
<i>Myoporum insulare</i>	■	■	■	■								■
<i>Billardiera cymosa</i>	■	■	■	■	■							
<i>Rhagodia candolleana</i>		■	■	■	■	■						
<i>Alyxia buxifolia</i>			■	■	■	■						
<i>Enchylaena tomentosa</i>			■	■	■	■						
<i>Amyema melaleucae</i>			■	■	■	■						
<i>Lycium ferocissimum</i> *			■	■	■	■						

**Figure 2.6.** The primary fruiting times of fleshy-fruited plants in the Younghusband Peninsula.

\* = introduced species. Figure adapted from Forde (1986), Young (1981) and pers. obs.

The plants on the Younghusband Peninsula also vary in the quantities of fruit produced from one year to the next (Fig. 2.7), which is similar to other Mediterranean temperate regions (e.g. Spain, Herrera 1998). The exact drivers of fruit variability in the region are not known, although winter frosts have some influence. When severe, frosts can cause considerable canopy dieback and reduce subsequent fruit production (Paton 2010). This reduction in fruit productivity was evident in *A. sophorae*, *E. syrticola* and *L. parviflorus* in January 2007 following severe frosts in August 2006 (Fig. 2.7). Thus, there is some potential that the abundances and richness of seeds dispersed to the perches could also vary between years.



**Figure 2.7.** Fruiting availabilities of four fleshy-fruited species determined from plants sampled at five sites along the Coorong National Park. Plants were sampled each January (i.e. mid-summer) between 2006 and 2017 and 30–50 plants were sampled per species at each site (Paton, unpubl. data). For each species, the figure depicts the mean percentage of plants with ripe fruit ( $\pm$  SE).

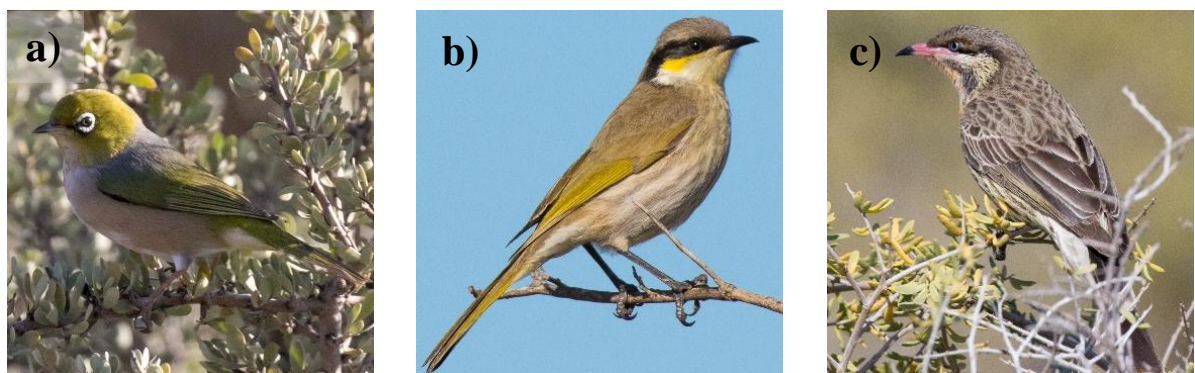
**Table 2.2.** Seed-dispersing birds of the Younghusband Peninsula and the fruits they potentially disperse, as determined from local data sources (1–3) and non-local data sources (4–12): 1) personal observation (scat collection); 2) Forde (1986); 3) local bird censuses (Paton, unpubl. data); 4) Gosper (1999); 5) Attiwill (1970); 6) Rose (1999); 7) Mellor (1931); 8) Lea and Gray (1935a); 9) Noble and Adair (2014); 10) Lea and Gray (1935b); 11) Stansbury (1996) and 12) Dunstan *et al.* (2013). The primary source of evidence was listed for each bird and plant combination, although there were often multiple sources that provided evidence for their relationship. \* = introduced species.

Dispersers	Plants														Total plant species				
	<i>Acacia sophorae</i>	<i>Alyxia buxifolia</i>	<i>Amyema melaleuca</i>	<i>Asparagus asparagoides*</i>	<i>Billardiera cymosa</i>	<i>Cassylha pubescens</i>	<i>Dianella revoluta</i>	<i>Enchylaena tomentosa</i>	<i>Exocarpos</i> spp	<i>Kunzea pomifera</i>	<i>Leucopogon parviflorus</i>	<i>Lycium ferocissimum*</i>	<i>Muehlenbeckia gunnii</i>	<i>Myoporum insulare</i>		<i>Rhagodia candolleana</i>	<i>Scaevola calendulacea</i>	<i>Tetragonia implexicoma</i>	<i>Threlkeldia diffusa</i>
Australian magpie <i>Cracticus tibicen</i>	4							1	2										3
Australian raven <i>Corvus coronoides</i>	4								2		3	3		3					5
black-faced cuckoo shrike <i>Coracina novaehollandiae</i>									2		4	7							3
brown thornbill <i>Acanthiza pusilla</i>	4																		1
common blackbird* <i>Turdus merula</i>				11					2		1	9		1					5
common starling* <i>Sturnus vulgaris</i>	6			2					2		6	9							5
emu <i>Dromaius novaehollandiae</i>	1	1		1	1	1	1	12	1	1	1	1	1	1	1	1	1	1	17
grey butcherbird <i>Cracticus torquatus</i>									2										1
grey currawong <i>Strepera versicolor</i>											2			2					2
little raven <i>Corvus mellori</i>											3	9							2
little wattlebird <i>Anthochaera chrysoptera</i>											2	2		1	2				4
mistletoebird <i>Dicaeum hirundinaceum</i>			2					2	2			2			2				5
purple-gaped honeyeater <i>Lichenostomus cratitius</i>	1								1		1	3		1	1			1	7
red wattlebird <i>Anthochaera carunculata</i>	1			11	2			2	1	2	1	2	2	1	1		2		12
rufous bristlebird <i>Dasyornis broadbenti</i>						2			2		10	2		2	10				6
singing honeyeater <i>Lichenostomus virescens</i>	1			5	2	2	2	1	1	2	1	1	1	1	1		2	1	15
spiny-cheeked honeyeater <i>Acanthagenys rufogularis</i>	1	2	2	5	2	2	2	2	1	2	1	1	1	1	1		2	1	17
superb fairy-wren <i>Malurus cyaneus</i>	4										2				2				3
silveryeye <i>Zosterops lateralis</i>	1	2		2	2		1	1	1	3	1	1	1	1	1		2	1	15
silver gull <i>Chroicocephalus novaehollandiae</i>				2							2				2				3
white-browed babbler <i>Pomatostomus superciliosus</i>								8							8				2
white-browed scrubwren <i>Sericornis frontalis</i>															2			1	2
<b>Total bird species</b>	<b>11</b>	<b>3</b>	<b>2</b>	<b>8</b>	<b>5</b>	<b>4</b>	<b>4</b>	<b>7</b>	<b>14</b>	<b>5</b>	<b>16</b>	<b>14</b>	<b>5</b>	<b>11</b>	<b>13</b>	<b>1</b>	<b>5</b>	<b>6</b>	



There are at least 22 bird species present in the study region that are known to disperse seed (Table 2.2). The mistletoebird (*Dicaeum hirundinaceum*) is the only specialised frugivore and feeds almost exclusively on mistletoe fruits (Reid 1986). In contrast, the other bird species consume fruit as part of their diet, although some to a greater extent than others (Table 2.2, Forde 1986). Those that frequently take fruit and consume the greatest range of plant species include the emu, silvereye (*Zosterops lateralis*, Fig. 2.8a), singing honeyeater (*Lichenostomus virescens*, Fig. 2.8b) and spiny-cheeked honeyeater (*Acanthagenys rufogularis*, Fig. 2.8c).

While the fruit-consuming birds of the Younghusband Peninsula consume many of the same species, they differ in their modes of dispersal. The large and flightless emu produces scats which often contain thousands of seeds and are deposited in open areas away from overhanging vegetation (Paton 2010; Nield *et al.* 2015). In contrast, silvereyes and the honeyeaters produce scats that typically contain a few seeds and are often deposited at trees or shrubs (Paton 2010). The perching birds are more important dispersers numerically speaking, as they disperse far greater quantities of seed per hectare and also dominate the terrestrial avifauna during summer, when fruit is most abundant (Paton 2010). Bird censuses conducted in January from 2004 to 2008 found the silvereye to be the most abundant frugivore (~25% of birds), followed by the singing and spiny-cheeked honeyeaters (each represent ~8% of birds, Paton 2010).



**Figure 2.8.** Common frugivorous birds in the Younghusband Peninsula, including a) the silvereye *Zosterops lateralis*, b) the singing honeyeater *Lichenostomus virescens* and c) the spiny-cheeked honeyeater *Acanthagenys rufogularis*.

Clearly, there are many seed-dispersing birds in the Younghusband Peninsula, although not all are expected to visit the artificial perches. This includes the flightless emu, ground-dwelling birds such as the rufous bristlebird (*Dasyornis broadbenti*) and birds that are

unlikely to rest on perches in terrestrial settings, such as the silver gull (*Chroicocephalus novaehollandiae*). The species more inclined to use the perches include those that are willing to enter open areas, such as the Australian magpie (*Cracticus tibicen*) and Australian raven (*Corvus coronoides*) (Higgins *et al.* 2006).

In addition to their willingness to use the perches, the seed-dispersing birds will need to be able to move seed over moderate distances (50–250 m), from the remnant vegetation in the dunes to the perches in the degraded site of Cantara. Tracking studies indicate that at least two seed-dispersing species in the study region — the silvereeye and the spiny-cheek honeyeater — are capable of dispersing some seed over such distances (Stansbury 2001; Paton 2010; Rawsthorne *et al.* 2011). Another study investigating the gut passage rate of silvereeyes found that they passed seeds of *Coprosma quadrifida* within 6–28 minutes (French 1996). Silvereeyes are unlikely to travel large distances over this time (maximum distances of 50–150 m over 10 minutes; Paton 2010), indicating that these birds appear to disperse most of the seed they consume over small to moderate distances.

#### **2.4 Recruitment barriers**

Apart from the occurrence of seed dispersal, regeneration at the artificial perches will depend upon the germination and recruitment of the deposited seed. In the Youngusband Peninsula, there are several barriers that will potentially prevent recruitment, including poor seed germination, competition with introduced plant species and seedling herbivory (Fig. 2.2). Poor germination is known to occur in some of the fleshy-fruited species in the region, such as *L. parviflorus* and *E. syraticola* (South Australian Seed Conservation Centre 2016). Native plant species recruitment is also likely to be limited through competition with introduced plant species. This includes non-native grasses such as *Avena barbata* and *B. diandrus*, which have been shown to limit the recruitment of native species in other parts of temperate Australia (Lenz *et al.* 2003; Ladd and Facelli 2005; Lenz and Facelli 2005; Standish *et al.* 2008). Recruitment will likely also be prevented by herbivorous mammals, which graze on seedlings in the Youngusband Peninsula and Coorong (Cooke 1987; Mutze *et al.* 2008; Bird *et al.* 2012; Moulton *et al.* 2018). This includes native herbivores such as western grey kangaroos (*Macropus fuliginosus*) and common wombats (*Vombatus ursinus*), as well as non-native herbivores such as European rabbits and feral fallow deer (*Dama dama*) (Bird *et al.* 2012).

## **2.5 Conclusion**

This chapter considered the potential function of artificial perches as a restoration tool within the ecological context of the Younghusband Peninsula. The local fleshy-fruit species and seed dispersing birds were examined for their potential role during the restoration process. Within the Younghusband Peninsula, there are at least 18 fleshy-fruited species present that can provide seed for regeneration and at least 22 bird species that can disperse seed. While there is a diversity of fleshy-fruited species, only some will have the potential to initiate vegetative restoration. This is because some plant species are unlikely to establish during the initial stages of regeneration, whereas others are of non-native origin. Similarly, only some of the seed-dispersing birds in the region are expected to assist in the restoration process. This is because some of the bird species do not use perches in terrestrial settings, whereas others are unlikely to venture into open and cleared areas. Regeneration at the artificial perches will also rely on the potential for the dispersed seed to recruit. In the Younghusband Peninsula, seedling recruitment could potentially be limited by barriers such as poor seed germination, competition with introduced grasses and seedling herbivory. The following three chapters now aim to observe and experimentally test the potential of the restoration tool within the cleared and degraded site of Cantara.

## Chapter 3. The use of artificial perches by birds on the Younghusband Peninsula

### 3.1 Introduction

Artificial bird perches are used to promote regeneration in cleared and degraded areas. They work by encouraging seed-dispersing birds to rest and defaecate seed, which may then result in the recruitment of plants. Birds play a critical role in this restoration process, although the birds that disperse the seed to the perches have only been occasionally identified (e.g. Holl 1998; Shiels and Walker 2003; Athiê and Dias 2016). Quantifying the use of artificial perches by birds is important for several reasons. First, these observations can identify the range of potential seed dispersers, which in turn can determine the quality of dispersal services available. This quality is influenced by the seed-dispersing abilities of birds, including their level of frugivory, fruit preferences, and ability to move between remnant and disturbed habitats (Levey 1986; Schupp 1993; Wunderle 1997). For example, birds that visited artificial perches located in tropical deforested peat swamps were found to be ineffective seed dispersers, as they failed to leave the degraded site and thus failed to disperse seed from areas of remnant vegetation (Graham and Page 2012). Rather, these birds predominantly dispersed seed from plants that had previously colonised the degraded site.

Observations of perch use may also determine the effectiveness of the perch design. For example, some studies have shown structurally complex perches (i.e. perches with a greater array of physical features) to attract more bird visitors than perches that were simple in design (Holl 1998; Athiê and Dias 2016). Perch observations may also determine if bird visitation varies seasonally, and if so, whether this visitation aligns with the peak period of fruit availability (Zanini and Ganade 2005). If bird visitation and fruit availability do not align, then seed deposition will be limited (Vogel *et al.* 2016). Finally, observations of perch use can identify the various uses that perches have for birds. For example, raptors can use the perches to hunt for prey, which in turn can help with the management of exotic species, including insects, snails and mice (Kay *et al.* 1994; Pias *et al.* 2012). Other studies have found that the provision of perches has allowed birds to enter landscapes which they were previously unwilling or unable to occupy (Horgan *et al.* 2016; Hannan *et al.* 2019).

In this study, artificial perches were erected in former grazing paddocks located on the Younghusband Peninsula, South Australia with the aim of enhancing vegetative restoration.

This chapter aimed to determine if seed-dispersing birds visited the perches, and if so, consider the influence that they would have on the restoration process. Furthermore, this chapter investigated the importance of perch design in influencing the use of perches by birds. Specifically, I asked the following questions:

- 1) Which bird species visited the artificial perches and of these which species were potential seed dispersers?
- 2) How do birds influence seed deposition through their fruit consumption and rates of visitation to the artificial perches?
- 3) Does the use of artificial perches by birds vary seasonally?
- 4) Does the structural complexity of the artificial perch influence the frequency of bird visitation?
- 5) What are the various uses that artificial perches have for birds?

## 3.2 Methods

### 3.2.1 Study location

This study was conducted in the southern paddocks of Cantara (Fig. 3.1), which cover an area of approximately 25 ha. These paddocks were located about 800 m inland from the Southern Ocean, on the Younghusband Peninsula, South Australia (36°20'S, 139°44'E). The climate is Mediterranean, with cool-moist winters (June–August) and hot-dry summers (December–February) (Australian Bureau of Meteorology 2021). Pastoral activities, such as horse-breeding and sheep grazing, were once conducted in the paddocks of Cantara (Paton 1977). These activities were initiated in the 1840s, although ceased by the 1970s, as the land was no longer viable for grazing (Rudduck 1982). The land has not recovered from the degradation in the 50 or so years that have followed.

Introduced grasses and herbs dominate the paddocks. At best, occasional patches of fleshy-fruited shrubs occur in the paddocks and consist of species such as *Acacia sophorae*, *Myoporum insulare* and *Rhagodia candolleana*, as well as the introduced species *Lycium ferocissimum*. The north, south and western sides of the paddocks are encompassed by the landward slopes of stabilised dunes, which are covered in a range of native fleshy-fruited plant species. To the east of the paddocks resides a thick stand of *Melaleuca halmaturorum*.

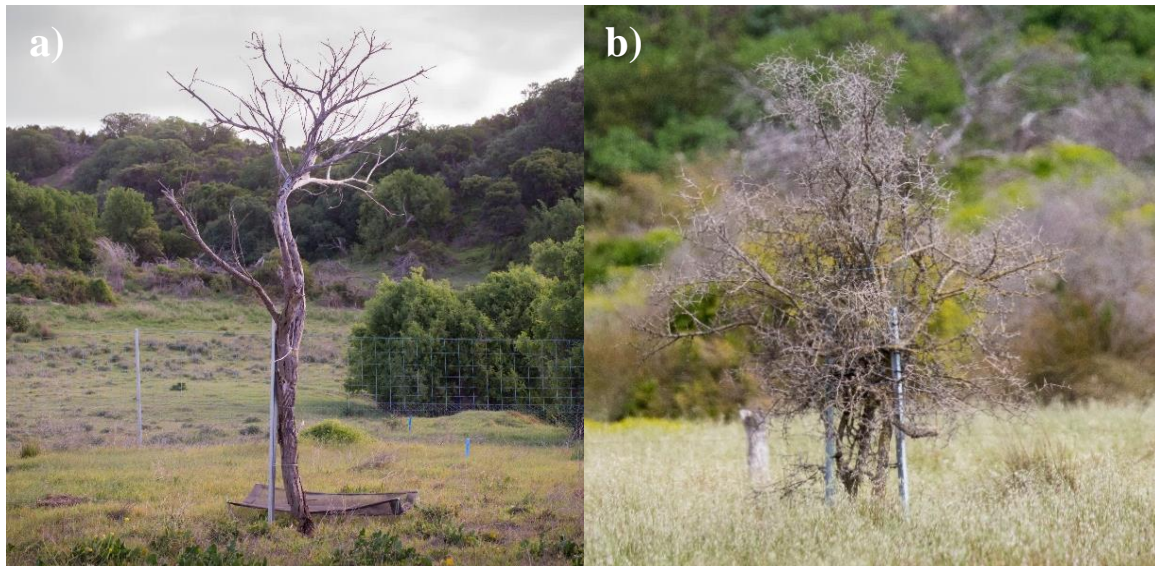


**Figure 3.1.** Aerial view of the southern paddocks associated with Cantara Homestead (top centre), where the artificial perches were erected. The locations of 12 simple perches (PS) and 2 complex perches (PC) are indicated with crosses. The slopes of the dunes that surround the paddocks are stabilised with native vegetation. Beyond these slopes reside non-vegetated mobile dunes.

### 3.2.2 Artificial perch implementation

Twelve artificial perches of simple design were erected in the southern paddocks of Cantara in July 2015. These perches were constructed from dead *A. sophorae* branches, which were wired to a metal stake that was driven into the ground (Fig. 3.2a). These structures were approximately 2.5 to 2.8 m in height. Two perches of complex design were erected in the paddocks in October 2016 as part of a preliminary experiment which considered the influence of perch complexity on bird attraction. They consisted of multiple dense branches of *L. ferocissimum* wired to a metal stake that was driven into the ground. The complex perches reached a similar height as the simple perches, although were denser and slightly wider (complex perches approximately 1.0–1.2 m in width and simple perches approximately 0.8–1 m in width; Fig. 3.2b). The complex and simple perches were placed

throughout open areas of the paddocks and were positioned at distances that varied between 50 and 250 m from the remnant dune vegetation (Fig. 3.1).



**Figure 3.2.** Artificial perch designs erected in the Cantara paddocks which consisted of: a) simple perch and b) complex perch. Surrounding remnant dune vegetation is evident in the background of both photos.

### 3.2.3 Perch observations

Bird visits to the 12 simple artificial perches were directly observed between mid-spring and early summer (October–December 2015). These observations occurred during periods of fruit availability (Chapter 2), meaning that birds had the potential to disperse seed to the perches at this time. Perches were observed from a vantage point that was 30–50 m away using 10 × 42 binoculars. Observations of perch use were conducted between dawn and dusk. All 12 simple perches could not be observed simultaneously at a given time, therefore perches were observed in sets of 4 over 2-hour sessions and the order of observation was then alternated each day. Each set of perches was observed for 6 hours in October, 14 hours in November and 14 hours in December (34 hours total per set of perches, 102 hours total observation time). Few birds were initially observed in October, so the hours of observation were increased in November and December. Each observation of perch use recorded the perch location, bird species, time of arrival and departure, and behaviour of the bird (e.g. agonistic displays, maintenance, vocalisation, defaecation). Individual birds from the same species could not be distinguished from one another, so perch use was defined by the number of bird visits rather than by the number of visitors. Observations also identified and

determined the abundance of any bird species that chose to fly past the perches within a 5 m proximity from ground level.

Between summer and autumn (December 2016–May 2017), remote cameras observed bird visitation to six simple perches (PS1, PS2, PS3, PS6, PS11, PS12) and two complex perches (PC1, PC2; locations of each perch are provided in Fig. 3.1). These observations coincided with the peak period of fruit availability (Chapter 2), meaning that birds had the potential to disperse many seeds to the perches during this time. These observations also occurred during the second year in which the artificial perches were deployed. Each perch was monitored with a single remote camera, which was attached to a small stake approximately 1–1.5 m tall and positioned several metres away from the perch. Cameras used consisted of six Moultrie M-999is and two Reconyx HC600 Hyperfires. Both camera models were set with high detection sensitivity and captured three photos whenever motion was detected. A 10 second detection delay occurred following capture, which helped to reduce the number of photos taken of the same bird. The infrared LED flash was also enabled, which allowed for the capture of bird visitation at night.

The visitation data collected from the remote camera imagery were similar to data collected from the direct observations. Each perch visit captured by a remote camera recorded the perch location, temperature, bird species, and the time that the bird was first and last observed on the perch. The cameras were not always able to capture the exact moment that the bird landed on the perch, so perching durations were categorically estimated according to the number of minutes that the bird was observed on the perch (e.g. <1 minute, 1 minute, etc.). Any obvious bird behaviour during the bird's visit was recorded, including agonistic displays, maintenance, vocalisation and defaecation. The cameras occasionally failed to operate, meaning that the perches differed in the number of days that they were observed. The days per month and season that each perch was observed is provided in Appendix 1.

#### 3.2.4 Faecal analysis

Faeces were collected from three common seed-dispersing bird species to determine how their fruit consumption and seed defaecation could potentially influence seed deposition at the perches. These species were the silvereeye (*Zosterops lateralis*), spiny-cheeked honeyeater (*Acanthagenys rufogularis*) and the singing honeyeater (*Lichenostomus virescens*). Faecal samples were collected in January 2015 and 2016 (i.e. in mid-summer), which coincided with the peak fruiting period. The samples were opportunistically collected



from birds that were captured in the Coorong as part of a long-term monitoring program (Paton, unpubl.). The birds were captured using mistnets and were then held individually in a calico bag for approximately 5–15 minutes, which was generally adequate time for the bird to produce a faecal sample. Each bird was banded, which helped to identify those that had been recaptured. The faecal sample was removed from the bag following its production and any defaecated seeds were counted and identified in the field. Unknown seeds were returned to the laboratory to allow for identification using seed guides. Faecal samples that did not contain seed were not considered for analysis, as the calico bags used to hold birds would absorb any non-solid faeces. The origins of these absorbed faeces were not always clear due to the re-use of the calico bags.

Faecal samples were collected from five sites across the Coorong National Park where the native vegetation is more-or-less intact. These sites consisted of Salt Creek (36°07'S, 139°38'E), Tommy's Track (36°08'S, 139°38'E), Tea Tree Crossing (36°11'S, 139°39'E), 4 km south of Tea Tree Crossing (36°13'S, 139°41'E) and 42 Mile Crossing (36°17'S, 139°42'E). Mistnets were in place over two days at each site and were opened for approximately eight hours a day. The honeyeaters produced few faecal samples at each of the sampling sites in both January 2015 and 2016 (Appendix 2), so faecal sample data were pooled across sites within each year of sampling. For each year of sampling, the influence that each frugivorous bird species had on seed deposition was examined by determining the species that they most abundantly and frequently passed seed from, as well as by determining the number of seeds and species they typically passed per faecal sample containing seed.

### *3.2.5 Statistical analysis*

Direct observations of perch visitation to 12 simple perches were pooled between mid-spring and early summer (October–December 2015). Following this, the mean hourly rate of visitation to a simple perch was determined for: 1) all birds and 2) seed-dispersing birds. The mean hourly rate in which seed-dispersing birds flew over a simple perch was also determined.

To determine if artificial perch complexity influenced bird visitation, Welch's *t*-tests compared the mean daily rates of perch visitation of the six simple perches and two complex perches as captured by the remote cameras between summer and autumn (December 2016–May 2017). The remote cameras were able to observe the perches throughout the day, so

visitation was determined through daily rates instead of hourly rates. The Welch's *t*-tests indicated that there were no significant differences between the two perch designs in their rates of visitation, including their rates of visitation from common seed-dispersers in the region. As a result, the visitation data for the two perch types were pooled to determine overall rates of visitation and seasonal rates of visitation.

Using the data collected by remote cameras, observations of visitation to eight artificial perches (six simple perches, two complex perches) were pooled between December 2016 and May 2017 to determine overall mean daily rates of visitation. The overall rates of visitation to a perch were determined for: 1) all birds, 2) seed-dispersing birds and 3) individually for three regionally abundant seed-dispersing species, which were the spiny-cheeked honeyeater, singing honeyeater and the silvereye.

Using the data collected by remote cameras, mean daily rates of bird visitation to a perch were determined for summer (December 2016–February 2017) and autumn (March 2017–May 2017). This analysis was conducted using observations obtained from seven of the artificial perches (six simple perches, one complex perch), as one of the remote cameras failed to operate in autumn (Appendix 1). For each season, the mean daily rate of visitation to a perch was determined for: 1) all birds, 2) seed-dispersing birds and 3) individually for seed-dispersing species that frequently visited the perches. Differences between the seasons in the rates of visitation to the perches were determined with paired *t*-tests.

Using the data collected by remote cameras between summer and autumn (December 2016–May 2017), diurnal visitation patterns were determined for all bird visitors, as well as for several bird species that commonly visited eight of the artificial perches (six simple perches, two complex perches). To account for differences in daylength, bird visits were distributed according to the percentage of daylight passed, where visits observed at <0% occurred before sunrise and visits observed at >100% occurred after sunset. Chi-square tests were used to determine whether visitation frequency varied throughout the day for the species that commonly visited the perches. To do this, the visit occurrences were separated into 11 classes. Each class represented 10% of the daylight passage, where the first class initiated at -5% and the last class ended at 105%.

The level of significance in all tests was set at  $\alpha < 0.05$  and means were presented with standard error except where otherwise noted. All tests were conducted in Graphpad Prism 8.0.0 (GraphPad software, Inc).

### 3.3 Results

#### 3.3.1 Direct observations of perch use

Following 102 hours of direct observation from mid-spring to early summer (October–December 2015), a total of 13 bird species were found to visit the 12 simple artificial perches and this included 8 bird species capable of consuming fruit and dispersing seed (Table 3.1). In total, 125 bird visits were recorded at the perches. The most frequent visitors included the insectivorous Australasian pipit *Anthus novaeseelandiae* (18.4% of visits), followed by two occasional fruit consumers, which were the Australian magpie *Gymnorhina tibicen* (16.8% of visits) and common starling *Sturnus vulgaris* (16.8% of visits) and one regular fruit consumer, which was the spiny-cheeked honeyeater (12.8% visits). Overall, birds made an average of  $0.34 \pm 0.07$  visits/perch/hour, with  $0.19 \pm 0.07$  of these visits made by seed-dispersing species. Seed-dispersing birds defaecated whilst perched on just two occasions.

The seed-dispersing birds were found to fly within 5 m of the perches at an average of  $0.36 \pm 0.07$  flights/hour. The seed-dispersing birds that recorded the most flights near the perches included spiny-cheeked honeyeaters (61 flights nearby compared to 16 landings), silvereyes (22 flights nearby compared to 2 landings), Australian ravens *Corvus coronoides* (21 flights nearby compared to 12 landings) and red wattlebirds *Anthochaera carunculata* (16 flights nearby compared to 2 landings).

### 3.3.2 Remote camera observations of perch use

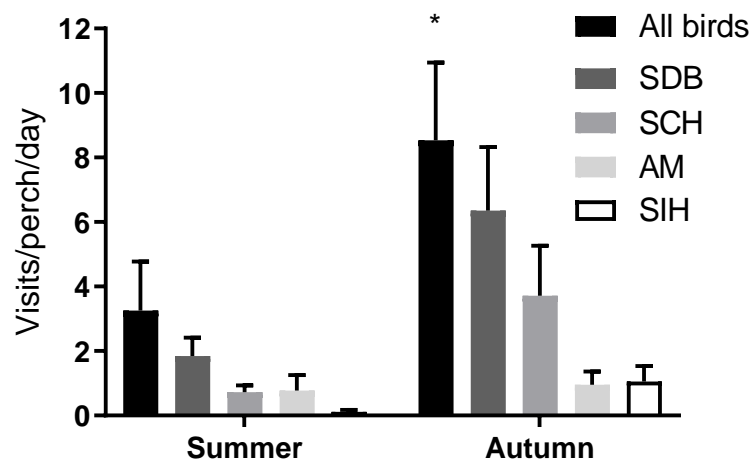
From summer to autumn (December 2016–May 2017), the remote cameras observed 24 bird species landing on 8 artificial perches (6 simple perches and 2 complex perches, Table 3.1). This included nine bird species capable of consuming fruit and dispersing seed, although only three of these species disperse seed regularly. Fifteen of the bird species that visited the perches were not known to disperse seed and they accounted for an average of  $1.74 \pm 1.20$  visits/perch/day. In comparison, the 9 species that were capable of dispersing seed made an average of  $3.60 \pm 0.88$  visits/perch/day.

Irrespective of seed-dispersing capability, birds made an average of  $5.34 \pm 1.55$  visits/perch/day and a total of 4862 visits to all combined perches (Table 3.1). Four bird species accounted for most of the visits recorded at the perches. This included 3 seed-dispersers, which were the spiny cheeked honeyeater (1736 visits, average of  $3.64 \pm 0.64$  visits/perch/day), singing honeyeater (511 visits, average of  $0.53 \pm 0.22$  visits/perch/day) and Australian magpie *Gymnorhina tibicen* (455 visits, average of  $0.76 \pm 0.40$  visits/perch/day). The insectivorous welcome swallow *Hirundo neoxena* was also a frequent perch visitor (1425 visits, average of  $1.25 \pm 1.24$  visits/perch/day), although their visitation rate was highly variable, as 93.2% of their visits occurred at a single perch located near a nesting site. Many bird species visited the perches infrequently, including 9 species that each recorded fewer than 20 visits (Table 3.1).

**Table 3.1.** Bird visitation to the artificial bird perches summarised from 102 hours of direct observation between mid-spring and early summer (October–December 2015) and 6 months of remote camera observation recorded between summer and autumn (December 2016–May 2017). Direct observations recorded bird visits at 12 simple perches, and remote cameras recorded bird visits at 6 simple perches and 2 complex perches. Bird species that visited the perches are listed with their diet, length (cm) and number of perch visits as determined by the two observation methods. Diet items: A = arthropod, F = fruit, N = nectar, P = plant material, S = seed, V = vertebrate. Size and dietary information was sourced from Barker and Vestjens (1990), Marchant and Higgins (1993), Higgins and Davies (1996), Higgins (1999), Higgins *et al.* (2001), Higgins and Peter (2002) and Higgins *et al.* (2006). \* = records of seed dispersal outside the study region.

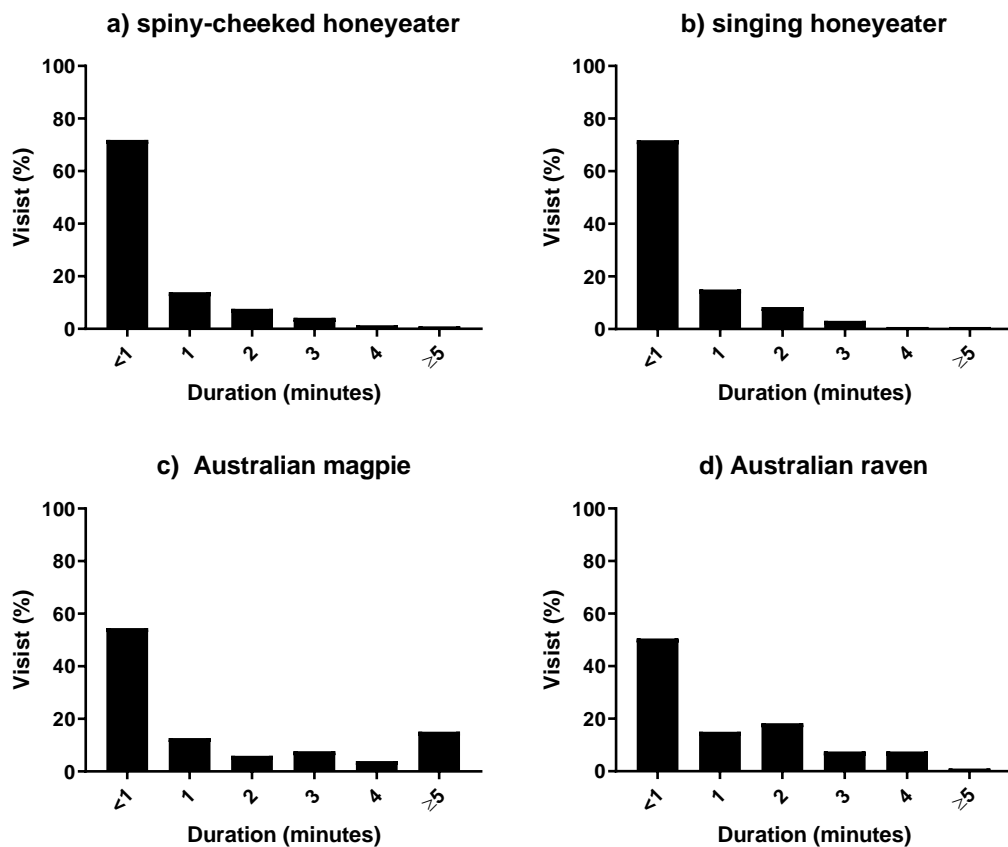
Common name	Scientific name	Diet items	Length (cm)	Visits per observation method		Total visits
				Direct	Camera	
<b>Species that regularly disperse seed in study region</b>						
spiny-cheeked honeyeater	<i>Acanthagenys rufogularis</i>	AFN	24	16	1736	1752
singing honeyeater	<i>Lichenostomus virescens</i>	AFN	19	1	511	512
Silvereye	<i>Zosterops lateralis</i>	AFN	12	2	34	36
<b>Species that occasionally or rarely disperse seed in study region</b>						
Australian magpie	<i>Gymnorhina tibicen</i>	AV	41	21	455	476
common starling	<i>Sturnus vulgaris</i>	AFN	21	21	112	133
grey butcherbird	<i>Cracticus torquatus</i>	AV	34	1	121	122
Australian raven	<i>Corvus coronoides</i>	AV	50	12	93	105
red wattlebird	<i>Anthochaera carunculata</i>	AFN	35	2	38	40
black-faced cuckoo-shrike	<i>Coracina novaehollandiae</i>	AV	33		16	16
<b>Species not known to disperse seed in study region</b>						
welcome swallow	<i>Hirundo neoxena</i>	A	16	6	1425	1431
willie wagtail	<i>Rhipidura leucophrys</i>	A	20	9	82	91
Australasian pipit	<i>Anthus novaeseelandiae</i>	AS	17	23	57	80
brown falcon	<i>Falco berigora</i>	AV	46		49	49
crested pigeon	<i>Ocyphaps lophotes</i>	S	33		44	44
yellow-rumped thornbill	<i>Acanthiza chrysorrhoa</i>	AS	11	10	23	33
grey shrike-thrush*	<i>Colluricincla harmonica</i>	AV	24		15	15
Australian kestrel	<i>Falco cenchroides</i>	AV	34	1	12	13
red-rumped parrot	<i>Psephotus haematonotus</i>	S	26		11	11
New Holland honeyeater*	<i>Phylidonyris novaehollandiae</i>	NA	18		8	8
elegant parrot	<i>Neophema elegans</i>	S	22		6	6
white-fronted chat	<i>Epthianura albifrons</i>	A	12		5	5
blue-winged parrot	<i>Neophema chrysostoma</i>	S	21		4	4
galah	<i>Eolophus roseicapilla</i>	PS	36		4	4
golden whistler*	<i>Pachycephala pectoralis</i>	A	17		1	1

Remote cameras observing 7 artificial perches (6 simple and 1 complex) found that the perches were visited significantly more so in autumn 2017 when compared to summer 2016–2017 (Fig. 3.3, paired  $t$ -test,  $t(6) = 2.64$ ,  $P = 0.04$ ). Seed-dispersing birds in particular also frequented the perches more often in autumn than in summer, although the difference between seasons was not significant (Fig. 3.3, paired  $t$ -test,  $t(6) = 2.24$ ,  $P = 0.07$ ). Common seed-dispersers such as the spiny-cheeked honeyeater and singing honeyeater visited the perches more frequently in autumn than in summer (Fig. 3.3), although these differences were not significant (paired  $t$ -test,  $t(6) = 2.07$ ,  $P = 0.08$  and  $t(6) = 1.99$ ,  $P = 0.09$  respectively). By contrast, the seed-dispersing Australian magpie visited the perches at a relatively similar rate in both seasons (Fig. 3.3, paired  $t$ -test,  $t(6) = 0.97$ ,  $P = 0.37$ ).

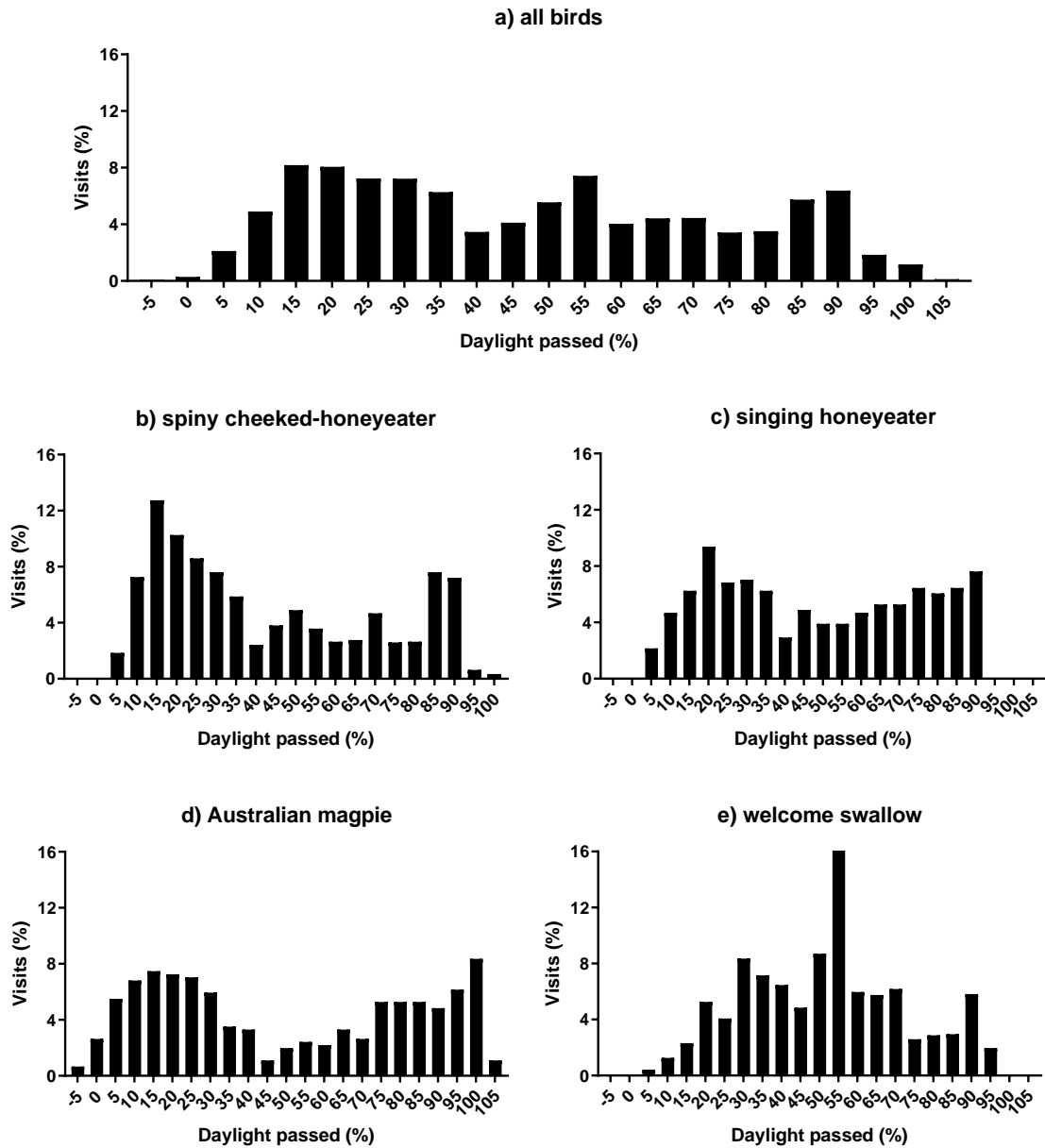


**Figure 3.3.** Daily perch visits (mean + SE) in summer (December 2016–February 2017) and autumn (March–April 2017) as determined for all birds, seed-dispersing birds (SDB), spiny-cheeked honeyeaters (SCH), Australian magpies (AM) and singing honeyeaters (SIH) at seven artificial perches (combined data from one complex perch and six simple perches). Visitation was recorded through the use of remote cameras. One artificial perch was excluded from the analysis as the remote camera observing it failed to operate throughout autumn (Appendix 1). Differences between seasons in bird visitation rates to perches were determined through paired  $t$ -tests, where: \* =  $P < 0.05$ .

Remote cameras observing 8 artificial perches (2 complex and 6 simple) found that 68.1% of the visits recorded by the seed-dispersing birds were <1 minute in duration. Short perching durations were evident in dispersers such as the spiny-cheeked honeyeater (Fig. 3.4a) and singing honeyeater (Fig. 3.4b). Larger seed-dispersing birds, such as the Australian magpie and Australian raven, comparatively occupied the perches for longer durations (Fig. 3.4c–d). Notably, 15.2% of the visits by Australian magpies were  $\geq 5$  minutes in duration.



**Figure 3.4.** Visits of varying durations (as a percentage of total visits) to eight artificial perches (combined data from two complex and six simple perches) between summer and autumn (December 2016–May 2017) as determined by remote cameras. Perching durations were depicted for four seed-dispersing species that frequently visited the perches, including a) spiny-cheeked honeyeater, b) singing honeyeater, c) Australian magpie and d) Australian raven. The total numbers of visits for each species are given in Table 3.1.

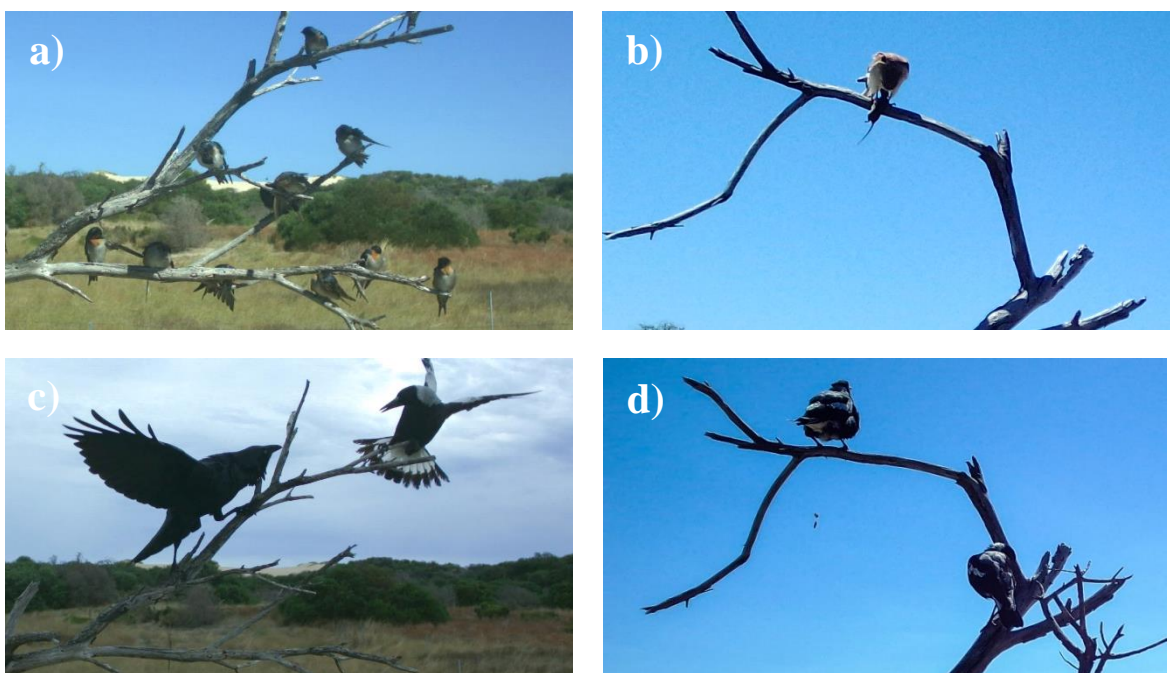


**Figure 3.5.** Diurnal patterns to visitation for eight artificial perches (combined data from two complex and six simple perches) between summer and autumn (December 2016–May 2017) as determined by remote cameras. Relative frequency of visits across the day were depicted for a) all bird species and b–e) bird species that most frequently visited the perches. To account for differences in daylength, visits were distributed according to the percentage of daylight passed, where visits observed at <0% occurred before sunrise and visits observed at >100% occurred after sunset.

Remote cameras observing eight artificial perches (two complex and six simple) found that the perches were visited by birds throughout the day, with few visits recorded during twilight and no visits detected during the night (Fig. 3.5a). Frequent perch visitors such as



the Australian magpie, spiny-cheeked honeyeater and singing honeyeater used the perches more frequently during mid-morning and again during mid-afternoon (Fig. 3.5b–d). In contrast, welcome swallows perched predominantly in the middle of the day (Fig. 3.5e), when temperatures were typically approaching a maximum. They would often visit the perches in small flocks of 2–15 birds and would preen and bask while resting on the perches (Fig. 3.6a). Chi-square tests determined that the frequency of visitation to the perches significantly differed throughout the day for the Australian magpie ( $\chi^2 = 84.48$ , d.f. =10,  $P < 0.0001$ ), spiny-cheeked honeyeater ( $\chi^2 = 846.0$ , d.f. =10,  $P < 0.0001$ ), singing honeyeater ( $\chi^2 = 133.1$ , d.f. =10,  $P < 0.0001$ ) and welcome swallow ( $\chi^2 = 694.1$ , d.f. =10,  $P < 0.0001$ ).



**Figure 3.6.** Bird behaviours observed on the artificial perches including: a) welcome swallows basking, b) Australian kestrel with prey, c) Australian raven antagonising an Australian magpie and d) an Australian magpie defaecating.

Most birds rested while using the perches, although some used them between foraging efforts. Eight species were observed with prey items on the perches, including two raptor species, which were the brown falcon *Falco berigora* and Australian kestrel *Falco cenchroides* (Fig. 3.6b). Eight species also displayed aggressive behaviours on the perches. This included the willie wagtail *Rhipidura leucophrys*, Australian raven and Australian magpie, which displayed interspecific aggression (Fig. 3.6c). Remote cameras captured defaecation at the perches, although very rarely. Seed-dispersing birds defaecated whilst perched on two occasions (Fig. 3.6d) and an Australian raven was once observed to regurgitate a pellet.

### 3.3.3 Perch complexity

Remote cameras were used to compare bird visitation at two complex and six simple perches from summer to autumn (December 2016–May 2017). Visitation rates were similar at the complex and simple perches (mean  $\pm$  S.E of  $4.74 \pm 2.31$  and  $5.54 \pm 2.03$  visits/perch/day respectively) and did not differ significantly (Welch's *t*-test,  $t(2.80) = 0.26$ ,  $P = 0.81$ ). Visitation rates from seed-dispersing birds were also similar for complex and simple perches (respectively  $3.9 \pm 2.67$  and  $3.46 \pm 0.95$  birds/day) and did not differ significantly (Welch's *t*-test,  $t(1.26) = 0.16$ ,  $P = 0.90$ ). Furthermore, Welch's *t*-tests found no significant differences between the perch designs in their visitation rates for regionally common seed dispersers, including the spiny-cheeked honeyeater ( $t(1.16) = 0.67$ ,  $P = 0.61$ ), singing honeyeater ( $t(1.97) = 0.28$ ,  $P = 0.81$ ) and silvereeye ( $t(5.56) = 1.96$ ,  $P = 0.10$ ).

### 3.3.4 Faecal analysis

In both January 2015 and 2016 (i.e. mid-summer), the silvereeye was the most frequently captured bird in mistnets (Table 3.2). This species also produced the most faecal samples containing seed. Singing and spiny-cheeked honeyeaters were captured far less frequently and fewer faecal samples were collected from these bird species.

**Table 3.2.** Number of captures (retraps in parentheses) and number of faeces collected from three bird species captured across five sites in the Younghusband Peninsula in January 2015 and January 2016. The table also gives the mean ( $\pm$ SE) and range in the number of seeds found in faeces, as well as the mean ( $\pm$ SE) and range in the number of species of seed found in faeces.

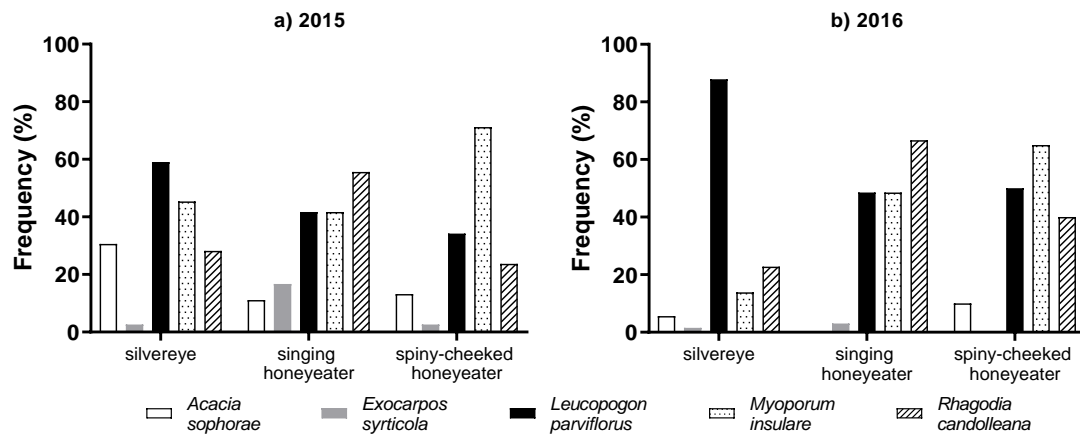
Bird species	Year	Captures	Faecal samples	Mean seeds per sample	Mean species per sample	Range of seeds per sample	Range of species per sample
silvereeye	2015	974 (161)	754	$4.60 \pm 0.13$	$1.69 \pm 0.03$	1–27	1–4
	2016	734 (114)	267	$4.78 \pm 0.22$	$1.37 \pm 0.04$	1–21	1–4
singing honeyeater	2015	61 (5)	36	$5.94 \pm 1.12$	$1.69 \pm 0.12$	1–29	1–4
	2016	70 (12)	33	$6.73 \pm 1.15$	$1.76 \pm 0.14$	1–31	1–4
spiny-cheeked honeyeater	2015	54 (1)	38	$5.21 \pm 0.58$	$1.45 \pm 0.11$	1–14	1–3
	2016	53 (2)	20	$8.45 \pm 1.51$	$2.00 \pm 0.21$	1–28	1–4

Small to moderate amounts of seed were found in the faeces of the three bird species (Table 3.2). The faeces mostly contained a few seeds from one to two plant species but on occasion included seeds from three or four species. The plant species that were most abundantly excreted included *L. parviflorus*, *M. insulare* and *R. candolleana* (Table 3.3). In both years of observation, the three bird species defaecated seed from many of the same fleshy-fruited plant species, although they varied in terms of the abundance and frequency with which they passed seeds of each of the plant species (Table 3.3, Fig. 3.7).

**Table 3.3.** Contribution of five fleshy-fruited species to the total number of seeds passed (with percentage of contribution to total in parenthesis) by three bird species captured across five sites in the Youngusband Peninsula in January 2015 and January 2016.

Bird species	Year	Total seeds	Total seeds (% of total)				
			<i>Leucopogon parviflorus</i>	<i>Myoporum insulare</i>	<i>Rhagodia candolleana</i>	<i>Acacia sophorae</i>	<i>Exocarpos syrticola</i>
silvereeye	2015	3465	1343 (38.8)	668 (19.2)	782 (22.6)	580 (16.7)	69 (2.0)
	2016	1259	938 (74.5)	58 (4.6)	197 (15.6)	33 (2.6)	7 (0.6)
singing honeyeater	2015	214	35 (16.4)	18 (8.4)	121 (56.5)	9 (4.2)	28 (13.1)
	2016	222	56 (25.2)	24 (10.8)	133 (59.9)		3 (1.4)
spiny-cheeked honeyeater	2015	198	58 (29.3)	86 (43.4)	42 (21.2)	9 (4.5)	3 (1.5)
	2016	166	64 (38.6)	45 (27.1)	32 (19.2)	10 (6.0)	

In both January 2015 and 2016, *L. parviflorus* was the most abundantly and frequently passed seed by silvereeyes, while *R. candolleana* was the most abundantly and frequently passed seed for singing honeyeaters (Table 3.3, Fig. 3.7). Notably, singing honeyeaters most abundantly and frequently defaecated the seeds of *R. candolleana* in both years (Table 3.3, Fig. 3.7). In 2015, spiny-cheeked honeyeaters most abundantly and frequently defaecated the seeds of *M. insulare* (Table 3.3, Fig. 3.7). In 2016, they most frequently passed the seeds of *M. insulare*, although overall, they passed more seeds of *L. parviflorus*.



**Figure 3.7.** Frequency of occurrence (%) of the seeds of five fleshy-fruited plant species in faecal samples containing seed produced by three bird species across five sites in the Younghusband Peninsula in a) January 2015 and b) January 2016.

### 3.4 Discussion

#### 3.4.1 Use of artificial perches by seed-dispersing birds

The artificial perches were visited by nine bird species capable of dispersing seed. These species for the most part were generalist frugivores. This appears to be a common finding in tropical systems where most studies of artificial perch use have been conducted (e.g. Pillatt *et al.* 2010; Vicente *et al.* 2010; Graham and Page 2012; Athiê and Dias 2016; Carlo and Morales 2016; Vogel *et al.* 2016; Freeman *et al.* 2021), although this has been observed in one study conducted in a temperate system (McLaughlin 2013). This result can be expected, since generalist birds are opportunistic species, which move into degraded habitats to take advantage of the food resources found there (e.g. insects, fruits of ruderal plants) (Wunderle 1997; Athiê and Dias 2016). In some tropical systems, restoration was limited by the lack of visitation from specialised frugivorous birds (e.g. hornbills and toucans), which either flew over the perches or did not enter the degraded site (Pillatt *et al.* 2010; Graham and Page 2012). Their absence limited restoration as these birds are useful dispersers of large-seeded plant species, which formed an important part of the remnant vegetation. Specialist frugivorous birds did not visit the perches at Cantara, although this was unlikely to be of consequence for restoration. This is because in temperate southern Australia there is only one specialist frugivore (mistletoebird, *Dicaeum hirundinaceum*) and the plant species in this region tend to have fruits adapted for general bird dispersal (Forde 1986; French 1991).

During the peak fruiting period of summer and autumn, the two seed-dispersing bird species that most frequently visited the perches were the spiny-cheeked honeyeater and singing honeyeater (1736 and 511 visits respectively as captured by remote cameras). Their visitation to the perches was significant given that they are capable of dispersing seed regularly but are also capable of dispersing seed from a range of plant species (at least 13 native species each, Chapter 2). Notably, these birds consume and defaecate seed from many of the same plant species, although as observed in January 2015 and 2016 (i.e. mid-summer), may do so with differing abundances and frequencies. This highlighted the importance of having both species of honeyeater visit the perches, as the diversity of seed arriving to the perches may have otherwise been reduced. The honeyeaters were also important perch visitors as they were capable of moving between the remnant and degraded sites (pers. obs.). Guevara and Laborde (1993) and Graham and Page (2012) emphasised the importance of such inter-site movements, as they promote the dispersal of seed from remnant vegetation. Although notably, the singing honeyeater mostly visited the perches during autumn. Thus, much of their contribution to the seed deposition at the artificial perches would have likely also occurred during this time.

In general, Australian magpies and Australian ravens were two other seed-dispersing species that visited the perches with some regularity (476 and 105 visits in total respectively). Compared to the honeyeaters, these large bird species consumed fruit less frequently and to a smaller extent (consuming fruit from 3–5 plant species, Chapter 2). Although, there is potential that these birds were useful dispersers of large seeds, as the species of fruit they consumed mostly included the larger-seeded species in the region (3–8 mm in width, e.g. *A. sophorae*, *E. syrticola*, *M. insulare*; Chapter 2). Other members of the Artamidae and Corvidae are important dispersers of large seeds, including the pied currawong (*Strepera graculina*, Artamidae) in north-eastern subtropical Australia (Moran 2007) and the large-billed crow (*Corvus macrorhynchos*, Corvidae) in Singapore (Corlett 2017). Ravens and magpies primarily forage on the ground in open habitats (as does the large and flightless emu, *Dromaius novaehollandiae*), so it is likely that these birds also contributed to seed deposition in open areas of Cantara. Ravens and magpies also offer a different kind of seed dispersal as they can void seed through the regurgitation of pellets. This regurgitation process may be important for regeneration as it can enhance seed germination (Traveset 1998), which for example occurred in seeds regurgitated by the common raven (*Corvus corax*) in the Canary Islands (Nogales *et al.* 1999).

### 3.4.2 Influence of visitation frequency on seed deposition

The artificial perches were able to attract seed-dispersing birds over the peak fruiting period of summer and autumn, receiving an average of 3.60 visits/perch/day. Although, not all of these visits would have resulted in the deposition of seed. Regular fruit consumers, such as the spiny-cheeked and singing honeyeaters, predominantly visited the perches for short durations (for both species only 28% of visits were >1 minute), as they often used them to cross the landscape or to briefly rest while hawking for insects. These short perching durations likely meant that only some of the visits made by the honeyeaters would have also resulted in defaecation. In comparison, the Australian ravens and magpies visited the perches for longer durations more frequently (49% and 46% of visits >1 minute respectively), as they would use them to rest while preening or socialising. There would have been a greater probability of defaecation or regurgitation occurring during the longer visits. Australian ravens and magpies, however, only occasionally consumed fruit, meaning that there was a lower probability that their excrement would have contained seed.

In general, seed deposition at the artificial perches may have also been limited by the lack of silvereye visitation (36 visits in total). This bird is one of the region's most important dispersers, given their abundance, ability to regularly and effectively disperse seed, and ability to disperse a variety of plant species (Table 3.2; Table 3.3; Fig. 3.7; Chapter 2; Stanley and Lill 2002; Paton 2010). Silvereyes likely avoided the perches given that they are small birds (11–12 cm long) and by resting in open areas they risk predation. The complex perches, which were implemented in the degraded site after few silvereyes were observed on simple perches, were expected to attract more silvereyes given the greater protection they offered. The two perch types, however, did not significantly differ in their ability to attract silvereyes, although this lack of difference may have been caused by small sample sizes used in the experiment. Thus, additional observations will be necessary to confirm if perch complexity influences bird visitation.

The lack of silvereye visitation to the artificial perches may have been due to the presence of scattered shrubs in the degraded site. As noted during the direct observations of perch use, silvereyes were more inclined to fly past the simple artificial perches rather than visit them (22 flights nearby compared to 2 landings). Instead, they chose to visit isolated patches of shrubs, which were likely more attractive due to their food resources (e.g. fruit, insects), as well as their larger physical volume and dense foliage, which would have better concealed the silvereyes from predators (Stanley and Lill 2002; Elgar *et al.* 2014; Freeman

*et al.* 2021). Systematic bird surveys conducted in January between 2008 and 2014 in the study region support the notion that silvereyes are not as inclined as other seed-dispersers to use bare perches (Paton, unpubl. data). These surveys recorded the substrates on which birds perched and silvereyes that were observed on perches were detected on dead branches only 6% of the time. In comparison, singing honeyeaters and spiny-cheeked honeyeaters when observed on perches were using dead branches 14% and 12% of the time respectively.

Evidently, some strategies may be required to entice silvereyes to use artificial perches given that they are important seed dispersers in the region. The attractiveness of the artificial perches could perhaps be enhanced if they were placed closer to areas of remnant vegetation. This would provide silvereyes with dense cover to retreat to when alarmed by predators. Additionally, the artificial perches may need to be taller than any proximate vegetation, as this has been shown to increase visitation by providing birds with a better lookout for predators (McDonnell 1986; Athiê and Dias 2016). In general, the ability of silvereyes to enter the paddocks of Cantara indicated that they could still contribute to seed deposition in the areas where perches were located, although only likely after some shrubby vegetation had established beneath the perch.

#### *3.4.3 Changes in visitation during the peak fruiting seasons*

From summer to autumn, birds significantly increased the rate in which they visited artificial perches (from 3.26 to 8.54 visits/perch/day). Seed-dispersing birds in particular also increased their rate of visitation from summer to autumn (from 1.82 to 6.35 visits/perch/day), although this increase was not to a significant extent. The lack of significant difference may have been due to a small sample size, so further observations may be necessary to determine the importance of season on the rates of visitation. In general, the slight increase in seed-dispersing bird visitation in autumn may have been related to changes in local food resources. For example, the spiny-cheeked and singing honeyeaters would have spent much of their time in summer foraging in the remnant vegetation, where fruit would have been abundant (Paton 2010). As the fruit availability declined in autumn, the honeyeaters may have then roamed further to find sufficient food resources, including throughout degraded areas. The numbers of singing honeyeaters in particular have been observed to fluctuate at sites within the Younghusband Peninsula, as they seemingly move in search of food (Patkin, unpubl. data). Notably, the Australian magpie was the most consistent in its perch use between seasons. The consistency in their

visitation rate was likely explained by their predominate use of open habitats, combined with their tendency to be sedentary (Higgins *et al.* 2006).

#### 3.4.4 Ecological services provided by perches

Artificial perches had a variety of uses for birds, demonstrating that they can provide ecological services besides the facilitation of seed dispersal. Perches were used throughout the day, although mostly so in the mid-morning and afternoon, which is when birds typically forage (Bednekoff and Houston 1994). The perches were observed to assist eight bird species with their foraging activities, including two raptor species, which were the Australian kestrel (*Falco cenchroides*) and brown falcon (*Falco berigora*). These raptors are thought to assist in the reduction of invasive mammals such as the house mouse (*Mus musculus*) (Kay *et al.* 1994), which is an abundant pest in the study region during cooler parts of the year (Caton *et al.* 2011).

Other birds, including the spiny-cheeked and singing honeyeaters, used the perches to rest while hawking for insects. The perches were also regularly visited by welcome swallows in the middle of the day, as temperatures approached a maximum. They basked on the perches during these warmer temperatures, which may have served to control ectoparasites (Blem and Blem 1993). Several other studies have also emphasised the importance of artificial perches in offsetting tree loss in the landscape, particularly in terms of the increases in bird species richness and abundance that the perches are able to facilitate (Vogel *et al.* 2018; Hannan *et al.* 2019). Evidently, if artificial perches are to be used to facilitate regeneration, then researchers and practitioners should acknowledge all the ecological services that the perches could potentially provide.

### 3.5 Conclusion

The artificial perches deployed in paddocks at Cantara were successfully able to attract nine seed-dispersing bird species. The spiny-cheeked honeyeater and singing honeyeater were the seed-dispersing species that most frequently visited the perches during the peak fruiting period of summer and autumn. These birds were likely to be important in dispersing seeds to artificial perches as they also frequently void the seeds of a variety of fleshy-fruited plant species. The honeyeaters tended to use the perches for short durations, which may have reduced their value as seed dispersers in degraded areas. Australian magpies and ravens were two other species that may have contributed to seed deposition at the perches, although not to the same extent as the honeyeaters, given that they only occasionally void seeds from



a few species. In general, the results of this chapter highlighted the important contribution that these four bird species have for the dispersal of seed into open and degraded areas of the Younghusband Peninsula. The following chapter, Chapter 4, now aims to document the quantities of seeds deposited beneath the artificial perches deployed in the paddocks of Cantara.

# **Chapter 4. The effectiveness of artificial perches in overcoming dispersal limitations for fleshy-fruited plants on the Younghusband Peninsula**

## **4.1 Introduction**

Artificial perches are implemented in disturbed or degraded areas as a means to overcome seed dispersal limitations and to accelerate regeneration. They work by encouraging frugivorous birds to rest in degraded areas, where they may defaecate the seeds of fruit they have consumed. The ability of artificial perches to effectively facilitate seed dispersal into degraded areas has been investigated through a variety of methods over the past few decades. Most commonly, researchers have investigated their effectiveness by measuring the abundance and richness of seed deposited beneath the perches (e.g. Shiels and Walker 2003; Vicente *et al.* 2010; Graham and Page 2012; Heelemann *et al.* 2012; de Almeida *et al.* 2016). Researchers have also often determined the origin and life forms of the species that were deposited beneath the perches (e.g. Shiels and Walker 2003; Athiê and Dias 2016; Tomazi and Castellani 2016). Taking these characteristics into account is important, as they influence restoration trajectories and the potential for restoration to occur in the degraded landscape (Guidetti *et al.* 2016). For example, de Almeida *et al.* (2016) found that the species that were dispersed to perches were mostly pioneering trees and shrubs, which was important for restoration as these species would help to colonise the degraded and fragmented landscape.

Some studies have also considered whether there was seasonal variation in the quantities and compositions of seed that were dispersed to the perches (e.g. Zanini and Ganade 2005; Vicente *et al.* 2010; Athiê and Dias 2016). Such observations may be used to determine the seasons in which artificial perches are most likely to effectively facilitate seed dispersal. This information is especially important if the perches are intended to be in place over a temporary period (Graham and Page 2012). Notably, very few studies have investigated the effectiveness of artificial perches in their ability to facilitate seed dispersal over multiple years (Bustamante-Sánchez and Armesto 2012; Zwiener *et al.* 2014). More long-term studies are required to determine the value of artificial perches throughout the different stages of vegetation recovery. For example, the restorative value of a perch could start to

diminish once some vegetation has established beneath it, so there may be a need to shift the perch throughout the degraded site over time.

When compared to artificial perches, natural perches (i.e. isolated trees and shrubs) have been as effective or even more effective than artificial perches in facilitating seed dispersal into degraded areas (e.g. Holl *et al.* 2000; Zwiener *et al.* 2014; Castillo-Escrivà *et al.* 2019). Although as pointed out by Zwiener *et al.* (2014), the number of studies directly comparing the facilitative effects of artificial perches and natural perches is currently limited and this comparison needs further exploration. Notably, very few studies have also measured seed deposition in the remnant vegetation that surrounds the degraded site (e.g. McClanahan and Wolfe 1987; Pillatt *et al.* 2010). Artificial perches are often deployed with the aim of enhancing seed arrival from areas of remnant vegetation (Guidetti *et al.* 2016), so measures of seed rain taken within this area may help to determine the compositions of seed that ought to be arriving at perches deployed in adjacent degraded areas.

The Youngusband Peninsula in the south-east of South Australia is a temperate coastal dune system that has been degraded through vegetation clearance and grazing by rabbits and domestic stock (Chapter 2). Many of these degraded areas have been slow to recover and some additional intervention, such as the deployment of artificial perches, is required to facilitate the re-establishment of native vegetation. In this chapter, I investigated the effectiveness of artificial perches to facilitate seed dispersal into formerly grazed paddocks located on the Youngusband Peninsula. This chapter asked the following questions:

- 1) Does the provision of artificial perches significantly increase rates of seed dispersal into degraded areas relative to adjacent open areas without perches?
- 2) What are the identities and life forms of the plants whose seeds are deposited at the artificial perches?
- 3) To what extent does seed deposition at the artificial perches vary between seasons and years?
- 4) How do artificial perches and natural perches such as shrubs compare in their ability to facilitate seed dispersal into the degraded site?
- 5) Within the degraded site, is there a difference in the composition of seed rain being detected beneath artificial perches, species of shrub and in open areas?
- 6) Is there a difference in the composition of seed rain being detected beneath species of shrub in the degraded site and the same species of shrub in the remnant

vegetation, and does the composition of seed rain vary with the shrub species that is serving as host?

## 4.2 Methods

### 4.2.1 Study location

Field research was conducted in the southern paddocks of Cantara (Fig. 4.1), which cover an area of approximately 25 ha. These paddocks were located about 800 m inland from the Southern Ocean, on the Younghusband Peninsula, South Australia (36°20'S, 139°44'E). The climate is Mediterranean, with cool-moist winters (June–August) and hot-dry summers (December–February) (Australian Bureau of Meteorology 2021). During the late 1840s and 1850s, parts of the Younghusband Peninsula were cleared for pastoral activities. This included Cantara, which was converted to pasture and used for stock grazing up until the 1970s (Rudduck 1982). Almost 50 years have passed since the paddocks were destocked. The land, however, has failed to recover during this time.

The paddocks are dominated by introduced grasses and herbs. Various fleshy-fruited shrubs are present in isolated patches across the paddocks, including *Acacia sophorae*, *Myoporum insulare* and *Rhagodia candolleana* and the introduced species *Lycium ferocissimum*. The north, south and western sides of the paddocks are surrounded by the leeward slopes of parabolic dunes. The dunes are densely covered in native vegetation, which includes many fleshy-fruited plant species, such as *M. insulare*, *Leucopogon parviflorus* and *Exocarpos syrticola*. In contrast, the eastern side of the paddocks are bordered by a thick stand of *Melaleuca halmaturorum*, which is parasitised by the mistletoe *Amyema melaleucae*.

### 4.2.2 Artificial perch and seed trap implementation

Twelve artificial perches of simple design were deployed throughout the southern paddocks of Cantara in July 2015 (Fig. 4.1). The perches were constructed from dead *A. sophorae* branches, which were wired to a metal stake that was driven into the ground (Fig. 4.2a). The perches were approximately 2.5 to 2.8 m in height and were placed throughout the open areas of the paddocks, at distances ranging between 50 to 250 m from the remnant dune vegetation. Seed was collected beneath each perch with a single seed trap. The seed traps were made with a 1 × 1 m of 0.25 mm fibreglass mesh, with a 5 cm rolled edge which prevented seed loss (Fig. 4.2b). Seed traps were propped at least 20 cm off the ground using 280 mm high metal pegs. Twenty-five seed traps were also placed in open areas of the

paddock (henceforth referred to as “open paddock”) to measure the seed rain in the absence of any perches (Fig. 4.1).



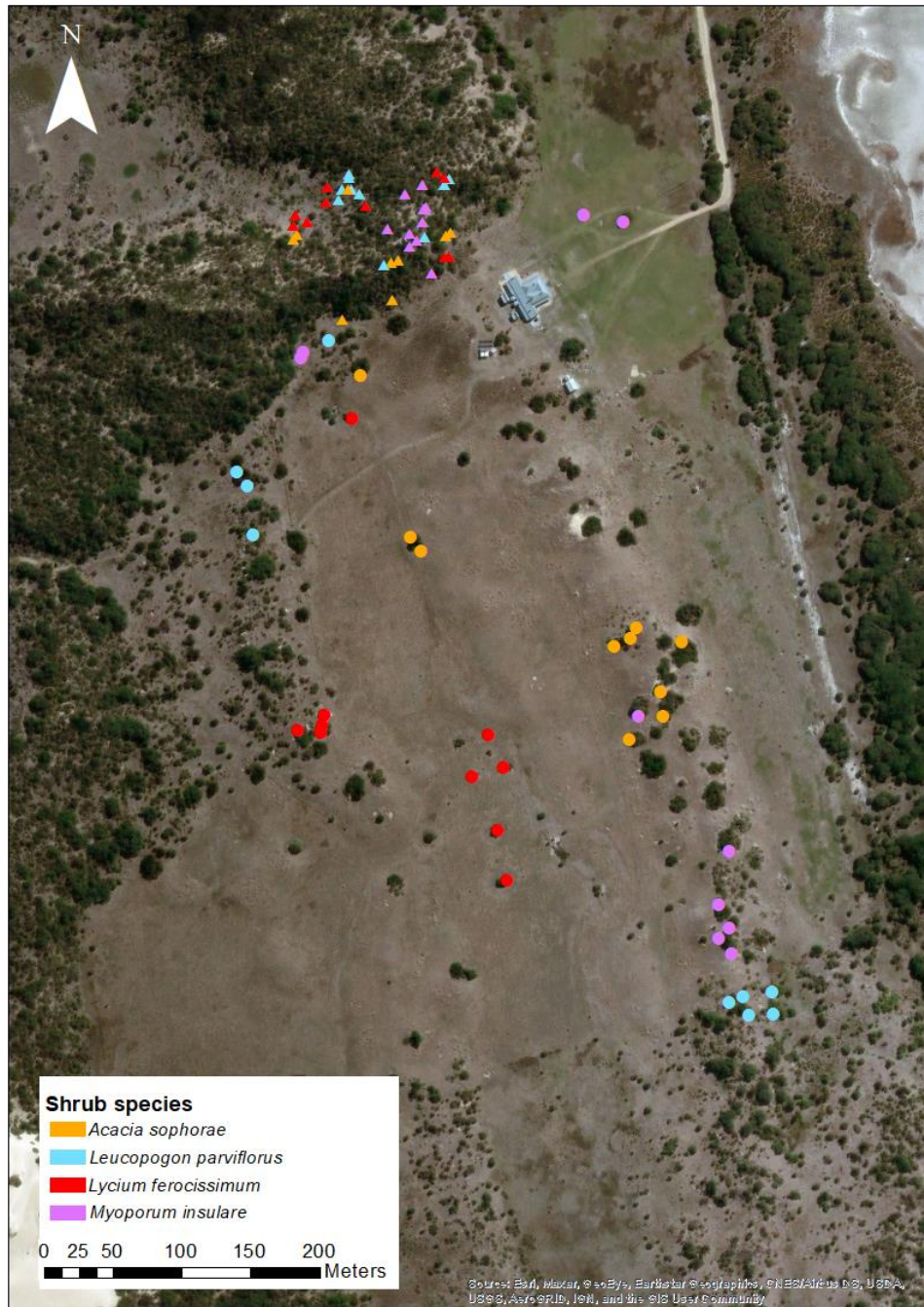
**Figure 4.1.** Aerial view of the experimental design deployed in the southern paddocks of Cantara, where 12 artificial perches of simple design were erected. A  $1 \times 1$  m seed trap was placed beneath each perch. Twenty-five  $1 \times 1$  m seed traps were also placed in open areas of the paddocks. The location of each perch is indicated with a cross, whereas the location of each seed trap in the open is indicated with a square.



**Figure 4.2.** An artificial perch located in the southern paddocks of Cantara with a  $1 \times 1$  m seed trap placed beneath it and remnant dune vegetation evident in background (a) and seed traps made from superfine 0.25 mm fibreglass mesh were used to capture defaecated seeds (b).

To investigate the ability of natural perches to facilitate seed dispersal, seed traps were placed beneath scattered shrubs in the paddocks (Fig. 4.3). Specifically, this consisted of ten adult plants from four shrub species, which were *A. sophorae*, *L. ferocissimum*, *M. insulare* and *L. parviflorus*. Seed rain was measured beneath ten adult plants of the same shrub species in the dunes to determine the species compositions and numbers of seed dispersed in remnant vegetation (Fig. 4.3). A single trap was placed beneath 10 individual shrubs of each of the four species in the dunes, and again in the paddocks, resulting in a total of 80 traps

Seeds collected by traps set under paddock shrubs, dune shrubs or set in the open paddock were collected monthly over a period of 12 months (September 2015–August 2016), encompassing the seasons of spring (September–November), summer (December–February), autumn (March–May) and winter (June–August). Seeds collected in traps set under artificial perches were collected monthly for 21 months (September 2015–May 2017). The seeds (or woody stones containing seeds) were placed into paper bags and were sorted, counted and identified back in the laboratory. Seeds which did not originate from fleshy-fruited species were discarded. The species of seed were identified using a reference collection, as well as through seed guides (Sweedman and Merritt 2006). For each month of seed collection, the seeds of each species were air-dried and then weighed to determine their dry biomass. The species of seed were categorised according to their origin (native, introduced) and life form (shrub, herb, climber, mistletoe).



**Figure 4.3.** Aerial view of the experimental design deployed in the southern paddocks of Cantara and adjacent dunes, where seed traps were placed under ten adult plants from four shrub species, both in the paddocks and in the remnant dune vegetation. The location of each shrub in the dunes is indicated with a triangle, whereas the location of each shrub in the paddocks is indicated with a circle.

#### 4.2.3 Statistical analysis

For the following analyses, the term 'seed' was inclusive of the woody stones of *L. parviflorus* and *M. insulare*. These woody stones potentially contain multiple seeds, however seed fill is variable (South Australian Seed Conservation Centre 2016), so in this chapter the woody stones are considered as single dispersal units and the number of seeds inside are not accounted for.

To determine the influence of perch treatment on seed deposition, seeds collected over 12 months from traps in four settings (beneath artificial perches, paddock shrubs, dune shrubs, and in the open paddock) were compared in terms of annual accumulated abundance and species richness. Two-way analysis of variance (ANOVA) with Tukey's multiple comparisons tested the main effects of perch treatment on the deposited seed abundance and seed richness. For the paddock shrubs and dune shrubs, measures of seed abundance and seed richness represented averaged means from the four shrub species whose seed rain were collected.

To determine the influence of perch treatment on the composition of seed rain in the paddocks, seeds accumulated over 12 months in traps from six settings (beneath artificial perches, four shrub species in the paddock, and in the open paddock) were assessed using one-way permutation multivariate analysis of variance (PERMANOVA) based on zero-adjusted Bray-Curtis similarities and 999 permutations. The PERMANOVAs were calculated using abundance data, as well as presence/absence data. The PERMANOVAs required a zero-adjusted Bray-Curtis measure as Bray-Curtis indices cannot be calculated using '0' values. This adjustment adds a 'dummy species', which takes the value of 1 for all samples. Pairwise comparisons were conducted for each PERMANOVA to explore significant differences between all possible pairs of perch treatments. The compositional differences based on seed abundance was visualised through two-dimensional non-metric multidimensional scaling ordination (NMDS) based on zero-adjusted Bray-Curtis indices of similarity.

To determine the influence of shrub location and shrub species on the composition of seed rain, seeds accumulated over 12 months in traps from two locations (paddock and dunes) and beneath four species of shrub were assessed through two-way PERMANOVAs based on Bray-Curtis similarities and 999 permutations. The PERMANOVAs were calculated using abundance data, as well as presence/absence data. Similarity percentage (SIMPER)



analysis was used to identify the species contributing most strongly to the compositional differences observed between the two locations and between the four shrub species.

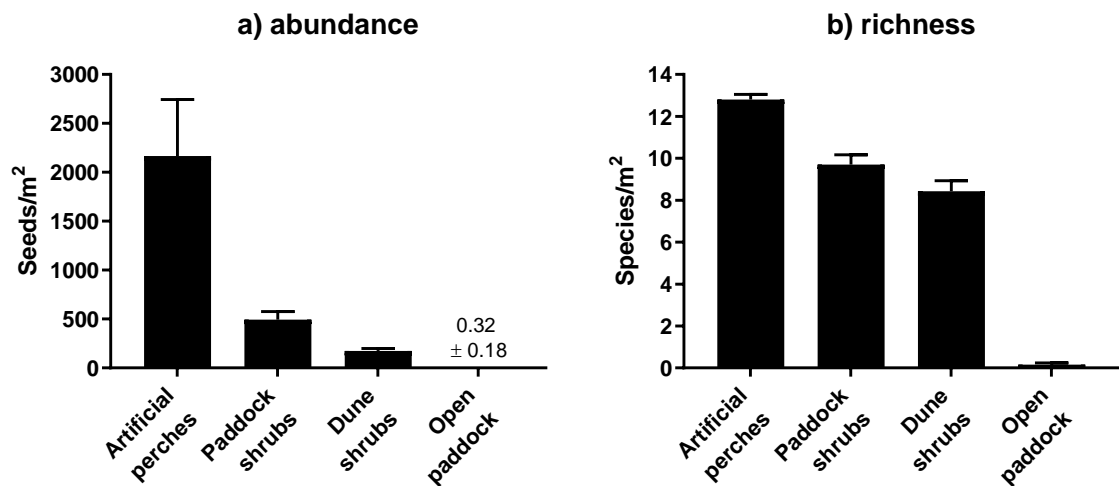
Seasonal variation in seed deposition at the artificial perches was investigated using data from the first year of observation. Specifically, seasons were compared in terms of deposited seed abundance, richness and dry biomass. These seed measures were compared between seasons using one-way repeated measures ANOVAs since the same perches were sampled each season. Seed deposition that occurred at the artificial perches during seasons of fruit availability (spring–autumn) were also compared between years. Using data collected after 21 months of observation, the two spring–autumn periods were compared in terms of deposited seed abundance, richness and dry biomass. The seed measures were compared between the two periods using two-way repeated measures ANOVAs since the same perches were sampled in each period. This also allowed for comparisons between years for individual seasons. The two spring–autumn periods were also compared for differences in deposited composition of seed using two-way PERMANOVAs based on Bray-Curtis similarities and 999 permutations. The PERMANOVAs were calculated using abundance data, as well as presence/absence data.

The level of significance in all tests was set at  $\alpha < 0.05$  and means were presented with standard error except where otherwise noted. One-way and two-way ANOVAs were conducted in Graphpad Prism 8.0.0 (GraphPad software, Inc). One-way and two-way PERMANOVAs, similarity percentages and NMDS analysis were conducted in PRIMER 7.0 (Clarke and Gorley 2015).

## 4.3 Results

### 4.3.1 Seed rain characteristics

After 12 months of seed collection, the artificial perches, dune shrubs, paddock shrubs and open traps in the paddocks significantly differed in the mean abundances of seed that they accumulated (Fig. 4.4a, two-way ANOVA,  $F(3, 110) = 28.88$ ,  $P < 0.0001$ ). Tukey's multiple comparisons found that significantly more seeds were collected in traps beneath the artificial perches (2161.2 seeds/m<sup>2</sup>/year) than those set under the paddock shrubs (493.3 seeds/m<sup>2</sup>/year), dune shrubs (174.9 seeds/m<sup>2</sup>/year) and in the open paddock (0.32 seeds/m<sup>2</sup>/year) ( $P < 0.0001$ ). In terms of detection, seed was recorded in traps beneath all 12 artificial perches, all 40 paddock shrubs and all 40 dune shrubs. In contrast, seed was recorded in only 4 of the 25 traps placed in the open paddock.



**Figure 4.4.** The abundance of seed (a) and species richness of seed (b) deposited in seed traps (both mean/m<sup>2</sup>/year + SE) beneath artificial perches ( $n = 12$ ), paddock shrubs ( $n = 4$  species, 10 shrubs per species; averaged mean), dune shrubs ( $n = 4$  species, 10 shrubs per species; averaged mean) and in the open paddock ( $n = 25$ ) during a 12-month period, between September 2015 and August 2016.

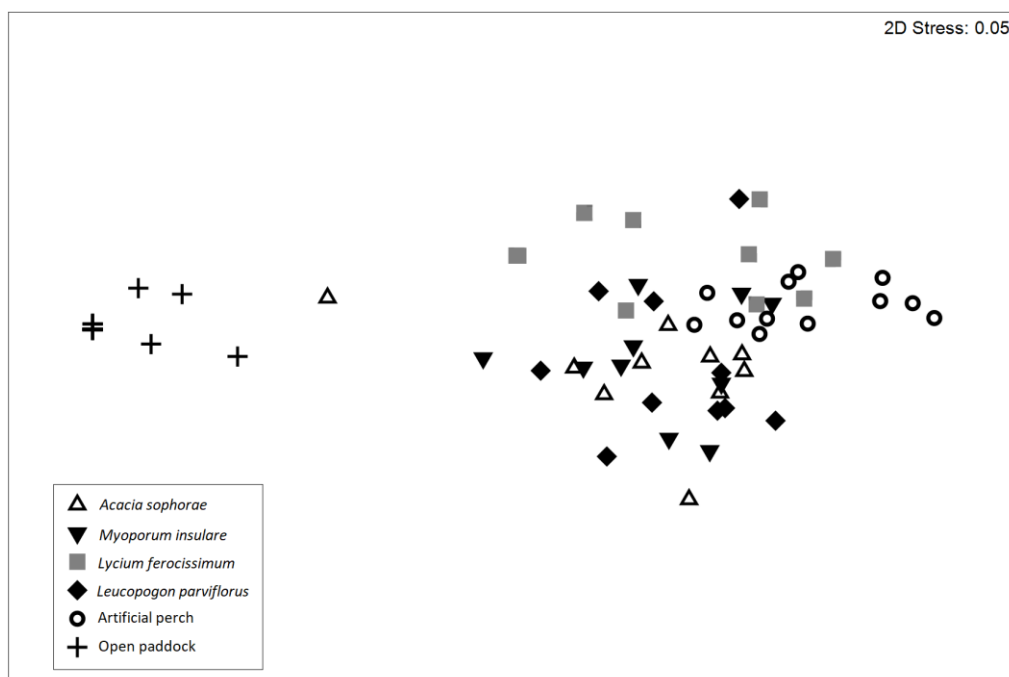
After 12 months of seed collection, the artificial perches, dune shrubs, paddock shrubs and open traps in the paddocks significantly differed in the mean number of species that they accumulated (Fig. 4.4b, two-way ANOVA,  $F(3, 110) = 157.5$ ,  $P < 0.0001$ ). Tukey's multiple comparisons found that significantly more species were collected in traps beneath the artificial perches (12.8 species/m<sup>2</sup>/year) than those set under the paddock shrubs (9.93 species/m<sup>2</sup>/year), dune shrubs (8.43 species/m<sup>2</sup>/year), and in the open paddock (0.16 species/m<sup>2</sup>/year) ( $P < 0.0001$ ).

**Table 4.1.** Species of seed present in seed traps beneath the artificial perches (AP;  $n = 12$ ), paddock shrubs ( $n = 4$  shrub species, 10 shrubs per species), dune shrubs ( $n = 4$  shrub species, 10 shrubs per species) and in seed traps set in the open paddock (OP;  $n = 25$ ) during a 12-month period, between September 2015 and August 2016. The four species of shrub were *Acacia sophorae* (AS), *Leucopogon parviflorus* (LP), *Lycium ferocissimum* (LF) and *Myoporum insulare* (MI). \* = introduced species. Life form (L): S = shrub, C = climber, H = herb, M = mistletoe. The mean deposition of each species at each of the perch treatments is listed in Appendix 3.

Species	L	AP	OP	Paddock shrubs				Dune shrubs			
				AS	LP	LF	MI	AS	LP	LF	MI
<i>Acacia sophorae</i>	S	×		×	×	×	×	×	×	×	×
<i>Alyxia buxifolia</i>	S	×		×	×	×	×	×	×	×	×
<i>Amyema melaleucae</i>	M	×		×			×	×		×	×
<i>Asparagus asparagoides</i> *	C	×		×	×	×	×			×	×
<i>Billardiera cymosa</i>	C			×		×				×	
<i>Dianella revoluta</i>	H	×		×	×	×	×	×	×	×	×
<i>Enchylaena tomentosa</i>	S	×	×	×	×	×	×	×	×	×	×
<i>Exocarpos syrticola</i>	S	×		×	×	×	×		×	×	×
<i>Leucopogon parviflorus</i>	S	×		×	×	×	×	×	×	×	×
<i>Lycium ferocissimum</i> *	S	×	×	×	×	×	×	×	×	×	×
<i>Muehlenbeckia gunnii</i>	C	×		×	×	×	×	×	×	×	×
<i>Myoporum insulare</i>	S	×	×	×	×	×	×	×	×	×	×
<i>Rhagodia candolleana</i>	S	×	×	×	×	×	×	×	×	×	×
<i>Scaevola calendulacea</i>	H	×									
<i>Tetragonia implexicoma</i>	C	×		×	×	×	×	×	×	×	×
<i>Threlkeldia diffusa</i>	S	×		×	×	×	×	×	×	×	×

In terms of range, 12–14 species (total of 15 species) were deposited in the traps beneath the 12 artificial perches, 5–14 species (total of 15 species) were deposited in the traps beneath the 40 paddock shrubs, 5–14 species (total of 15 species) were deposited in the traps beneath the 40 dune shrubs and 0–1 species (total of 4 species) were deposited in the 25 traps set in the open paddock (Table 4.1). In total, 16 species were deposited beneath the 4 perch treatments (Table 4.1). Fourteen of the species were native to the region, whereas two were introduced species (*L. ferocissimum* and *Asparagus asparagoides*). Of the native species identified, eight were shrubs, two were herbs, three were climbers and one was a mistletoe. The mean deposition of each species at each of the perch treatments is listed in Appendix 3.

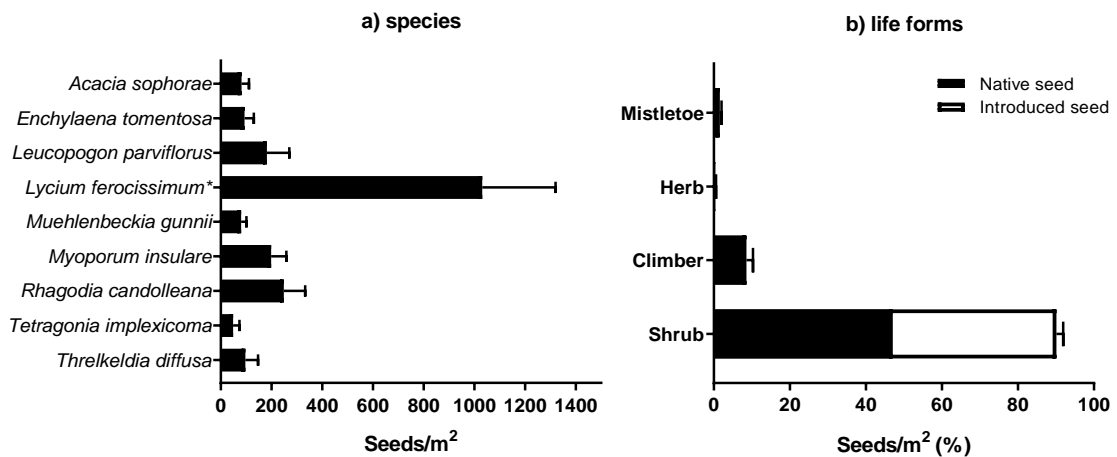
After 12 months of seed collection, the six perch treatments in the paddock (traps set beneath artificial perches and four paddock shrub species, and traps set in open areas of the paddock) significantly varied in the abundances of species that they accumulated (one-way PERMANOVA, pseudo- $F(5, 71) = 20.2$ ,  $P = 0.001$ ; Fig. 4.5). Significant differences were also detected in the identity of species that they accumulated (i.e. presence/absence of species; one-way PERMANOVA, pseudo- $F(5, 71) = 129.7$ ,  $P = 0.001$ ). Pairwise comparisons found that the artificial perches and the four species of paddock shrub significantly differed from the traps set in the open paddock in terms of the abundances and identities of species received ( $P = 0.001$ ).



**Figure 4.5.** Two-dimensional non-metric multidimensional scaling ordination visualising differences in the compositions of seed (based on species abundance) that were collected in traps set under the artificial perches ( $n = 12$ ), four species of paddock shrub ( $n = 10$  shrubs per species) and in the open paddock ( $n = 25$ ) during a 12-month period, between September 2015 and August 2016. Points closer together in ordination space indicate that they received relatively more similar compositions of seed based on zero-adjusted Bray-Curtis indices of similarity.

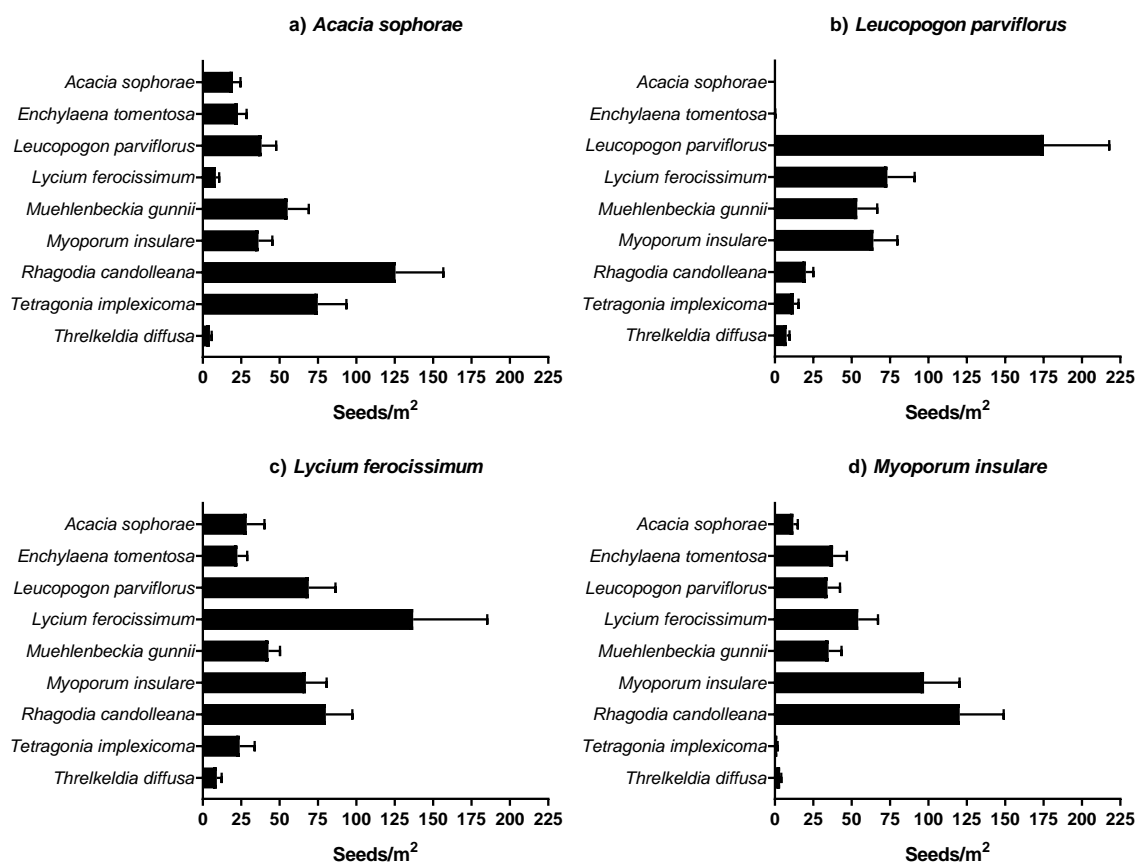
After 12 months of observation, the species that was on average most abundantly deposited in the traps beneath the artificial perches was the introduced shrub *L. ferocissimum* (1031.0 seeds/m<sup>2</sup>/year, equivalent to 42.4% of the seed, Fig. 4.6a). The deposition of this species beneath artificial perches was somewhat variable, ranging from 19–2565 seeds.

Cumulatively, native species accounted for 1128.6 seeds/m<sup>2</sup>/year (equivalent to 57.4% of seed) and those that were most abundantly deposited included the shrubs *R. candolleana* (248.9 seeds/m<sup>2</sup>/year, equivalent to 15.3% of seed), *M. insulare* (198.8 seeds/m<sup>2</sup>/year, equivalent to 8.8% of seed) and *L. parviflorus* (181.8 seeds/m<sup>2</sup>/year, equivalent to 7.7% of seed) (Fig. 4.6a). On average, shrub species accounted for most of the seed deposited at the artificial perches (90.2% of seed, where 47.1% was native seed), followed by climbers (8.6% of seed) (Fig. 4.6b).



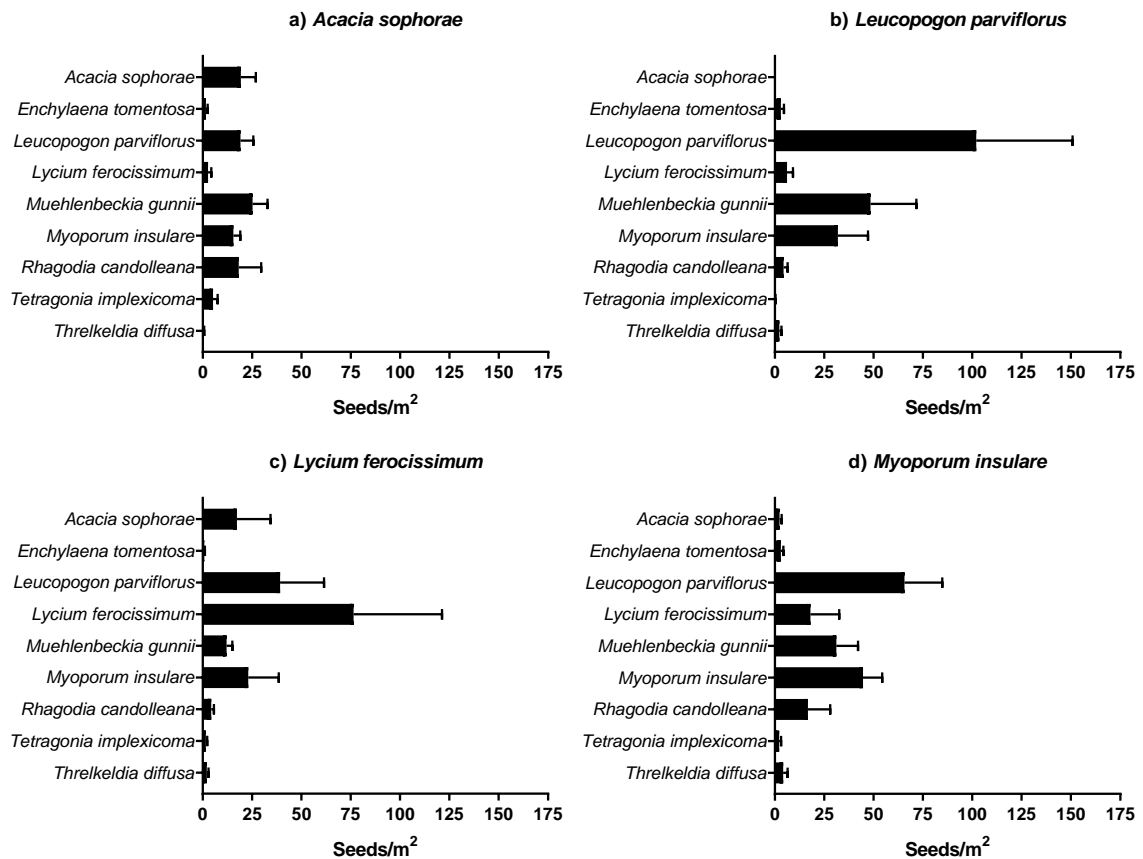
**Figure 4.6.** Seeds commonly deposited beneath the 12 artificial perches in the paddocks of Cantara, according to a) species (mean seed/m<sup>2</sup>/year + SE) and b) life form (mean percentage of seed/m<sup>2</sup>/year + SE, seed categorised according to origin). Seeds were collected during a 12-month period, between September 2015 and August 2016.

After 12 months of measurements, the traps set under the paddock shrubs of *L. parviflorus* and *L. ferocissimum* largely caught seeds belonging to these two species respectively (Fig. 4.7a–b). In comparison, the traps set under paddock shrubs of *A. sophorae* and *M. insulare* most abundantly received seed from *R. candolleana* (Fig. 4.7c–d). *Leucopogon parviflorus* and *M. insulare* shrubs also appeared to receive a considerable amount of seed rain from the introduced species *L. ferocissimum*, although by contrast *A. sophorae* shrubs did not. For each of the shrub species, some of the intraspecific seed deposited in the seed traps beneath the shrubs was likely seed that had been dislodged from desiccated and unconsumed fruits, which fell from branches located above the traps.



**Figure 4.7a–d.** Quantities of seed (mean seed/m<sup>2</sup>/year + SE) from different plant species that were commonly collected in traps set under four shrubs species ( $n = 10$  shrubs per species) in the paddocks of Cantara. Seeds were collected during a 12-month period, between September 2015 and August 2016.

Notably, when compared to the paddock shrubs, the traps set under dune shrubs tended to receive proportionally fewer *L. ferocissimum* seeds (Fig. 4.6a, Fig. 4.7, Fig. 4.8). Species of seed that were commonly deposited beneath most of the dune shrubs included *L. parviflorus*, *M. insulare* and *Muehlenbeckia gunnii*. Similar to the paddock shrubs, some of the intraspecific seed deposited in the traps beneath the dune shrubs likely originated from desiccated and unconsumed fruits, which fell from branches located above the traps.



**Figure 4.8a–d.** Quantities of seed (mean seed/m<sup>2</sup>/year + SE) from different plant species that were commonly collected in traps set under four shrubs species ( $n = 10$  shrubs per species) located in the dunes surrounding Cantara. Seeds were collected during a 12-month period, between September 2015 and August 2016.

Comparisons between four species of shrub present in the paddocks and dunes (*A. sophorae*, *M. insulare*, *L. parviflorus* and *L. ferocissimum*) revealed that the location of the shrub and the species of shrub had a significant influence on the abundances of species being deposited beneath the shrub (two-way PERMANOVA, pseudo- $F(1, 72) = 5.69$ ,  $P = 0.001$  and pseudo- $F(3, 72) = 8.75$ ,  $P = 0.001$  respectively). The interaction between these two factors, however, was not significant (pseudo- $F(3, 72) = 0.99$ ,  $P = 0.47$ ). SIMPER analysis revealed that only three species contributed up to 50% to the seed rain compositional differences between the paddock shrubs and the dune shrubs based on the abundances of species received (Table 4.2a).

**Table 4.2** Similarity percentage (SIMPER) analysis, showing the species that contributed the most (up to 50%) to the average Bray-Curtis dissimilarity between paddock shrubs and dune shrubs in their compositions of seed rain, based on a) the abundance of species in the seed rain and b) the identity of species in the seed rain (i.e. species presence/absence). Deposited seeds were collected beneath the four species of shrub present in the paddocks and dunes (*Acacia sophorae*, *Myoporum insulare*, *Leucopogon parviflorus*, *Lycium ferocissimum*) during a 12-month period from September 2015 to August 2016.

Species	Average dissimilarity	Dissimilarity/standard deviation	Contribution (%)
a) Species abundance; average dissimilarity between paddock and dunes = 67.66%.			
<i>Lycium ferocissimum</i>	13.92	0.65	20.58
<i>Leucopogon parviflorus</i>	11.45	0.92	16.92
<i>Myoporum insulare</i>	11.38	0.80	16.82
b) Species presence/absence; average dissimilarity between paddock and dunes = 24.24%.			
<i>Enchylaena tomentosa</i>	3.02	1.03	12.46
<i>Dianella revoluta</i>	2.81	0.97	11.61
<i>Tetragonia implexicoma</i>	2.77	0.92	11.44
<i>Exocarpos syrticola</i>	2.59	0.93	10.69
<i>Alyxia buxifolia</i>	2.52	0.92	10.39

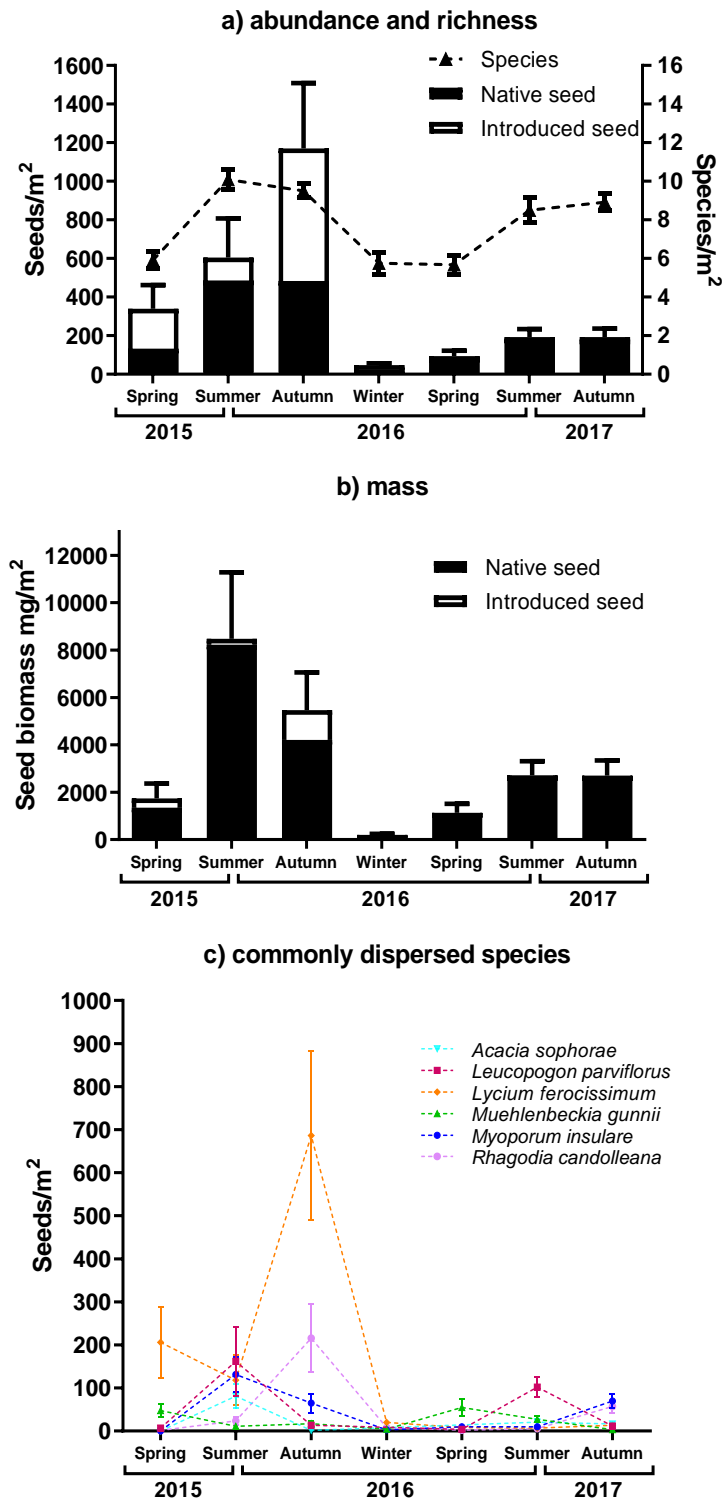
The identity of species (i.e. species presence/absence) being deposited beneath the shrub was also influenced by the species of shrub and by the location of the shrub (two-way PERMANOVA, pseudo- $F(1, 72) = 6.99$ ,  $P = 0.001$  and pseudo- $F(3, 72) = 2.74$ ,  $P = 0.045$  respectively), where the interaction between these two factors was significant (pseudo- $F(3, 72) = 2.56$ ,  $P = 0.007$ ). SIMPER analysis revealed that five species contributed up to 50% to the seed rain compositional differences between the paddock shrubs and the dune shrubs based on the identity of species received (Table 4.2b).



#### 4.3.2 Annual and seasonal variation in seed deposition

During the first year of observation, seed deposition in the traps beneath the artificial perches clearly varied between seasons (Fig. 4.9). This variation proved significant in terms of seed abundance (one-way repeated measures ANOVA,  $F(3, 33) = 7.82, P < 0.001$ ), species richness ( $F(3, 33) = 25.99, P < 0.0001$ ) and dry seed biomass ( $F(3, 33) = 8.01, P = 0.008$ ). The deposited seed was most abundant, most species rich and had the greatest dry biomass in summer and autumn (Fig. 4.9a–b). The species that contributed to peak deposition during these seasons included the native species *L. parviflorus*, *M. insulare*, *A. sophorae* and *R. candolleana*, as well as the introduced species *L. ferocissimum* (Fig. 4.9c, Fig. 4.10). From these species, *L. ferocissimum* contributed by far the most seed, although did not contribute much in terms of the overall biomass of seeds deposited (Fig. 4.9b).

At the artificial perches, seed deposition significantly differed between the first spring–autumn and the following spring–autumn period in terms of seed abundance (repeated measures two-way ANOVA,  $F(2, 22) = 4.37, P = 0.03$ , Fig. 4.9a), dry seed biomass ( $F(2, 22) = 3.74, P = 0.04$ , Fig. 4.9b), species abundance and species identity (two-way PERMANOVA pseudo- $F(2, 66) = 3.23, P = 0.001$  and pseudo- $F(2, 66) = 4.28, P = 0.001$  respectively). The species richness of seed, however, did not differ significantly (repeated measures two-way ANOVA,  $F(2, 22) = 1.20, P = 0.32$ , Fig. 4.9a). Evidently, fewer seeds were deposited at the perches in the second spring–autumn period and this largely reflected a decline in deposition of the introduced species *L. ferocissimum* (Fig. 4.9a, c). Most native species also experienced declines in seed deposition, although clearly not to the same extent (Fig. 4.9c).



**Figure 4.9.** Seasonal variation in the seeds collected in traps set under the 12 artificial perches over 7 seasons between 2015 and 2017, including in the a) abundance and species richness of seed deposited (mean seed/m<sup>2</sup>/season + SE), b) dry biomass of seed deposited (mean mg/m<sup>2</sup>/season + SE) and c) abundances of commonly deposited species (mean seed/m<sup>2</sup>/season ± SE). The seed abundance and seed biomass recorded in each season was also categorised according to the origin of the seed (native or introduced).



**Figure 4.10.** Seed trap located beneath an artificial perch that is abundant with seed from the introduced species *Lycium ferocissimum*. The trap contains 1 month of deposited seed, captured in April 2016 (i.e. mid-autumn), during the peak deposition of *L. ferocissimum*. Each seed trap had a rolled edge to minimise seed loss from rain and seed predators.

## 4.4 Discussion

### 4.4.1 Seed dispersal limitation

The artificial perches were effective at facilitating the dispersal of seed into open areas of the paddocks where native vegetation had been lost. Over the course of a year, 2161.2 seeds/m<sup>2</sup> were deposited at the perches, which was significantly greater than the 0.32 seeds/m<sup>2</sup> that arrived in open areas without perches. This result exceeds that which has been observed in previous studies of artificial perches, including Holl (1998), Vicente *et al.* (2010) and de Almeida *et al.* (2016), who respectively observed 161, 181 and 680 seeds/m<sup>2</sup>/year being deposited under perches in tropical and subtropical systems. Primarily, the abundant deposition observed in this study may have been due to the presence of fleshy-fruited shrubs, which occurred in isolated patches in the paddocks and were able to act as sources of seed. This most notably included the introduced shrub *L. ferocissimum*, whose seed accounted for 42.4% of the seed deposited beneath the perches during the first year of observation. In general, the shrubs also increased the structural complexity of the grassy

paddocks at Cantara and this likely helped to entice seed-dispersing birds to venture into the degraded site (McDonnell and Stiles 1983; Toh *et al.* 1999). Studies conducted in tropical and temperate systems have emphasised the importance of scattered vegetation on seed arrival in degraded areas, observing greater inputs of bird-dispersed seed in sites where there were greater complexities of vegetation, particularly when that vegetation contained fleshy-fruited species (McDonnell and Stiles 1983; Guevara *et al.* 1986; Da Silva *et al.* 1996).

In this study, flying frugivorous birds deposited a few seeds into open areas of the paddocks. This was not unexpected, as studies elsewhere have also observed flying frugivorous birds to deposit small amounts of seed into open and disturbed habitats (e.g. McDonnell and Stiles 1983; McClanahan and Wolfe 1987; Willson and Crome 1989; Holl 1998; Cavallero *et al.* 2013). Furthermore, this is because birds tend to defaecate seed more whilst perched than during flight (Jordano 2000). While this study focused on the seed dispersal facilitated by flying frugivorous birds, some of the seeds that arrived in the paddocks (although were unable to be collected in seed traps) were dispersed by the flightless emu (*Dromaius novaehollandiae*). Their scats were occasionally observed in open areas of the paddocks and were found to contain thousands of seeds, which were typically from 3–5 plant species (McCarron, unpubl. data).

Similar to the artificial perches, the shrubs in the paddocks were also able to act as dispersal foci, receiving 493.3 seeds/m<sup>2</sup>/year. Fewer seeds were deposited per m<sup>2</sup> at the paddock shrubs when compared to the artificial perches, although, this may have been because the shrubs possessed larger crowns. This would have increased the area of seed deposition and thus reduced the potential for seed to fall into the seed trap (McClanahan and Wolfe 1987; Zwiener *et al.* 2014). Thus, there is potential that the abundances of seed deposited over the entire crowns of the paddock shrubs would have exceeded those that were deposited at the artificial perches. Notably, the shrub species in the paddocks differed in the abundances and identities of species which accumulated beneath them. This may have occurred as the species of shrub differed in the nature of the fruits they provided (e.g. size, reward, ease of harvest) and because they varied in the timing of their ripe fruit availability (Chapter 2). These characteristics have the potential to strongly influence the timing of bird visitation and the range of birds attracted to the shrub (Stiles and White 1986; Jordano 2000; Izhaki 2002). The birds in turn influence the composition of seed rain deposited beneath the shrub through their fruit choice, which is influenced by factors such as their dietary requirements,

as well as the seasonal availability of ripe fruit in the local area (e.g. as found in other systems; Stiles and White 1986; Jordano 2000).

#### 4.4.2 Species deposition

The artificial perches were also effective at increasing the richness and composition of seed being deposited in the degraded site. Over 12 months, the perches received seed from 15 plant species, including 13 native species. This represented most of the fleshy-fruited species present in the Youngusband Peninsula (Chapter 2). The native species that were most abundantly deposited beneath the perches were the summer–autumn fruiting shrubs *R. candolleana*, *M. insulare* and *L. parviflorus*, which respectively accounted for 248.9, 198.8 and 181.8 seeds/m<sup>2</sup>/year under the perches. Realistically, *M. insulare* and *L. parviflorus* would have contributed more seeds at the perches than indicated since only the woody stones of these two species were counted. The woody stones of *M. insulare* may contain up to three seeds, whereas those of *L. parviflorus* may contain up to five seeds (Black 1952). The abundant deposition of *R. candolleana*, *M. insulare* and *L. parviflorus* seed beneath the perches reflects the abundance of these species in the vegetation of the Youngusband Peninsula (Paton 2010). Furthermore, their fruits are consumed by a range of seed-dispersing birds (Chapter 2, Chapter 3), including the spiny-cheeked honeyeater (*Acanthagenys rufogularis*) and singing honeyeater (*Lichenostomus virescens*), which were the seed-dispersing species that most frequently visited the perches during summer and autumn (Chapter 3).

Overall, the introduced shrub *L. ferocissimum* contributed the most seeds to the seed rain that fell beneath the artificial perches (1031.0 seeds/m<sup>2</sup>/year, equivalent to 42.4% of deposited seed). The predominant deposition of this species likely occurred for several reasons. First, *L. ferocissimum* fruits contain many seeds (20–70, Noble and Adair 2014), whereas the fruits of most other species in the region contain only one seed. Second, *L. ferocissimum* produced fruit in autumn when native fruit availability began to decline, meaning that their fruit may have more readily been consumed and dispersed by frugivorous birds (Gosper *et al.* 2005). Lastly, and perhaps most importantly, the *L. ferocissimum* shrubs resided in closer proximity to most of the perches than other fleshy-fruited plant species. This may have accounted for the high quantities of *L. ferocissimum* seed being deposited beneath artificial perches since most bird-dispersed seeds are transported over short distances from the parent plant (Debussche and Isenmann 1994; Jordano *et al.* 2007). Other studies of artificial perches have also noted the influence of the proximity of source plants

on seed rain, with most of the seeds deposited at artificial perches likely to have originated from the plants present within the disturbed site (McDonnell and Stiles 1983; McClanahan and Wolfe 1987; Bustamante-Sánchez and Armesto 2012).

Similar to the artificial perches, *L. ferocissimum* seed was abundantly dispersed to two native shrub species in the paddock, which were *L. parviflorus* and *M. insulare*. Few *L. ferocissimum* shrubs occurred in the remnant dune vegetation, which explains why this species was not as abundantly dispersed to the native shrubs found there. In general, the species of shrubs in the dunes significantly differed from the same shrub species in the paddocks in terms of the identities of species which were detected in their seed rain. The shrubs in the dunes were more likely to receive seed from the fleshy-fruited plant species that were common there, such as *M. gunnii*, *L. parviflorus* and *M. insulare*. Seed from these native species were deposited in the traps beneath the artificial perches, although clearly not to the same extent as *L. ferocissimum*, as they resided further from the degraded site. Despite their distance, most of the fleshy-fruited plant species in the surrounding remnant vegetation contributed to the seed rain beneath the perches. In fact, some of these species were known to reside at least 150–200 m away from some of the artificial perches (e.g. *A. melaleucae* found in the *M. halmaturorum* stand, *Scaevola calendulacea* and *Alyxia buxifolia* found on dune crests) which indicated that birds can disperse some seeds over moderate distances (locations of habitats observed in Fig. 2.3; Chapter 2).

#### 4.4.3 Temporal variation in seed deposition

Seed deposition at the artificial perches was found to vary between seasons. Seed deposition was most abundant, most species rich and had the greatest dry biomass in summer and autumn, which is when most fleshy-fruited species in the study site produced fruit (Chapter 2). Very few species produced fruit in winter, which explains the lack of seed deposition during this time. Seasonal variation in fruit availability has influenced seed deposition in three studies of artificial perches, two of which were conducted in tropical Brazil (Zanini and Ganade 2005; Athiê and Dias 2016) and one which was conducted in temperate North America (McDonnell and Stiles 1983). In contrast, Graham and Page (2012) in tropical Indonesia found no effect of seasonality on deposited seed biomass at their perches, as fruit was consistently available throughout the year.

Seed deposition at the artificial perches was also found to vary between years. Most notably, the perches received far fewer seeds over the second spring–autumn fruiting period, which

was largely due to a decline in the deposition of seed from the introduced species *L. ferocissimum*. This decline occurred following the control (i.e. poisoning) of *L. ferocissimum* shrubs at Cantara in the winter of 2016. This control was not an intentional part of this study but was carried out as part of a regional management program (South East Natural Resources Management Board 2018). All the native species that contributed to the seed rain beneath the artificial perches in the first spring–autumn fruiting period also contributed to the seed rain in the second period, although for most species this was to a smaller extent. This decline in native seed deposition was likely to have been influenced by the control of *L. ferocissimum* shrubs in the paddocks. The *L. ferocissimum* shrubs were no longer producing fruit, so seed-dispersing birds had less incentive to move into the paddocks. Degraded sites with fruit-producing plants have been shown to attract more seed-dispersing birds and have greater amounts of seed deposition when compared to sites that lack fruit resources (McDonnell and Stiles 1983; Guevara *et al.* 1986; Da Silva *et al.* 1996). For some native species, their decline in seed deposition beneath the perches may have been due to a decline in fruit production in the nearby vegetation. Fruit production has the potential to vary between years in the Younghusband Peninsula, although the exact drivers of this variation are not known (Chapter 2). Inter-annual variation in fruit production in the surrounding vegetation matrix also appeared to explain changes in seed deposition to artificial perches in temperate Chile (Bustamante-Sánchez and Armesto 2012). Perhaps to a small extent, the decline in native seed deposition may have been the result of perch degradation. Branches gradually broke off the perches over time and this may have decreased their attractiveness to seed-dispersing birds (Vogel *et al.* 2016). Notably, native seed deposition only slightly decreased from the first spring to the next, so perch degradation was unlikely to have been a substantial factor in the overall decline in seed deposition.

#### 4.4.4 Implications for restoration

The abundant deposition of *L. ferocissimum* seed at the artificial perches was clearly to the detriment of restoration. The establishment of this introduced species at the perches would have only caused further degradation to the paddocks of Cantara, as it is able to displace native vegetation but it is also extremely difficult and expensive to control (Noble and Adair 2014; Ireland *et al.* 2019). The dispersal of seeds from introduced species to artificial perches has limited the potential for restoration to occur elsewhere, including in subtropical North America (Prather *et al.* 2017) and Mediterranean South Africa (Heelemann *et al.*

2012). The results of these studies, as well as this study, indicate that it may not be appropriate to erect perches in sites where introduced fleshy-fruited species are present unless some form of control is carried out. This control would increase the costs of a supposedly cost-effective restoration method, although such control is typically required before the initiation of most restoration efforts (Berger 1993). At Cantara, the control of the introduced shrub *L. ferocissimum* was largely effective at reducing the dispersal of its seed to the artificial perches. This species recorded 28.08 seeds/m<sup>2</sup> beneath the perches in the spring–autumn period that followed its control, which was a substantial decline from the 1010.7 seeds/m<sup>2</sup> recorded in the previous spring–autumn period. If left intact in the paddocks, the poisoned *L. ferocissimum* shrubs could be used to assist with restoration. The dead shrubs would provide suitable perches for birds and so would help to facilitate seed dispersal into the paddocks. Such use of dead shrubs has been explored in former pastures in tropical north-eastern Australia, where poisoned strands of *Solanum mauritianum* (in combination with grass suppression) were able to facilitate seed dispersal and enhance plant recruitment (Elgar *et al.* 2014).

To the benefit of restoration, the artificial perches were able to receive abundant amounts of seed from native species (from up to 13 species, 1128.6 seeds/m<sup>2</sup>/year). Assuming that recruitment barriers were not severe in the paddocks, then these quantities of seed should have been more than enough to allow for some germination and establishment to occur in due course. Evidently, much of the native seed originated from shrub species, which importantly included shrubs such as *A. sophorae*, *M. insulare* and *R. candolleana* (accounting for 529.9 seeds/m<sup>2</sup>/year). Their deposition beneath the perches was important for regeneration processes as they are hardy species which can establish in degraded or disturbed coastal habitats (Chladil and Kirkpatrick 1989; Heyligers 2009; Liney 2011; Kelsall 2015). If these shrubs establish and mature at the perches, then they should be able to in turn promote the establishment of other species, including shade-tolerant shrubs (e.g. *L. parviflorus*), as well as understorey shrubs (e.g. *Enchylaena tomentosa*, *Dianella revoluta*) and climbers (e.g. *Tetragonia implexicoma*, *M. gunnii*) which establish in the shelter of their crowns (Hazard and Parsons 1977; Forde 1986; Croft *et al.* 2006; Heyligers 2009). Of course, there is no certainty as to whether this restoration trajectory, or recruitment in general will occur, without long-term monitoring. The following chapter, Chapter 5, aims to remove some of this uncertainty by investigating the potential for several



of the common fleshy-fruited plant species to germinate, recruit and survive in the degraded site.

The results of this chapter have provided some practical considerations towards the deployment of artificial perches for the regeneration of the cleared and degraded parts of the Youngusband Peninsula. In this study, 12 artificial perches were planted over 25 ha, which evidently is very few perches for such a large area. With this setup, only a small proportion of the degraded site would have potentially been assisted with regeneration over the short-term. If artificial perches are to be used as a restoration tool, then they will need to be deployed in far greater numbers to ensure that seed will be deposited over many areas within the degraded site. Furthermore, as observed at Cantara, deploying a small number of perches also meant that there were high densities of seed being deposited beneath each perch as birds had few perches to choose from. High seed densities may not be particularly ideal if they result in competition between germinants (Münzbergová 2012). Deploying many perches would reduce the density of seed rain at each perch (as a result of fewer bird visits) and would reduce potential competition between germinants. Although, as to whether such competition (and recruitment in general) occurs when there is a high density of seed rain can only be confirmed through testing and monitoring. Alternatively, the number of areas where seeds are dispersed could be increased if the artificial perches were shifted throughout the degraded site over time.

This study has also indicated that the perches would need to be in place at least over summer and autumn when most of the fleshy-fruited plant species in the region are producing fruit. In terms of longevity, the results of this study indicated that artificial perches constructed from dead *A. sophorae* branches may only be useful over a short period of time, as the branches were prone to breaking. The longevity of artificial perches could be improved if they were constructed from species with sturdier wood or constructed with freshly cut branches. Castillo-Escrivà *et al.* (2019) for example constructed branch piles using branches from native pine (*Pinus halepensis*), which were sourced from thinning works conducted in local afforested areas. These branch piles were still intact and functional two years after their construction.

As observed at Cantara, natural perches such as shrubs also act as important facilitators of seed dispersal. Where seedlings of large shrubs such as *A. sophorae*, *M. insulare* and *L. parviflorus* can be obtained, then these too could be planted to increase the likelihood of

seed-dispersing birds venturing into heavily cleared paddocks in the Younghusband Peninsula. This restoration method would be expensive. Although, costs could be reduced if the shrubs were planted in clumps rather than planting over the entire degraded area. Fewer seedlings are planted using this method, thereby reducing planting and maintenance costs (e.g. smaller area of weed control, fewer replantings required) (Rey Benayas *et al.* 2008; Cole *et al.* 2010; Holl *et al.* 2011; Holl *et al.* 2020). Over time, these islands would be expected to spread and coalesce, as they facilitate the recruitment of seed deposited beneath their canopies (Zahawi and Augspurger 2006). Planting several species in the degraded site would also help to attract a greater diversity of seed dispersers, which in turn would increase the richness of deposited seed (Janzen 1988; Slocum and Horvitz 2000). Experiments may be required to investigate the potential for recruitment beneath each species of shrub, as it could vary depending on the resources and space monopolised by the shrub (Janzen 1988).

#### **4.5 Conclusion**

In conclusion, the artificial perches facilitated the dispersal of seed into a cleared and degraded temperate coastal site. Most of the perches predominantly received seed from the introduced species *L. ferocissimum*, which suggests that perches should not be implemented in degraded sites where this species is present. The artificial perches did, however, receive large amounts of seed from up to 13 native species. In the absence of recruitment barriers, then this should have been more than enough seed to allow for eventual germination and establishment. Importantly, the species that were deposited at the perches included hardy shrubs such as *M. insulare*, *R. candolleana* and *A. sophorae*. The establishment and recruitment of such species would benefit regeneration, as their presence would help to facilitate the establishment of other species. This chapter also highlighted the potential importance of shrubs in enhancing seed deposition in degraded areas. Planting shrubs in degraded areas may be an effective strategy to overcome dispersal limitations in conjunction with erecting bare branches to act as perches. The following chapter, Chapter 5, now considers the potential for the deposited seed to germinate, survive and establish.

# Chapter 5. Seed germination and seedling survival on the Younghusband Peninsula

## 5.1 Introduction

Artificial perches are erected in cleared and disturbed environments with the aim of enhancing seed dispersal and increasing the chances of plant recruitment. Perches can overcome seed dispersal limitations by encouraging frugivorous birds to move into open areas of disturbed sites, where they may rest and defaecate the seeds from the fruits they have consumed. For regeneration to occur, these seeds then need to germinate and recruit. Researchers have most commonly evaluated the effectiveness of the restoration tool by determining the extent to which seed arrival is enhanced in the disturbed or degraded site (Guidetti *et al.* 2016). Many researchers, however, have neglected to monitor and report on the stages that occur after seed dispersal, including seed germination and seedling survival (Reid and Holl 2013; de Almeida *et al.* 2016). Monitoring plant recruitment is crucial in the evaluation of restoration success, especially since there is no guarantee that seed deposition will result in plant recruitment (e.g. Holl 1998; Graham and Page 2012; Heelemann *et al.* 2012). There are many post seed-dispersal barriers that can prevent seedling recruitment in degraded areas, including poor germination rates, seed predation, competition with introduced grasses and herbivory (Aide and Cavellier 1994; Holl *et al.* 2000; Dey *et al.* 2019). Thus, to avoid the same short-comings as previous studies, this chapter now considers the fate of seed dispersed to artificial perches erected in a degraded temperate coastal environment, located on the Younghusband Peninsula, South Australia.

The recruitment barriers investigated in this chapter were poor seed germination, competition from introduced grasses and seedling herbivory. These barriers were selected as they are known to influence plant recruitment in the region, however, there are still aspects of each barrier that need to be understood. For example, germination probabilities have been reported in *ex situ* germination trials for some but not all fleshy-fruited species of the region (South Australian Seed Conservation Centre 2016). There is also potential that the seeds defaecated at the perches experience different germination probabilities than those reported in the germination trials, particularly as the seeds have passed through the gut of a bird. This process can enhance germination as it is able to scarify the seed coat, making it more permeable to water and gases (Traveset 1998). Furthermore, germination probabilities may also differ in the field as they are influenced by the conditions of the local environment (e.g.

soil moisture, light, disturbance) (Traveset *et al.* 2007). Poor seed germination has limited recruitment in two other studies of artificial perches. In Mediterranean South Africa, seed germination was limited following seed predation and poor soil conditions (Heelemann *et al.* 2012), whereas in semi-arid Spain seed germination was limited by a stressful microclimate (Martínez-López *et al.* 2019).

There is also limited knowledge on the ability of native plant species to recruit when in competition with introduced grasses in degraded areas of the Youngusband Peninsula. Vegetation surveys conducted in the Youngusband Peninsula and the nearby Coorong and Murray Mouth regions have found that introduced species, such as *Avena barbata* and *Ehrharta calycina*, dominate the ground cover of degraded sites and appear to prevent the regeneration of native vegetation (Alcock and Symon 1977; Brandle 2002; Milne 2015). Experiments are required to determine whether introduced grasses limit the establishment of fleshy-fruited plants through competition in the Youngusband Peninsula. Competition from introduced grasses has limited seedling recruitment in studies of artificial perches conducted elsewhere, including in tropical Costa Rica (Holl *et al.* 2000) and in tropical north-eastern Australia (Elgar *et al.* 2014).

Plant herbivory is currently the most extensively explored recruitment barrier in the Youngusband Peninsula. Field experiments conducted in the region found that native seedling survival was improved when mammalian herbivores, such as European rabbits (*Oryctolagus cuniculus*), were controlled or fencing excluded them from accessing seedlings (e.g. Cooke 1987; Bird *et al.* 2012). These studies, however, did not assess the ability of any seedlings of fleshy-fruited species to tolerate and survive grazing in cleared landscapes. The field experiments also neglected to consider how seedling survival was influenced by size, which is important because plants may display increased survival as they grow larger, particularly as the impacts of herbivory are reduced (Allcock and Hik 2004; Boege *et al.* 2011).

The aim of this chapter was to determine the potential for seed deposited at artificial perches located on the Youngusband Peninsula to overcome recruitment barriers and to establish. The following questions were asked:

- 1) What were the germination probabilities of the seeds of the species that were commonly deposited under perches and were these germination probabilities influenced by passage through the bird gut?

- 2) Do introduced grass species limit the emergence and establishment of seedlings from fleshy-fruited plant species?
- 3) Do herbivorous grazers limit the survival of seedlings of fleshy-fruited plant species in the Youngusband Peninsula and is height important for seedling survival?
- 4) What is the overall likelihood of establishment in the degraded site?

## 5.2 Methods

### 5.2.1 Study location

Field research was conducted in the southern paddocks of Cantara, which cover an area of approximately 25 ha. These paddocks were located about 800 m inland from the Southern Ocean, on the Youngusband Peninsula, South Australia (36°20'S, 139°44'E). The climate is Mediterranean, with cool-moist winters (June–August) and hot-dry summers (December–February) (Australian Bureau of Meteorology 2021). Average annual rainfall is 521.8 mm (measured at Salt Creek's Pitlochry Outstation, 36.28° S, 139.84° E). Total rainfall during 2016, the year that field experiments were conducted, was 545.8 mm. The soil on the Youngusband Peninsula is comprised mostly of sandy calcareous soils (Gilbertson and Foale 1977).

Pastoral activities were once conducted in the paddocks of Cantara, approximately between the mid-nineteenth century to the late twentieth century (Rudduck 1982). Grazing and trampling resulted in a loss of native vegetation and further damage followed with the introduction of rabbits in the late nineteenth century. Oats (*Avena* spp) were also sown in the southern paddocks of Cantara and this introduction is thought to be partly responsible for the dominance of introduced grasses on the previously cleared land (Rudduck 1982). Other introduced grasses that are currently abundant in the study site include *Vulpia* spp, *Bromus diandrus* and *Lagurus ovatus*. Apart from rabbits, grazing mammals currently present in the study site include the western grey kangaroo (*Macropus fuliginosus*), common wombat (*Vombatus ursinus*) and feral fallow deer (*Dama dama*). Bird *et al.* (2012), Mutze *et al.* (2014) and Moulton *et al.* (2018) have provided long-term density estimates for some of these animals (particularly rabbits) in the study region, where fluctuations in density appeared to occur in response to rainfall and/or biocontrol measures.

### 5.2.2 Experimental design

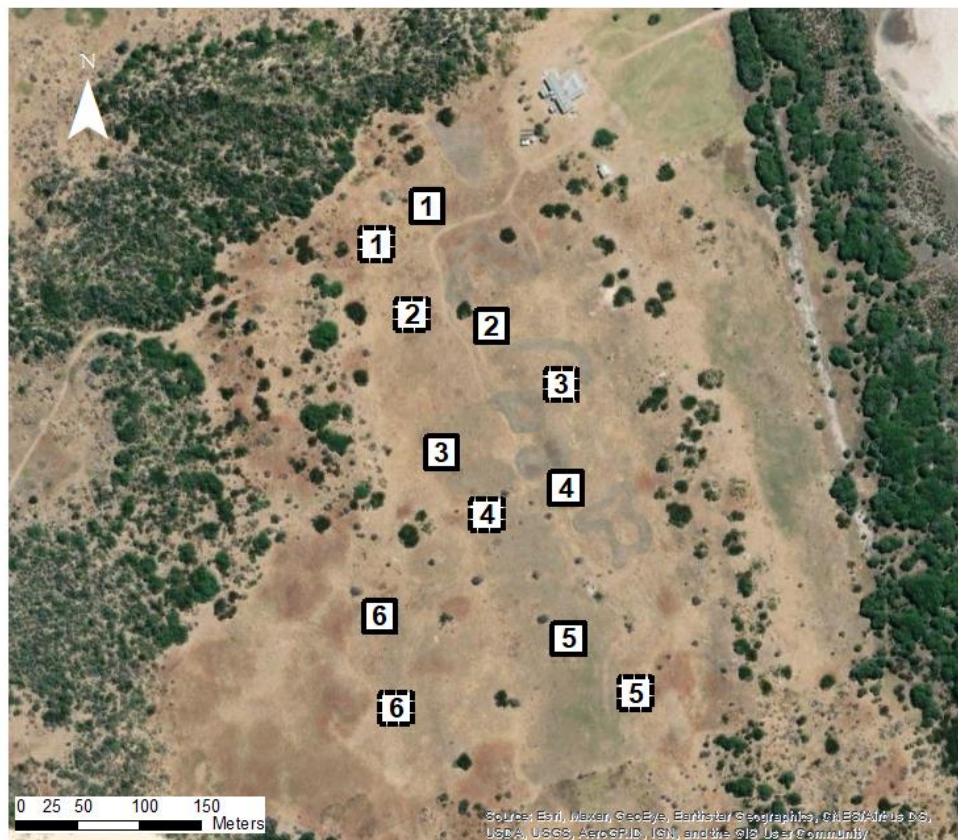
Twelve artificial perches were deployed throughout the open areas of the southern paddocks of Cantara in July 2015. Several studies have tested the importance of certain recruitment barriers by manipulating the conditions beneath or near the artificial perches and observing the effect that this would have for the seeds deposited there (e.g. Elgar *et al.* 2014; Martínez-López *et al.* 2019). This was not possible to replicate in this study, as the seeds that were deposited beneath the perches were collected in traps, so they could be counted and identified (Chapter 4). Therefore, this chapter tested the influence of recruitment barriers through glasshouse experiments, as well as through field experiments which were conducted in areas proximate to the artificial perches (Fig. 5.1). The native fleshy-fruited species involved in these experiments were those whose seed were commonly deposited beneath the perches. The species consisted of the shrubs *Acacia sophorae*, *Myoporum insulare*, *Rhagodia candolleana*, *Exocarpos syrticola* and *Leucopogon parviflorus*.

### 5.2.3 Seed germination in the glasshouse

Seed germination probabilities were determined for the species *A. sophorae*, *E. syrticola*, *L. parviflorus*, *M. insulare* and *R. candolleana*. In this experiment, the term 'seed' was inclusive of the woody stones of *L. parviflorus* and *M. insulare*, which potentially contain multiple seeds. For each species, germination ability was tested for gut-passed seeds, as well as for seeds that were extracted from fruit collected from plants ("fruit-extracted seeds" hereafter). Gut-passed seeds were collected from the regionally abundant silvereye (*Zosterops lateralis*), which was trapped at five sites along the Coorong in January 2015 as part of a long-term monitoring program (Paton, unpubl. data). While waiting to be banded, the birds were individually held in a calico bag for approximately 5–15 minutes, which was generally adequate time for the bird to pass seed. The seeds were collected, sorted according to species and then stored dry at ambient room temperature for 3 months until experimentation commenced. The fruit-extracted seeds were also sourced in January 2015 from plants in the study region. Seeds were collected from several plants to minimise possible maternal effects on germination. Seeds were removed of flesh and then stored dry in paper bags at ambient temperature for 3 months until experimentation commenced.

Seed germination was tested in 9 cm Petri dishes that were filled with sterilised sand. For each species, there were two Petri dishes containing 25 fruit-extracted seeds (50 seeds total) and four Petri dishes containing 25 gut-passed seeds (100 seeds total). The Petri dishes were

placed in a glasshouse, which was set to evaporatively cool when the room temperature exceeded 20 °C. Petri dishes were moistened with distilled water when required and the seeds were checked every 1–2 days for germination (i.e. radicle emergence from the seed coat). Germinated seeds were removed from the Petri dishes to prevent interference with the remaining seeds. The experiments commenced in April 2015 (mid-autumn) and were terminated in June 2016 (early winter), running for a total of 450 days. The experiments were conducted over a long period as the seeds of *E. syrticola* and *L. parviflorus* were expected to experience delayed germination.



**Figure 5.1.** Aerial view of the southern paddocks associated with Cantara Homestead (top centre), including the locations of six 25 × 25 m fenced plots (solid perimeter) and six 25 × 25 m open plots (dashed perimeter) where field experiments were conducted.

#### 5.2.4 Effect of introduced grasses on seedling emergence and establishment

The effects of the introduced grasses on the emergence and survival of seedlings were investigated for the shrubs *R. candolleana* and *A. sophorae*. For both species, the effects of the introduced grasses on these species were tested by comparing seedling emergence and recruitment in subplots exposed to grasses (control treatment,  $n = 4$ ) to emergence and recruitment in subplots cleared of introduced grasses ("grass-cleared subplots",  $n = 4$ ). Each

subplot was  $2.5 \times 2$  m in size. Throughout each of these subplots, a total of 500 seeds were sown. Both species had a single subplot of each treatment placed inside of a  $25 \times 25$  m plot that had been enclosed in a 1.6 m fence to exclude mammalian grazers (fenced plots 1, 2, 4 and 6 were used; Fig. 5.1). The top section of the fence consisted of prefabricated wire mesh netting (1.1 m high), which deterred kangaroos from entering. The bottom section of the fence consisted of galvanised wire mesh (40 mm hexagonal holes) that was 0.60 m high, with a 0.3 m apron that projected outward to deter rabbits and wombats from burrowing underneath. The large and small mesh overlapped by 10 cm.

Seed for these experiments were collected from plants in the study region in January 2016. Seeds were removed of flesh and then stored dry in paper bags at ambient temperature for 7 months until required. The grass-cleared subplots were initially prepared through an application of 540 g/L glyphosate (at a mix ratio of 6.5 mL per litre of water) in May 2016. They were then lightly raked to remove dead grasses in June 2016 and were raked again in early October 2016. The control subplots containing grasses were not disturbed except during sowing, when small holes were created for seeds to be sown in. The seeds were sown into the grass-cleared and control subplots in early October 2016 (i.e. mid-spring). The numbers of seedlings that emerged (i.e. protruded above the soil surface) in each of the subplots were then recorded at 2, 6, 10, 14 and 20 weeks after the seeds were sown. Ideally, the seeds in this experiment should have been sown at a similar time to their deposition at artificial perches between December and April (i.e. between summer and mid-autumn, Chapter 4). However, the need to control introduced grasses in this experiment delayed the deployment of seeds until spring, as the introduced grasses were best controlled following their emergence in autumn and winter.

#### *5.2.5 Effect of herbivory on seedling survival*

The effect of mammalian herbivory on seedling survival was investigated for the shrubs *A. sophorae*, *M. insulare* and *R. candolleana*. This effect was investigated by comparing the survival of seedlings that were excluded from mammalian herbivory to those that were left open to herbivory. The seedlings that were excluded from herbivory were placed inside the fenced  $25 \times 25$  m plots, which excluded mammalian herbivores. The seedlings exposed to mammalian herbivory were placed in open plots that were also  $25 \times 25$  m in size. Seedlings were scattered throughout each plot and were placed at least 1.5–2 m apart from one another. Each species had seedlings placed in two fenced plots and two open plots. Each



plot received 50 seedlings, thereby resulting in a total of 100 seedlings per treatment. *Acacia sophorae* seedlings were placed in fenced and open plots 1–2, *M. insulare* seedlings were placed in fenced and open plots 2–3, and *R. candolleana* seedlings were placed in fenced and open plots 5–6 (location of plots in Fig. 5.1).

Seedlings were grown from seeds that were sourced from the study region and were propagated in the glasshouse between spring 2015 and winter 2016. The seedlings were grown to a range of heights to test the influence of height on survival. Prior to deployment, seedling height ranged from 1.5–58.5cm (mean 19.1 cm) in *A. sophorae*, 1.4–33.0 cm (mean 12.1 cm) in *M. insulare* and 1.3–58.9 cm (mean 22.0 cm) in *R. candolleana*. To avoid biasing the survival estimates of each species, each plot received seedlings across the range of heights available.

Seedlings were deployed in the field in late August 2016 (i.e. late winter) and were kept in the pots in which they were grown in to avoid disturbing their root systems and to prevent competition with introduced grasses. Each pot was numbered, which allowed individual seedling survival to be tracked over time. Each pot was placed in a small augured hole, which was deep enough to allow the top of the pot to be flush with the ground. Seedlings were checked at 3, 5 and 7 weeks after deployment. At each census, the data recorded consisted of seedling survival, seedling height, signs of damage (e.g. grazed, trampled, uprooted, desiccated) and the grazers responsible for damage (insect/snail, mammal) were noted. Mammals were considered responsible for the damage when the stem or the leaves of the seedling had been ripped or sharply grazed. Snails or insects were considered responsible for the damage when the leaves of the seedling had irregular holes or grazed edges and when grazing scars were apparent on tender stems. Seedling death was attributed to grazing when the seedling was completely grazed or grazed with only a desiccated stem remaining. Seedling death was attributed to moisture stress when the seedling was desiccated but showed little or no sign of having been grazed. The seedlings were not watered during site visits, as 90.2 mm of rain fell over the 7 weeks that the seedlings were deployed (rainfall recorded at Salt Creek's Pitlochry Outstation).

#### 5.2.6 Statistical analysis

For each species tested in the glasshouse experiment, the Kaplan-Meier method was used to estimate the germination probabilities of 100 gut-passed seeds and 50 fruit-extracted seeds. The replicates for each treatment were combined in this circumstance, as replication is not

required for time-to-event analysis (McNair *et al.* 2012). The Kaplan-Meier method is a non-parametric method that is typically used to estimate survival, however, it is also useful for estimating germination probabilities as it takes the temporal patterns of germination into account (Onofri *et al.* 2010; McNair *et al.* 2012). Furthermore, the method is useful as it accommodates right-censored data, which in this circumstance are seeds that did not germinate before the end of the experiment. For right-censored data, the exact time until the event (i.e. germination) occurs is unknown, although what is known is the duration in which the event did not occur. Accommodating right-censored data is important as complete germination (100%) is rare and the length of time required for germination to occur in viable seeds can exceed that of the experimental period (Pérez and Kettner 2013).

The Kaplan-Meier estimator of the survival function, denoted  $\hat{S}_{(t)}$ , estimated germination probability (Kaplan and Meier 1958). Assuming there are  $k$  distinct ordered event times  $t_1 < t_2 \dots t_k$ , then  $\hat{S}_{(t)}$  for  $t_1 \leq t \leq t_k$  is given by:

$$\hat{S}_{(t)} = \prod_{j: t_j \leq t} \left( 1 - \frac{d_j}{n_j} \right)$$

where  $d_j$  is the number of individuals that experienced the event (i.e. seeds that germinated) in a given time interval  $t_j$ ; and  $n_j$  is the number of individuals at risk of experiencing the event (i.e. seeds "at risk" of germination) up to time  $t_j$ . For each species, the germination curves of the two treatments were compared using a log-rank test, except for when the curves crossed. When curves are crossed, the hazard ratio is not constant and the log-rank test loses its power to detect differences. In these circumstances, the Tarone-Ware test can be more powerful than the log-rank test and thus was used instead (Etikan *et al.* 2018). For each species, Fisher's exact test (FET) was used to compare the final germination percentages of gut-passed and fruit-extracted seeds.

For species of seedlings grown in the introduced grass experiment, a repeated measures two-way analysis of variance (ANOVA) was conducted to compare the number of seedlings observed in the four subplots with grasses to those observed in the four subplots cleared of grasses (between-subjects factor) at the censuses that coincided with and followed first seedling emergence (within-subjects factor). A repeated measures two-way ANOVA was performed instead of survival analysis, as survival was not tracked for individual seeds/seedlings. This was due to the large number of seeds used in the experiment (500

seeds were sown per subplot) and because some of the young seedlings may have been lost to insect or snail predation before they could have been detected at a census.

For three fleshy-fruited plant species, the influence of herbivory on seedling survival was investigated through Cox proportional hazards (Cox PH) semi-parametric models. The Cox PH model estimates the change in the hazard function  $h(t)$ , or in this case the risk of dying at time  $t$ . The hazard function is defined as:

$$h(t|X, \beta) = h_0(t)e^{X^T \beta}$$

where  $h(t|X, \beta)$  is the hazard rate conditional on covariates  $X$  and regression parameters  $\beta$ , with  $h_0(t)$  as the baseline hazard function. The hazard rate was estimated by using the survival times of the seedlings (i.e. the dependent variable). These data were interval censored (i.e. survival time is only known to occur between two observation times), so Turnbull's estimator was used to estimate the baseline hazard function. Turnbull's estimator, also known as the non-parametric maximum likelihood estimator, was used as it allows for interval censored data but it also kept the model semi-parametric (Anderson-Bergman 2017). For each species, a Cox PH model compared the survival of 100 seedlings excluded from mammal herbivory (reference group) to the survival of 100 seedlings open to mammal herbivory using the data collected from the three censuses. The replicates for each treatment were combined in this circumstance, as replication is not required for time-to-event analysis (McNair *et al.* 2012). Seedlings that did not die during the experiment were treated as right-censored observations, meaning that they could die at an unknown time after the experiment. Initial seedling height was included as a covariate in the model to determine if height had an influence on the survival of grazed seedlings. The significance of the covariates on seedling survival was estimated by using 200 bootstrapped samples of Turnbull's estimator. For the seedlings open to herbivory that were grazed by mammals, simple linear regressions were used to examine the relationship between initial seedling height and change in seedling height.

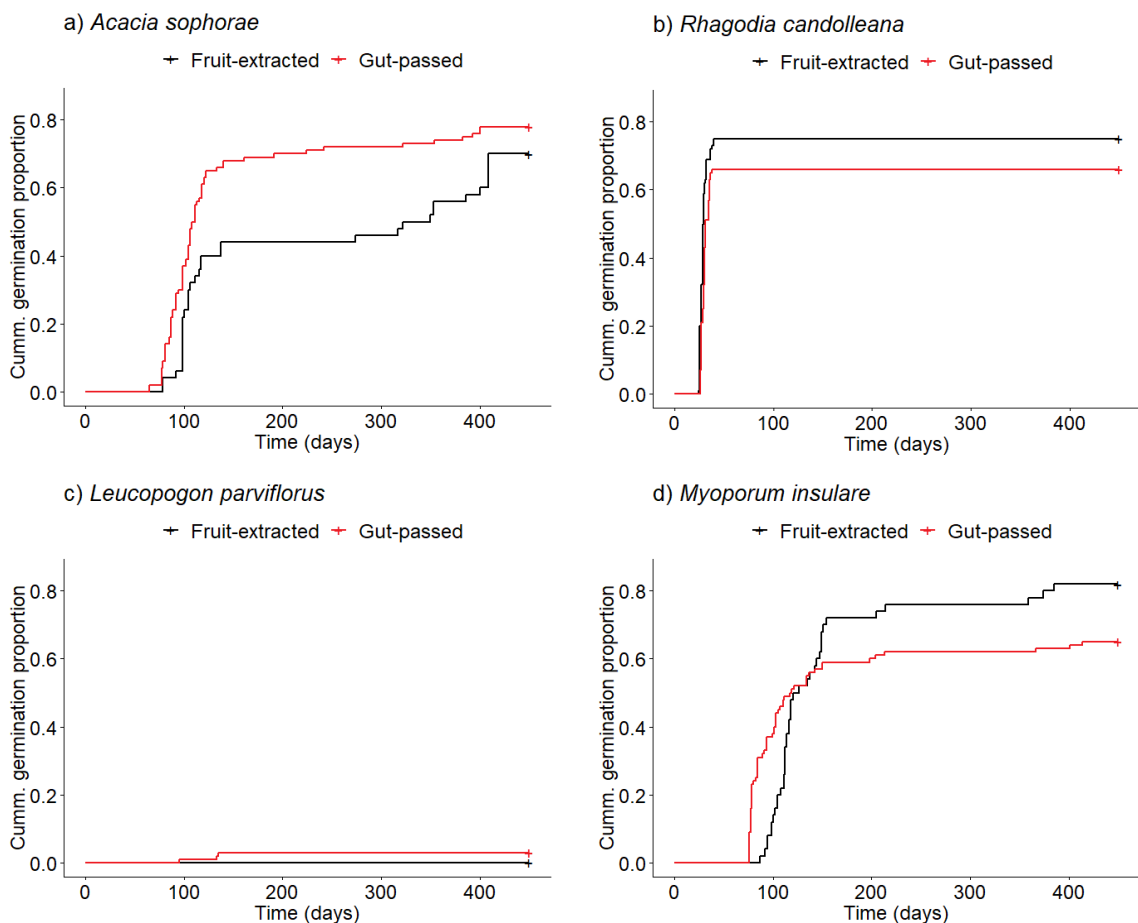
Survival analyses were performed with R 3.5.2 (R Core Team 2018). Kaplan-Meier curves were produced with the *survminer* package (Kassambara *et al.* 2018). Log-rank tests and Tarone-Ware tests that compared the Kaplan-Meier curves were conducted with the *survMisc* package (Dardis 2018). Cox PH models were produced with the *icenReg* package (Anderson-Bergman 2018). Two-way ANOVAs and linear regressions were performed in

Graphpad Prism 8.0.0 (GraphPad software, Inc). The level of significance in all tests was set at  $\alpha < 0.05$  and means were presented with standard error except where otherwise noted.

### 5.3 Results

#### 5.3.1 Seed germination in the glasshouse

Gut-passage was found to have a significant influence on the germination of *A. sophorae*, as the gut-passed seeds germinated significantly faster than fruit-extracted seeds (Fig. 5.2a, log-rank  $Z = 2.14$ ,  $P = 0.033$ ). Time taken to reach median germination ( $T_{50}$ , as obtained from the germination curve) for the gut-passed seeds was 109.5 days (95% CI = 104–118 days) while for the fruit-extracted seeds the time taken was 336 days (95% CI = 117–409 days).



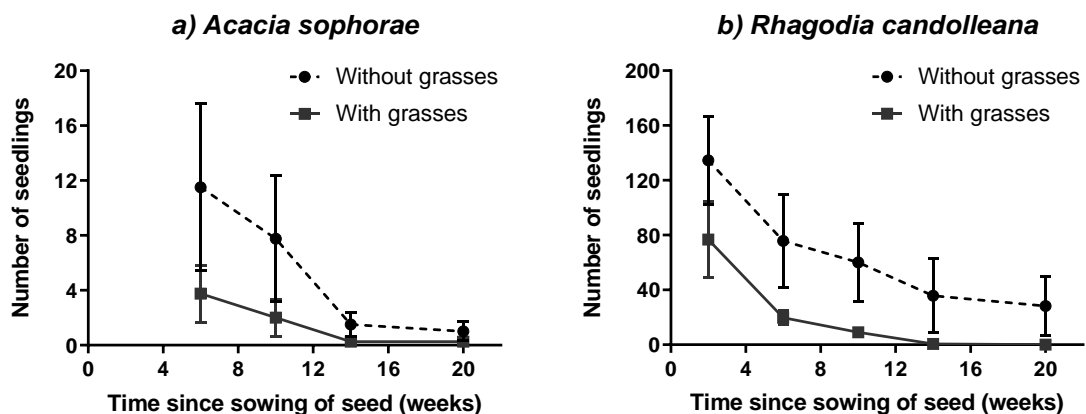
**Figure 5.2.** Cumulative germination proportion (1-Kaplan-Meier estimates) for seeds of a) *Acacia sophorae*, b) *Rhagodia candolleana*, c) *Leucopogon parviflorus* and d) *Myoporum insulare* that were passed through the gut ( $n = 100$  seeds) or were extracted from fruit ( $n = 50$  seeds). *Exocarpos syrticola* was excluded as this species did not germinate in either treatment. Seeds were germinated in an evaporatively cooled glasshouse over 450 days.

For *A. sophorae*, the final germination percentage was high for both gut-passed and fruit-extracted seeds (78% and 70% respectively) and did not differ significantly between the treatments (FET,  $P = 0.42$ ). Gut-passage was also found to have a significant influence on the germination of *R. candolleana*, although in contrast to *A. sophorae*, germination was significantly slower in the gut-passed seeds when compared to the fruit-extracted seeds (Fig. 5.2b,  $Z = -2.29$ ,  $P = 0.022$ ).  $T_{50}$  for the fruit-extracted seeds was 28.5 days (95% CI = 28–30 days), while for the gut-passed seeds the time taken was 31 days (95% CI = 30–35 days). For *R. candolleana*, the final germination percentage was high for both fruit-extracted and gut-passed seeds (75% and 66% respectively) and did not differ significantly between the treatments (FET,  $P = 0.22$ ).

In this experiment, the term 'seed' also referred to the woody stones of *L. parviflorus* and *M. insulare*, which potentially contain multiple seeds. For *L. parviflorus*, germination did not occur in fruit-extracted seeds and only 3% of the gut-passed seeds germinated. For this species, germination probabilities of gut-passed and fruit-extracted seeds did not differ significantly (Fig. 5.2c, log-rank  $Z = 1.23$ ,  $P = 0.22$ ) nor did the final germination percentage (FET,  $P = 0.55$ ). Gut-passage appeared to initially accelerate the germination of *M. insulare*. Overall, however, the germination probabilities of gut-passed and fruit-extracted seeds did not differ significantly (Fig. 5.2d, Tarone-Ware  $Z = 1.31$ ,  $P = 0.19$ ).  $T_{50}$  for the fruit-extracted seeds was 123 days (95% CI = 114–149 days), whereas the  $T_{50}$  for the gut-passed seeds was 118 days (95% CI = 103–204 days). For *M. insulare*, the final germination percentage was high for both fruit-extracted and gut-passed seeds (85% and 66% respectively) and did not differ significantly between the treatments (FET,  $P = 0.055$ ). In contrast to the other species, both gut-passed and fruit-extracted seeds of *E. syrticola* failed to germinate.

### 5.3.2 Effect of introduced grasses on seedling emergence and establishment

Emerged *A. sophorae* seedlings were first observed in the subplots with introduced grasses (control treatment) and the subplots without introduced grasses during the second census, which occurred 6 weeks after sowing (Fig. 5.3a). More seedlings were observed in the subplots without grasses, although overall, seedling emergence was low for both treatments (Fig. 5.3a). With 500 seeds sown per subplot, a mean of  $11.50 \pm 6.10$  seedlings were observed in the subplots with grasses, whereas a mean of  $3.75 \pm 2.10$  seedlings were observed in the subplots without grasses. Seedling recruitment was poor in both treatments, as very few seedlings were present at the end of the 20-week experiment (i.e. 14 weeks after the seedlings were initially observed). By this point, a mean of  $1.00 \pm 0.70$  seedlings were observed in subplots without grasses, whereas a mean of  $0.25 \pm 0.25$  seedlings were observed in subplots with grasses. Overall, the removal of introduced grasses had no significant effect on seedling emergence and recruitment (repeated measures two-way ANOVA,  $F(3, 18) = 1.342$ ,  $P = 0.29$ ).



**Figure 5.3.** The number of seedlings (mean  $\pm$  SE) recorded in subplots with introduced grasses and subplots cleared of introduced grasses ( $n = 4$  subplots per treatment) at Cantara for a) *Acacia sophorae* and b) *Rhagodia candolleana*. A total of 500 seeds were sown per subplot in early October 2016. Seedling abundance was recorded at 2, 6, 10, 14 and 20 weeks after the seeds were sown.

Emerged *R. candolleana* seedlings were first observed in both treatments during the first census, which occurred 2 weeks after sowing. After 500 seeds were sown per subplot, moderate amounts of seedlings (mean of  $134.5 \pm 32.48$ ) were observed in the subplots without grasses and low to moderate amounts of seedlings (mean of  $76.75 \pm 27.69$ ) were observed in the subplots with grasses (Fig. 5.3b). Both treatments observed declines in seedling abundance over time. Seedling recruitment was particularly poor in the plots with grasses, where no seedlings were found to survive at the end of the 20-week experiment (i.e.

18 weeks after the seedlings were initially observed). In comparison, a mean of  $28.25 \pm 21.29$  seedlings were observed in subplots without grasses at the end of the 20-week experiment. Overall, the removal of introduced grasses had no significant effect on seedling emergence and recruitment (Fig. 5.3b, repeated measures two-way ANOVA,  $F(4, 24) = 0.7070$ ,  $P = 0.60$ ).

### 5.3.3 Effect of herbivory on seedling survival

*Acacia sophorae* seedlings open to mammalian herbivory were at a significantly greater risk of dying when compared to the seedlings that were excluded from mammalian herbivory (Cox PH,  $P < 0.001$ , Table 5.1a). Within 7 weeks, 84% of *A. sophorae* seedlings exposed to mammals had died, whereas 31% of seedlings excluded from mammals had died. Mammals had grazed 95% of the *A. sophorae* seedlings that were exposed to mammalian herbivory, which resulted in the death of 83% of the seedlings (Table 5.2a). For the *A. sophorae* seedlings excluded from herbivory, 11% had died from desiccation and 20% had died from insect/snail herbivory (Table 5.2a).

**Table 5.1.** Cox proportional hazards semi-parametric models for a) *Acacia sophorae*, b) *Myoporum insulare* and c) *Rhagodia candolleana* seedling survival. The model shows the effect of herbivory treatment and initial seedling height on seedling survival time (i.e. the dependent variable). Seedlings excluded from mammalian herbivory were the reference group. Parameters given are: regression coefficient ( $\beta$ ; negative values indicate a reduced hazard rate and an increased survival time), standard error of  $\beta$ , hazard ratio ( $\text{Exp}(\beta)$ ), Z-score, and the significance of the regression coefficient (significant values are bold). Seedlings were deployed in the paddocks of Cantara in late August 2016 and mortality was monitored after 3, 5 and 7 weeks ( $n = 100$  seedlings per treatment).

Species/variable	Estimate $\beta$	Standard error of $\beta$	Hazard ratio $\text{Exp}(\beta)$	Z	P
a) <i>A. sophorae</i>					
Open to herbivory (ref: excluded)	2.847	0.465	17.24	6.125	<b>&lt;0.001</b>
Initial height	0.014	0.011	1.014	1.266	0.206
Initial height $\times$ Open to herbivory	-0.047	0.019	0.954	-2.527	<b>0.012</b>
b) <i>M. insulare</i>					
Open to herbivory (ref: excluded)	2.171	0.483	8.771	4.500	<b>&lt;0.001</b>
Initial height	-0.055	0.037	0.946	-1.499	0.129
Initial height $\times$ Open to herbivory	-0.915	0.049	0.900	-2.114	<b>0.034</b>
c) <i>R. candolleana</i>					
Open to herbivory (ref: excluded)	1.111	0.568	3.037	1.956	0.051
Initial height	0.002	0.015	1.002	0.163	0.871
Initial height $\times$ Open to herbivory	-0.043	0.025	0.958	-1.687	0.092

*Myoporum insulare* seedlings open to mammalian herbivory were also at a significantly greater risk of dying when compared to the seedlings that were excluded from mammalian herbivory (Cox PH,  $P < 0.001$ , Table 5.1b). Within 7 weeks, 46% of *M. insulare* seedlings exposed to mammals had died, whereas 20% of seedlings excluded from mammals had died. During this period, mammals had grazed 83% of the *M. insulare* seedlings that were exposed to mammalian herbivory, which resulted in the death of 44% of the seedlings (Table 5.2b). *Myoporum insulare* seedlings that were grazed by mammals demonstrated some regrowth. Within 5 weeks, resprouting occurred in 18% of grazed seedlings and within 7 weeks, resprouting occurred in 40% of grazed seedlings. This resprouting appeared to help the seedlings withstand and recover from grazing damage. For the *M. insulare* seedlings excluded from herbivory, 15% had died from desiccation and 5% died from insect/snail herbivory (Table 5.2b).

**Table 5.2.** The percentage of a) *Acacia sophorae* and b) *Myoporum insulare* and c) *Rhagodia candolleana* seedlings at each census that were damaged or dead under two grazing treatments: excluded from mammal herbivory and open to mammal herbivory. Seedlings were deployed in the paddocks of Cantara in late August 2016 and mortality was monitored after 3, 5 and 7 weeks ( $n = 100$  seedlings per treatment). Seedlings were classified according to their damage type: D = desiccated, I/S = grazed by insect/snail, M = grazed by mammal, O = other mammal damage (trampled, uprooted). Some individuals experienced several types of damage and thus fell under multiple classifications. Seedling death was attributed to the main cause of damage.

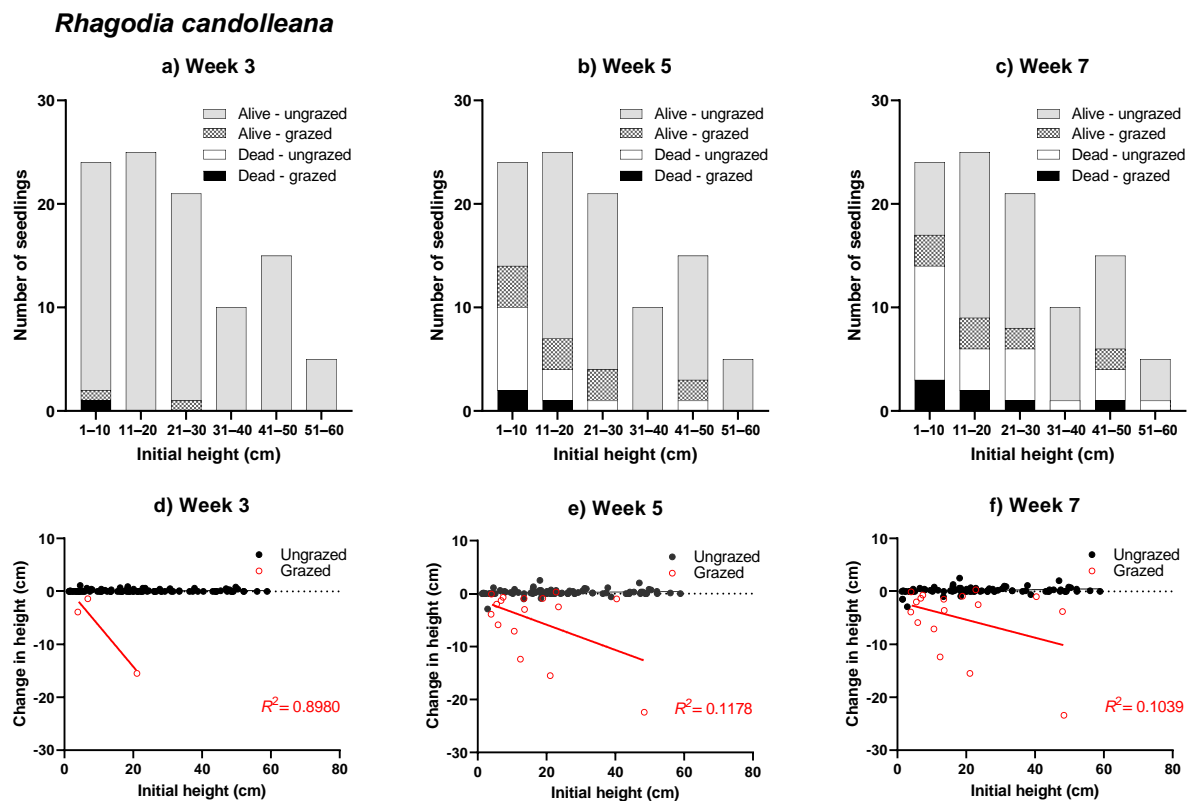
Damage class:	Damaged (%)						Dead (%)					
	Excluded		Open				Excluded		Open			
	D	I/S	D	I/S	M	O	D	I/S	D	I/S	M	O
a) <i>A. sophorae</i>												
Week 3	0	7	0	0	78	2	0	2	0	0	37	0
Week 5	3	32	1	1	92	2	3	6	0	0	78	0
Week 7	13	39	2	1	95	2	11	20	1	0	83	0
b) <i>M. insulare</i>												
Week 3	0	2	0	4	31	1	0	0	0	0	10	0
Week 5	9	6	0	4	77	6	6	3	0	0	33	0
Week 7	20	11	0	5	83	6	15	5	0	0	44	2
c) <i>R. candolleana</i>												
Week 3	3	0	1	0	3	2	1	0	0	0	1	0
Week 5	18	3	15	0	16	5	14	0	14	0	3	0
Week 7	31	5	31	0	17	5	24	2	26	0	7	0







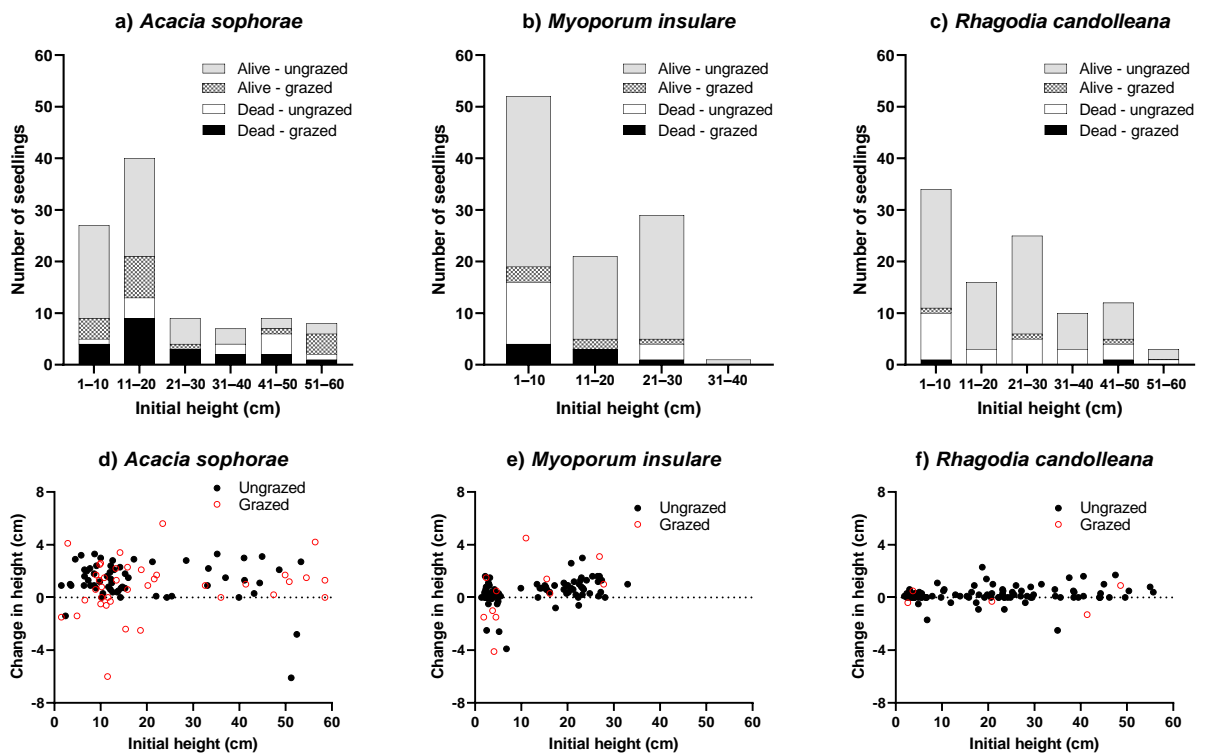
5.5). Most larger seedlings (>10 cm tall) had also been grazed, although appeared to have better survival, as they did not lose as much of their height to grazing. For seedlings of *R. candolleana*, there was no significant interaction between initial seedling height and grazing treatment (Cox PH,  $P = 0.092$ , Table 5.1c). After 7 weeks, many of the smaller seedlings (<10 cm tall) had died, although this was mainly the result of desiccation (Fig. 5.6).



**Figure 5.6.** For seedlings of *Rhagodia candolleana* that were open to mammal herbivory ( $n = 100$ ), a–c) the condition of seedlings from different height classes after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals, and d–f) initial seedling height versus change in seedling height after 3, 5 and 7 weeks for ungrazed seedlings and seedlings grazed by mammals. In d–f), simple linear regressions examined the relationship between initial height and change in height for seedlings that were grazed. Seedlings were deployed in the paddocks of Cantara in late August 2016.

For *A. sophorae* seedlings excluded from mammalian herbivory, the larger seedlings (>20 cm tall) did not appear to survive any better than the smaller seedlings (<20 cm tall) after 7 weeks, particularly as some of the larger seedlings died as a result of desiccation (i.e. dead and ungrazed, Fig. 5.7a). For *M. insulare* seedlings excluded from mammalian herbivory, seedling death was mostly observed in small seedlings (<10 cm tall) after 7 weeks following

desiccation, although some desiccation also occurred in larger seedlings (>20 cm tall, Fig. 5.7b). For *R. candolleana* seedlings excluded from mammalian herbivory, seedling death was observed throughout the range of height classes after 7 weeks, where desiccation was the main cause of death (Fig. 5.7c). The changes in height were relatively small after 7 weeks for many of the *A. sophorae*, *M. insulare* and *R. candolleana* seedlings that were excluded from mammalian herbivory, with most seedlings recording a slight increase in height (Fig. 5.7d–f). Each of the three species had seedlings which were grazed by insects or snails (particularly those of *A. sophorae*), although this grazing did not often appear to result in a reduction of seedling height. On average, the surviving *A. sophorae* seedlings that were excluded from herbivory had the greatest net growth in height ( $1.32 \pm 0.19$  cm), followed by *M. insulare* ( $0.58 \pm 0.09$  cm) and *R. candolleana* ( $0.25 \pm 0.07$  cm).



**Figure 5.7.** For seedlings of three species that were excluded from mammal herbivory, a–c) the condition of seedlings from different height classes after 7 weeks for ungrazed seedlings and seedlings grazed by insects or snails, and d–f) initial seedling height versus change in seedling height after 7 weeks for ungrazed seedlings and seedlings grazed by insects or snails. Seedlings ( $n = 100$  seedlings per species) were deployed in the paddocks of Cantara in late August 2016.

## 5.4 Discussion

### 5.4.1 Seed germination in the glasshouse

From the seeds that were extracted from fruit, those of *E. syrticola* and *L. parviflorus* experienced the greatest germination difficulty. These species have complex germination requirements (e.g. depend on temperature stratification and fire cues) and display morphophysiological dormancies (Dixon *et al.* 1995; Bell 1999; South Australian Seed Conservation Centre 2016), which likely accounted for their very low rates of germination. In addition, seeds of *L. parviflorus* can also suffer from poor development and seed fill (South Australian Seed Conservation Centre 2016). In comparison, *A. sophorae* and *M. insulare* fruit-extracted seeds germinated more readily, and their final germination percentages were high (70% and 66% respectively after 14 months). Their seeds germinated after 2 months, which indicated that some dormancy had occurred (Baskin and Baskin 2004). *Myoporum insulare* seeds are thought to have physiological dormancy (Guja *et al.* 2010), whereas *Acacia* seeds typically experience physical dormancy (Baskin and Baskin 1998). From the species tested, *R. candolleana* fruit-extracted seeds appeared to have the least difficulty germinating, as 75% of their seeds germinated and most of this germination occurred within 30 days. This germination time would suggest the species lacks dormancy, although physiological dormancy is known to occur in other species of *Rhagodia*, including *Rhagodia preissii* and the closely related *Rhagodia baccata* (Guja *et al.* 2010; Nichols *et al.* 2014). There is potential that the *R. candolleana* seeds were physiologically dormant at collection but this dormancy was relieved during the 3-month storage prior to the germination tests (Bewley *et al.* 2012). In general, there is potential that a few of the seeds from each of these species may have died during storage, which may have effected germination probabilities. The storage behaviour of seeds from most Australian species is unknown, although the viability of seeds collected for this experiment was unlikely to be greatly reduced during the short storage time and under the dry storage conditions (Sweedman and Merritt 2006; Commander 2008). Furthermore, Seeds from Australian shrubs also tend to be longer-lived than seeds from other life forms (Ooi *et al.* 2007; Merritt 2014).

The passage of the seed through the bird gut only significantly accelerated the germination of *A. sophorae*. Gut passage was able to enhance the germination of *A. sophorae* by breaking its physical dormancy (i.e. scarifying the seed coat, making it permeable to water and gases) but did not break the physiological dormancies experienced by the other species,

which were likely caused by conditions within the embryo itself (Traveset 1998). In contrast to *A. sophorae*, gut-passage significantly reduced the germination probability of *R. candolleana* seeds. This may have been due to their small size (<3 mm), as small seeds are generally retained in the gut longer than large seeds and thus are more likely to be excessively abraded (Verdú and Traveset 2004). Whether the small *R. candolleana* seeds were retained in the gut for longer, however, can only be confirmed through gut-retention experiments.

While gut passage influenced the timing of germination for two species during the observed time course, it had no effect on the final germination percentages of all species tested. Of course, birds may influence seed germination through means beside gut-passage, including through the removal of pulp (Samuels and Levey 2005; Logan and Xu 2006), which the glasshouse experiments did not consider. Furthermore, the glasshouse experiments also only tested the influence that one bird species (the silvereye) had on germination response. The influence of gut passage on seed germination, however, can vary between bird species following differences in seed retention time (Traveset 1998; Traveset *et al.* 2001). While not considered in the glasshouse experiments, there was also potential that the germination responses varied between individual plants or plant populations, which occurs when there are differences in seed traits, such as seed coat thickness or seed size (Traveset 1998; Rodríguez-Pérez *et al.* 2005). Additionally, the application of germination rates observed in the glasshouse experiments to the context of the field is limited, as the experiments did not replicate the likely field conditions experienced, such as temperature and water availability, which have an influence on germination. Future experiments will need to consider assessing germination rates under the conditions experienced in the field, where germination rates may be much lower. Lastly, future studies will likely need to conduct germination experiments with larger sample sizes to confirm the results observed, particularly as germination was difficult to observe for species with complex germination requirements such as *E. syrticola* and *L. parviflorus*.

#### 5.4.2 Effect of introduced grasses on seedling emergence and establishment

The removal of introduced grasses has improved native seedling establishment in several Australian studies of old fields (e.g. Hobbs and Atkins 1991; Yates *et al.* 2000; Standish *et al.* 2008), although no significant benefits were observed for seedlings of *A. sophorae* and *R. candolleana* at Cantara. This was perhaps due to the condition of the soil at Cantara, as well as the harsh conditions that occur in the Younghusband Peninsula during summer,

when the seedlings were attempting to establish. The sandy carbonate soils present in Cantara have poor water-holding capacity, limiting the moisture available for seedlings. The soil moisture is further reduced in summer, when temperatures are high and dry sand-laden winds tend to be frequent (Bennett and Hails 1981; Barron and Dalton 1996). These conditions are particularly challenging for seedlings that are attempting to establish in the presence of introduced grasses (e.g. as they compete with the grasses for soil moisture; Barron and Dalton 1996; Standish *et al.* 2008), but even those that are trying to establish in these soils in the absence of competition from introduced grasses may struggle from the harsh conditions of summer.

#### 5.4.3 Effect of herbivory on seedling survival

During spring, herbivorous mammals were found to significantly increase the risk of mortality for two species: *A. sophorae* and *M. insulare*. From the seedlings that were exposed to mammalian herbivory, those belonging to *A. sophorae* were the most quickly grazed by mammals (95% grazed within 7 weeks), which resulted in the death of 83% of *A. sophorae* seedlings. Comparably, *M. insulare* seedlings were not as quickly grazed (83% grazed by mammals within 7 weeks). Fewer *M. insulare* seedlings died as a result, with 44% dead from mammalian grazing within 7 weeks. Greater survival in *M. insulare* seedlings may have also been due to its ability to resprout, which allowed some seedlings to recover from the grazing. The ability for resprouting to improve seedling survival has been observed in other species in Australia, including *Eucalyptus albens* and *Diploglottis diphylostegia* (Osunkjoya *et al.* 1992; Allcock and Hik 2004). For *A. sophorae* and *M. insulare* seedlings open to mammalian herbivory, the risk of mortality significantly decreased as the initial height of a seedling increased. Smaller seedlings had poorer survival as they were wholly grazed more quickly than the larger seedlings. Mammals did not frequently graze the exposed seedlings of *R. candolleana* (17% grazed within 7 weeks), which suggests that they were not as favoured as the other species. As a result, the survival of *R. candolleana* was not significantly limited by mammalian grazers. In Australia, there are several other species of *Rhagodia* that appear to escape heavy grazing by mammalian herbivores (sheep, rabbits, goats, kangaroos), including *Rhagodia parabolica*, *Rhagodia eremaea* and *Rhagodia spinescens* (Tiver *et al.* 2008).

The mammalian grazers of the three plant species were not determined in this study, although they may have included rabbits, western grey kangaroos, common wombats, and deer, as they were all observed at Cantara. For seedlings of *A. sophorae*, western grey

kangaroos were perhaps the primary suppressors of seedling recruitment. In south-eastern Australia, *A. sophorae* was commonly detected in the diets of eastern grey kangaroos (*Macropus giganteus*) and swamp wallabies (*Wallabia bicolor*) but was not commonly observed in the diet of rabbits or common wombats (Davis *et al.* 2008). In contrast, seedlings of *M. insulare* are thought to be highly palatable to rabbits (Gillham 1963; Cooke and McPhee 2007). Additional experiments are likely required to identify the specific grazers of the fleshy-fruited species in the Youngusband Peninsula, particularly as there tends to be a high degree of overlap in food use between rabbits, kangaroos and wombats (Davis *et al.* 2008; Mutze *et al.* 2016). Additional experiments will also be required to determine seedling survival in other seasons, particularly in summer and autumn, when grazing intensity would be expected to be higher (and seedling survival lower) due to the lack of other green feed (Cooke 1987; Martin *et al.* 2007).

For the most part, the seedlings that were excluded from mammalian herbivory grew in height. After 7 weeks, the surviving seedlings of *A. sophorae* on average had the greatest net growth in height when protected from mammalian herbivores (1.32 cm), followed by the seedlings of *M. insulare* (0.58 cm) and *R. candolleana* (0.25 cm). While the seedlings of each of these species were protected from grazing mammals, they were unable to escape grazing damage caused by insects or snails. One of the main grazers of these seedlings may have been the introduced snail *Theba pisana*, as it was often observed on the seedlings. The impact that these snails have on Australian native flora is largely unknown (Clarke *et al.* 2000), although they are problematic for some coastal native species in South Africa, another country in which they have been introduced (Odendaal *et al.* 2008; van Elden *et al.* 2015). The damage caused by the snails may have contributed to seedling death, although clearly, they do not have the same level of impact as the mammalian grazers.

#### 5.4.4 Likelihood of germination and recruitment beneath artificial perches

Following seed deposition beneath the artificial perches, germination could be most anticipated for species such as *M. insulare*, *A. sophorae*, and *R. candolleana*, as they have simpler germination requirements and higher short-term germination potentials. Enhanced germination would be expected for *A. sophorae* following passage through the bird gut, although whether this translates to an increase in plant fitness (e.g. survival, growth) can only be determined by comparing the fate of seedlings establishing from ingested and un-ingested seeds (Traveset 1998). Germination beneath the perches appears less likely for



species with complex dormancies and poorer initial germination rates, such as *L. parviflorus* and *E. syrticola*.

The germination potentials of the fleshy-fruited species considered in this chapter were determined through experiments that were conducted in the glasshouse. Although in the field, there are many more factors that would influence germination and emergence. For example, seeds that are deposited intact under the perches must survive post-dispersal predation in order to germinate. At Cantara, such predation may occur from several types of insect, including moth larvae (Paton 2010) and ants (Berg 1975; Andersen and Ashton 1985). Assuming that seeds are able to enter the soil, they would then need to overcome stressful microclimatic conditions to germinate (Holl *et al.* 2000). This would include the stressful conditions induced by introduced grasses, which are able to deplete soil moisture (Standish *et al.* 2008). Even if the seeds deposited beneath the perches were able to overcome numerous limitations to germinate, the emerged seedlings would be unlikely to recruit given the high levels of herbivory, coupled with likely competition from introduced grasses and moisture stress in summer. These factors combined are likely to prevent plant recruitment for most fleshy-fruited species at Cantara. While not explored in this chapter, significant competition for resources would have also existed between the seeds that were deposited under the artificial perches at Cantara, particularly since the density of seed falling beneath each perch was high (Chapter 4; Schupp 1993).

Recruitment beneath artificial perches could be improved through the use of additional treatments, which would aim to reduce the effects of these different recruitment barriers. For example, herbicide can be applied to reduce the effects of competition with introduced species (Elgar *et al.* 2014) and fencing has been used to prevent herbivory by mammalian herbivores (Cooke 1987; Martínez-López *et al.* 2019). Similar treatments could be used at Cantara to enhance plant recruitment beneath perches, although these would have to be applied with consideration for the local conditions. At Cantara, the most logical approach in deploying artificial perches and supporting treatments for vegetative restoration may be to: 1) fence out herbivores in areas targeted for restoration, 2) spray and reduce introduced grasses and other non-native ground-dwelling plants within the fenced areas, 3) slash the adjacent grassy areas to reduce seed release and reinvasion into fenced areas, 4) use a dense array of artificial perches to allow seed to be deposited in many areas, and 5) water areas beneath the artificial perches to promote germination and establishment. The suppression of introduced grasses appeared necessary in the management regime, as there is considerable

evidence from studies conducted within temperate systems in Australia to suggest that such control can significantly improve the establishment of native woody seedlings (Hobbs and Atkins 1991; Barron and Dalton 1996; Knight *et al.* 1997; Yates *et al.* 2000; Standish *et al.* 2008). As a result, continued management of introduced grasses in the areas around the artificial perches may also be required to minimise competition for any seedlings that start to emerge. A perch could then be shifted once a seedling or two has established underneath it. A similar approach would be required if seedlings were grown and planted out instead of the deployment of artificial perches. Some assessment may be required to determine the cost-effectiveness and potential restoration outcomes associated with each approach.

## **5.5 Conclusion**

In conclusion, the results of this chapter suggest that artificial perches in the Younghusband Peninsula, despite having the capacity to increase seed dispersal, are unlikely to facilitate the recruitment of fleshy-fruited plant species on their own. This was due to the presence of multiple recruitment barriers, including poor germination, harsh establishment conditions during summer and high levels of grazing. This study then adds to the list of other studies of artificial perch use that have experienced limited recruitment because of post-dispersal barriers (e.g. Holl *et al.* 2000; Shiels and Walker 2003; Graham and Page 2012; Heelemann *et al.* 2012; de Almeida *et al.* 2016). If artificial perches are to be deployed to facilitate seed dispersal in cleared and degraded areas along the Younghusband Peninsula, then additional treatments will be required to secure the recruitment of fleshy-fruited plants beneath the perches. This at the very least includes a treatment which prevents herbivory and likely also a treatment that reduces the competitive effects of introduced grasses.

## Chapter 6. General discussion

### 6.1 Summary of findings

This thesis aimed to determine the effectiveness of artificial perches in aiding the regeneration of cleared and degraded coastal environments, which were located on the Younghusband Peninsula, South Australia. Their potential effectiveness was assessed by documenting the frequency in which seed-dispersing birds used the perches, by measuring the quantities of seed rain that fell beneath the perches and by considering the potential for subsequent plant recruitment beneath the perches.

The artificial perches attracted nine seed-dispersing bird species, none of which were obligate frugivores but rather consumed fruit as part of their diet (Chapter 3). Over the period of peak fruit availability (summer and autumn), the seed-dispersing species that most frequently visited the perches were the spiny-cheeked honeyeater (*Acanthagenys rufogularis*) and the singing honeyeater (*Lichenostomus virescens*). The honeyeaters were important visitors to the perches, as they were capable of dispersing seed regularly but also capable of dispersing seed from at least 13 of the local native fleshy-fruited plant species.

The seed-dispersing birds that rested on the artificial perches evidently used them as a place to void seed, as seeds from fleshy-fruited species were found in seed traps set beneath the perches (Chapter 4). Following 12 months of measurements, the artificial perches were found to effectively enhance the dispersal of seed in the degraded site, as the quantities of seed arriving beneath the perches were significantly greater than the quantities arriving in open areas in the paddocks. Importantly, large quantities of seeds from native plants were deposited under the perches, great enough to suggest that some germination could occur in due course. In all, seeds from up to 13 native species were recorded in seed traps beneath the perches. Importantly this included seeds from shrubs which are capable of establishing in degraded environments, such as *Myoporum insulare* and *Acacia sophorae*. The establishment and maturation of such shrubs beneath the perches would have been ideal for revegetation processes, as they in turn can facilitate the establishment of other species beneath their crowns, thereby further promoting regeneration (Chapter 4; Croft *et al.* 2006; Heyligers 2009). Although to the detriment of restoration, the seed traps beneath the perches also accumulated large numbers of seeds from the introduced shrub *Lycium ferocissimum*, which was likely due to its presence in the degraded site. This result suggested that artificial perches have the potential to facilitate the spread of introduced species in degraded areas.

Thus, it may not be appropriate to deploy artificial perches in sites with introduced fleshy-fruited species unless some form of control is carried out beforehand.

While many seeds were deposited beneath the artificial perches, very few of these were likely to establish either because of low germination rates, harsh establishment conditions or grazing by herbivores (Chapter 5). This was particularly true for species with complex germination requirements and low initial germination rates, such as *Leucopogon parviflorus* and *Exocarpos syrticola*. Germination difficulties were not experienced by *Rhagodia candolleana*, *M. insulare* and *A. sophorae* but recruitment for the latter two species was hindered by grazing. Although not clearly demonstrated in this study, there was potential that introduced grasses also limited the establishment of native seedlings at Cantara (Chapter 5). This is because there is considerable evidence to suggest that this limitation occurs in temperate Australia, particularly in disturbed habitats or abandoned agricultural lands (Hobbs and Atkins 1991; Barron and Dalton 1996; Knight *et al.* 1997; Yates *et al.* 2000; Standish *et al.* 2008). The control of recruitment barriers will be necessary if artificial perches are to be used as a restoration tool in the cleared and degraded areas of the Youngusband Peninsula.

In general, some of the findings arising from this study were limited by the low numbers of replicates and sample sizes used in some experiments. This would have decreased the statistical power of the experiment, thereby increasing the risk of rejecting a significant effect. Future studies will need to avoid a similar shortcoming by ensuring that the study design has adequate statistical power. This would then increase the confidence that can be placed into the conclusions drawn from the study.

## **6.2 Limitations with artificial perches and recommendations for future research**

### *6.2.1 Overcoming post-dispersal barriers*

In order to improve the effectiveness of artificial perches as a restoration method, future research should address some of the limitations that occurred in this study and other studies of artificial perch use (e.g. Holl *et al.* 2000; Shiels and Walker 2003; Bustamante-Sánchez and Armesto 2012; Graham and Page 2012). The primary limitation found in the Youngusband Peninsula, and in many other studies, is that the seedling recruitment beneath artificial perches is unlikely to occur as a result of difficult establishment conditions (e.g. seedling competition with introduced grasses, grazing pressure from herbivorous mammals). Thus, in many cases, additional interventions (e.g. herbicide application,

exclusion fencing) will likely be necessary to greatly increase the likelihood of successful establishment of fleshy-fruited plants across degraded areas. This would firstly require the identification of the recruitment barriers present in the sites targeted for restoration. Small-scale experiments may then be necessary to determine the most effective combination and application of treatments before restoration works are implemented over a larger scale (Holl *et al.* 2000).

#### 6.2.2 Evaluation of bird and plant species before perch deployment

Apart from the presence of recruitment barriers, artificial perches have shown limited potential as a restoration tool when the fleshy-fruited species desired for regeneration (i.e. native species from areas of remnant vegetation) are not dispersed to the perches. This can occur when seed-dispersing birds fail to move out of areas of remnant vegetation to visit the perches but may also occur when the birds that use the perches predominantly reside within the degraded site and thus fail to disperse seed from areas of remnant vegetation (Holl 1998; Graham and Page 2012). Restoration may also be limited when species that are not desired for regeneration, such as introduced fleshy-fruited species, are abundantly dispersed to the perches. This occurs when these species form a common part of the vegetation present in the degraded site or occur in close proximity to the perches (Chapter 4; Prather *et al.* 2017).

Artificial perches could be used more successfully for restoration if greater efforts were made prior to perch deployment to 1) determine the bird and plant species likely involved in the seed dispersal process and 2) consider their ability to facilitate restoration. In regards to birds, their ability to facilitate restoration will primarily depend upon their ability to disperse seed from areas of remnant vegetation to the artificial perches. This of course is influenced by their willingness to enter and rest in the degraded site. Several studies have indicated that habitat specialists or specialist frugivorous birds are unlikely to enter degraded habitats (Da Silva *et al.* 1996; Wunderle 1997; Moran 2007). Thus, it may be unwise to expect such species to deposit seed at the artificial perches, at least in tropical rainforest ecosystems, where there are often many strong habitat specialists (Wunderle 1997). Habitat generalists and generalist fruit consumers on the other hand appear to be far more frequent facilitators of seed dispersal at artificial perches (e.g. Chapter 2, Zanini and Ganade 2005; Vicente *et al.* 2010; Athiê and Dias 2016; Vogel *et al.* 2018; Freeman *et al.* 2021), as these birds opportunistically move into open and degraded areas to forage (Wunderle 1997; Moran 2007; Carlo and Morales 2016). In the temperate ecosystem of the Younghusband Peninsula, generalist frugivorous birds were required to carry out seed dispersal to artificial

perches, as only one obligate frugivorous bird occurs in the region. These birds, however, were useful dispersers as they were able to disperse seed to all of the artificial perches, including those that resided far from the remnant vegetation (furthest perch resided ~250 m away; Chapter 4). They also appeared to disperse some seed over moderate distances from the remnant vegetation (at least 150–200 m, Chapter 4), which was important as birds tend to disperse most seeds over short distances of less than 100 m from the parent plant (Debussche and Isenmann 1994; Wunderle 1997).

Besides their willingness to enter degraded areas, some generalist bird species have been shown to be important dispersers by dispersing seed regularly and by dispersing seed from a variety of plant species. In the Younghusband Peninsula, such dispersers include the singing honeyeater and the spiny-cheeked honeyeater, as they frequently disperse seed and are both capable of dispersing seeds from at least 13 native species each (Chapter 2, Chapter 3). Generalist frugivorous birds, however, are often responsible for the invasion of introduced fleshy-fruited plant species (Stansbury and Vivian-Smith 2003; Ramaswami *et al.* 2016; Bitani *et al.* 2020). Introduced plant species that have fruits adapted for generalised dispersal can be consumed by many bird species, who then disperse seeds to a large variety of habitats, including into disturbed or degraded areas (Izhaki *et al.* 1991; Renne *et al.* 2002; Noble and Adair 2014; Bitani *et al.* 2020). This was evident in the Younghusband Peninsula, where generalist frugivorous birds were responsible for the abundant dispersal of *L. ferocissimum* to artificial perches (Chapter 4). Some generalist frugivorous birds may also be less useful dispersers in tropical climates, where they can be restricted in the types of seed that they disperse (e.g. some cannot disperse large seeds, Pillatt *et al.* 2010; Graham and Page 2012). Although, this may not necessarily be a problem for restoration if the birds are at least able to disperse seeds from a few species that have the potential to initiate regeneration. If some vegetation is able to establish at the perches, then a greater diversity of seed-dispersers may be enticed to eventually enter the degraded site.

The willingness of birds to visit and disperse seed to artificial perches will likely also be influenced by the availability of food resources and the structural complexity of the vegetation within the disturbed or degraded area (McDonnell and Stiles 1983; Wunderle 1997; de Almeida *et al.* 2016). In the Younghusband Peninsula, scattered fleshy-fruited shrubs appeared to facilitate the movement of seed-dispersing birds into and throughout the degraded site (pers. obs.), likely because the shrubs acted as a source of food (e.g. fruit, insects) but also provided some cover from predators (Bustamante-Sánchez and Armesto

2012; Elgar *et al.* 2014; Athiê and Dias 2016). In contrast, birds appear less inclined to visit and disperse seed to perches in disturbed areas that are largely devoid of woody plants, particularly if the site contains few food resources (McDonnell and Stiles 1983; Da Silva *et al.* 1996). In sites such as these, fewer seeds may arrive at perches that are placed far (>150–200 m) from remnant vegetation, as they reside further from the source of seed (McDonnell and Stiles 1983; McClanahan and Wolfe 1993; Athiê and Dias 2016). Furthermore, frugivorous birds may be unwilling to venture too far in sites devoid of vegetative cover, as such movements would increase their exposure to predators (McDonnell and Stiles 1983; Elliott *et al.* 2013). For degraded sites devoid of woody vegetation, artificial perches may initially need to be placed in areas that are adjacent to existing native vegetation. Following the establishment of some vegetation, the perches could then be deployed further into the degraded site. Alternatively, a series of structurally complex perches need to be deployed out into the cleared areas where the complexity of the perches affords effective cover to the birds that use them.

In regards to fleshy-fruited plant species, their ability to facilitate regeneration at the artificial perches will depend upon their life history traits, such as their life form. During the initial stages of regeneration, the dispersal of life forms such as shrubs and trees will be more beneficial than the dispersal of other life forms such as herbs or climbers. This is because if trees and shrubs are to establish and mature at the artificial perches, then they themselves can act as perches, further enhancing bird movement and seed dispersal in the degraded site. Furthermore, mature shrubs and trees may help to facilitate the emergence and survival of other species by ameliorating the local conditions (e.g. improving soil fertility, shading out competitive grasses; Toh *et al.* 1999; Gómez-Aparicio *et al.* 2005; Gómez-Aparicio 2009). Shrubs in particular are important facilitators of seedling recruitment, as observed in temperate coastlines in Australia (Croft *et al.* 2006; Heyligers 2006), semiarid shrublands in South Africa (Blignaut and Milton 2005) and montane forests in Spain (Gómez-Aparicio *et al.* 2005). In some systems, shrubs are not as strong competitors as other life forms for resources (e.g. ground water, light), allowing the benefits of facilitation to be received by plant neighbours at a small cost in regards to competitive effects (Gómez-Aparicio 2009).

Some consideration should also be given to the ability of the fleshy-fruited species to arrive and establish in the degraded site, as those with the most potential will be relied upon to initiate regeneration processes. For example, in the Youngusband Peninsula the dispersal

of seeds from the shrubs *M. insulare*, *A. sophorae*, and *R. candolleana* to perches was important, as these hardy species would have been most capable of germinating in the degraded site (Chapter 5). Importantly, if some seedlings of these species were able to establish, then they in turn would have promoted the eventual establishment of other species, including climbers and shade-tolerant shrubs (Forde 1986; Croft *et al.* 2006; Heyligers 2009). There was considerable potential for seeds from *M. insulare*, *A. sophorae*, and *R. candolleana* to arrive at the artificial perches, as these species occurred in small amounts in the degraded site (consistent with being early colonisers) and occurred more abundantly in the nearby remnant vegetation. Furthermore, the seeds of these shrubs are dispersed by a range of bird species, including common seed-dispersing birds such as the singing honeyeater and spiny-cheeked honeyeater (Chapter 2, Chapter 3). These factors when combined ultimately allowed large amounts of seed from the three shrub species to accumulate beneath the perches (Chapter 4).

Lastly, the potential for fleshy-fruited species to facilitate regeneration beneath artificial perches will depend upon their origin. As observed in the Younghusband Peninsula, subtropical North America and in tropical Brazil, introduced species can dominate the seed rain being deposited beneath the perches and thus undermine restoration efforts (Chapter 4; Athiê and Dias 2016; Prather *et al.* 2017). For the Younghusband Peninsula, the dispersal of the introduced species *L. ferocissimum* to artificial perches was concerning given its ability to exclude native vegetation and degrade fauna habitat (Noble *et al.* 2013; Weber 2017). Similarly, the abundant dispersal of *Tridacia sebifera* to artificial perches in tallgrass prairies on the Gulf Coast of the United States was problematic, as this species aggressively invades grassland ecosystems (Prather *et al.* 2017). These results have demonstrated that introduced fleshy-fruited species may need to be controlled in the sites targeted for restoration before artificial perches can be deployed.

### *6.2.3 Considerations for practical implementation*

Another short-coming arising from studies of artificial perches is the lack of consideration towards the practical implementation of the restoration method, especially in cases where the method has been recommended for potential use (e.g. Athiê and Dias 2016; Ferreira and de Melo 2016). There are several scientific and practical considerations that need to be addressed if artificial perches are to be deployed on a large-scale for restoration. Firstly, as discussed in Chapter 4, there needs to be consideration towards the number of perches required for restoration. Practitioners could expect to deploy large numbers of perches to



ensure that seed deposition, and in turn regeneration, could potentially occur over many areas in the degraded site. Many perches may also need to be erected or continually shifted to reduce the density of seed being deposited beneath each perch. Having large numbers of seeds deposited at the one place may not be ideal for restoration if it results in competition between the potentially many germinants. Consideration should also be given to the design of the perch. As shown at Cantara, perches of simple design can effectively attract seed-dispersing birds and facilitate seed dispersal, although they are unable to assist with seedling recruitment as they do not ameliorate the local conditions (Chapter 3, Chapter 4, Chapter 5). As observed in studies elsewhere, perches of complex design (e.g. branch piles) can potentially assist seedling recruitment by creating favourable soil conditions (through the provision of shade and the accumulation of litter) and by providing seedlings with some protection from herbivores (McLaughlin 2013; Castillo-Escrivà *et al.* 2019). Once the number of perches required has been estimated and the optimal perch design has been determined, researchers and practitioners could then focus on addressing other limiting factors, such as whether treatments are also required to help overcome recruitment barriers, and if so, how these treatments should be applied. The restoration works would be carried out best with an adaptive management approach, where monitoring would inform the following steps in the restoration process, including any additional or modified actions. This approach allows resources to be used more efficiently and ensures that restoration goals can be more successfully met (Hobbs *et al.* 2007).

Secondly, a cost-benefit analysis could also be conducted to determine the feasibility of artificial perch deployment. In the Youngusband Peninsula, 2.5–2.8 m tall perches were erected (similar height as mature coastal shrublands, typically 2–4 m tall), which consisted of a dead branch wired to a metal stake. The cost per perch for materials was low (approximately \$10 AUD each in 2014) as the branches were sourced from dead vegetation next to the degraded area. Although, these perches were not particularly robust as they began to degrade after 1–2 years (Chapter 4). While the cost per perch was relatively low, additional costs would be expected in terms of labour and possible ongoing management. Another important aspect that could be considered is the number and size of the areas that require restoration, which determines the potential economies of scale (Armsworth *et al.* 2011). Some assessment could also be given to the feasibility of artificial perches when compared to other assisted natural regeneration methods, as they could prove to be more suitable in terms of ongoing costs and associated outcomes. Although, as pointed out by

Shoo and Catterall (2013), this comparison may be difficult given the lack of cost and long-term outcome reporting that occurs in studies of assisted natural regeneration.

Lastly, when scaling up restoration efforts from small-scale studies such as this one, it is important to consider whether the practical recommendations arising from the study can be generalised and applied throughout the region targeted for restoration. Some studies have indicated that such generalisations may not be practical if the degraded sites within the region differ in their environmental conditions (e.g. soil type, elevation, land-use history etc.), as these conditions are able to influence restoration trajectories and rates of restoration (Holl *et al.* 2000; Bustamante-Sánchez and Armesto 2012; Zahawi *et al.* 2013; Elgar *et al.* 2014). In this study, the use of artificial perches was limited to a single site in the coastal shrublands Youngusband Peninsula and so the potential effectiveness of this restoration tool in other degraded shrubland areas of the region was not determined. Although, many of these degraded areas could be anticipated to be in similar condition as they have undergone an identical land use history (i.e. short-term agricultural attempts) and have experienced the same pressures from introduced animal and plant species (Butcher and Rogers 2013).

#### *6.2.4 Alternatives to artificial perches*

As noted in several studies, future research and practice may be best focused towards the use of natural perches as dispersal and recruitment foci in degraded areas (Zanini and Ganade 2005; Graham and Page 2012; Zwiener *et al.* 2014; Freeman *et al.* 2021). Scattered plantings of trees and shrubs in such areas, planted either singly or in clumps, can eventually provide natural perches for frugivorous birds (often known as applied nucleation techniques). Such plantings would take several years to establish. However, this investment may be worthwhile as natural perches have been shown to effectively facilitate seed dispersal (e.g. Elgar *et al.* 2014; Zwiener *et al.* 2014). This was observed in the abandoned paddocks of Cantara on the Youngusband Peninsula, where the density of seed rain recorded beneath paddock shrubs was considerably greater than the density of seed rain recorded in the open (Chapter 4).

Importantly, natural perches allow for the outwards expansion of vegetation, as the seeds that are dispersed near the crown germinate and establish and/or as the vegetation spreads out clonally (Cole *et al.* 2010). Natural perches are able to facilitate plant recruitment by ameliorating the local conditions and by creating an environment more conducive for seedling recruitment. They do this by suppressing competitive grasses, increasing nutrient

availability and by maintaining lower soil temperatures, which in turn helps to prevent the evaporative loss of soil water (Holl *et al.* 2000; Shumway 2000; Elgar *et al.* 2014; Zwiener *et al.* 2014). Natural perches may also enhance water availability through hydraulic lift, where water from deep soil layers are taken up by root systems and then transported and released into shallow soil layers (Prieto *et al.* 2011). In comparison, artificial perches are unable to provide such facilitative conditions until some vegetation has established beneath them (Graham and Page 2012). Although, Toh *et al.* (1999) point out that the conditions that occur beneath natural perches may only benefit some seedlings. In their study, conducted in abandoned farmlands in southern Queensland, large numbers of seedlings were found to establish beneath a tree, although only a small proportion of the seedlings survived to maturity following competition within or near the plant crown.

As discussed in Chapter 4, natural perches could potentially be used to promote regeneration in the temperate coastal environments of Australia. For example, in the Younghusband Peninsula, large fleshy-fruited shrubs such as *A. sophorae*, *M. insulare* and *L. parviflorus* are effective facilitators of seed dispersal (Chapter 4; Paton 2010). They also promote the recruitment of many other fleshy-fruited species (e.g. climbers, shade-tolerant herbs and subshrubs), which take advantage of the protection and shade offered beneath the shrub canopy (Forde 1986; Croft *et al.* 2006). In contrast, the seedlings of larger shrubs may struggle to establish if they are suppressed beneath a dense canopy (Hazard and Parsons 1977). Establishing beneath a mature shrub, however, may be more beneficial than establishing within the surrounding grassland, where soil temperatures, moisture stress and competitive effects may be greater (Shumway 2000; Gómez-Aparicio 2009). A vegetation survey conducted in mature shrublands on the Younghusband Peninsula appeared to support this notion. Here, the seedlings of fleshy-fruited species (while typically rare) were much more likely to occur beneath the canopy of a mature shrub than in the open areas adjacent to the shrub (Patkin, unpubl. data). As discussed by Toh *et al.* (1999), the most ideal approach when using shrubs to facilitate seedling recruitment could be to foster the seedlings that occur near the outer margins of the canopy, where competition with the shrub would be reduced. Importantly, this would then help to enhance the outward spread of plant cover from the shrub. Seedlings occurring on the periphery of the shrub would endure greater competition with introduced grasses, although this could be reduced with some form of control during months of active grass growth.

Some studies have also indicated that widespread non-native woody weeds could be used to enhance seed dispersal and recruitment of native plants in disturbed or degraded areas. For example, camphor laurel (*Cinnamomum camphora*, an exotic fleshy-fruited tree) was found to facilitate the dispersal and recruitment of a wide variety of native rainforest species in abandoned pastures located in eastern Australia (Neilan *et al.* 2006; Kanowski *et al.* 2008). In another study conducted by Elgar *et al.* (2014), stands of the wild tobacco *Solanum mauritianum* (both poisoned and alive) were able to enhance seed dispersal and plant recruitment in abandoned pastures located in north-eastern Australia. As discussed by both Kanowski *et al.* (2008) and Elgar *et al.* (2014), using living woody weeds for regeneration carries some uncertainties, particularly in regards to the timeframes required for native species to overtake their exotic counterparts. Both studies indicated that the transition may need to be accelerated through the removal of the woody weeds, which could occur either extensively (which would help to reduce competition for existing recruits) or more gradually (which would help to maintain a complex and shaded habitat).

Similar to Elgar *et al.* (2014), poisoned shrubs of *L. ferocissimum* could also be used to facilitate regeneration in the Younghusband Peninsula. In recent years, large-scale efforts have taken place to poison and eradicate this widespread woody shrub (South East Natural Resources Management Board 2018). The dead *L. ferocissimum* shrubs could be left in place to act as perching sites for birds and in the process aid the dispersal of seeds and plant recruitment. Unlike the previously mentioned studies, using living *L. ferocissimum* shrubs to facilitate regeneration would not be an option, given its ability to exclude native plant species (Noble *et al.* 2013; Weber 2017). Evidently, very few studies in Australia have explored value of non-native woody weeds in restoration, despite their ability to potentially assist with seed dispersal and plant recruitment. Future studies should further consider their value in restoration efforts but will also need to continue to explore the timeframes or methods required for native vegetation to take over the landscape.

### **6.3 Conclusion**

In conclusion, this thesis demonstrated that artificial perches can be used to facilitate the dispersal of seed into open and degraded areas of the Younghusband Peninsula, South Australia. Despite the deposition of large amounts of native seed, recruitment beneath the perches appeared unlikely due to the presence of post-dispersal barriers, including poor seed germination, seedling herbivory and likely competition from introduced grasses. Additional

interventions, such as herbicide application and exclusion fencing, appear necessary to allow seedling recruitment to occur beneath artificial perches. As a result, future research may be best focused on the use of natural perches (including woody weeds) for restoration, as they have demonstrated a greater potential to facilitate plant recruitment in several studies conducted elsewhere. Ideally, the knowledge gained from this thesis will inform the future use of artificial perches as a restoration tool, as well as future efforts to restore the degraded areas of the Youngusband Peninsula.

## References

- Aide TM, Cavelier J (1994) Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* **2**, 219–229.
- Alcock C, Symon D (1977) The flora. In 'The southern Coorong and lower Youngusband Peninsula of South Australia.' (Eds DD Gilbertson, MR Foale.) pp. 25–44. (Nature Conservation Society of South Australia: Adelaide)
- Allcock KG, Hik DS (2004) Survival, growth, and escape from herbivory are determined by habitat and herbivore species for three Australian woodland plants. *Oecologia* **138**, 231–241.
- Andersen A, Ashton D (1985) Rates of seed removal by ants at heath and woodland sites in southeastern Australia. *Australian Journal of Ecology* **10**, 381–390.
- Anderson-Bergman C (2017) icenReg: regression models for interval censored data in R. *Journal of Statistical Software* **81**, 1–23.
- Anderson-Bergman C (2018) 'icenReg. R package version 2.0.9.'
- Armsworth PR, Cantú-Salazar L, Parnell M, Davies ZG, Stoneman R (2011) Management costs for small protected areas and economies of scale in habitat conservation. *Biological Conservation* **144**, 423–429.
- Aronson J, Clewell AF, Blignaut JN, Milton SJ (2006) Ecological restoration: a new frontier for nature conservation and economics. *Journal for Nature Conservation* **14**, 135–139.
- Athiê S, Dias MM (2016) Use of perches and seed dispersal by birds in an abandoned pasture in the Porto Ferreira state park, southeastern Brazil. *Brazilian Journal of Biology* **76**, 80–92.
- Attiwill A (1970) On the spread of pines and bridal creeper by birds. *South Australian Ornithologist* **25**, 212.
- Australian Bureau of Meteorology (2021) 'Long-range weather and climate.' Available at <http://www.bom.gov.au/climate/> [Accessed 24 March 2021].
- Barker RD, Vestjens WJM (1990) 'The food of Australian birds 2. Passerines.' (CSIRO Publishing: Lyneham)
- Barron P, Dalton G (1996) Direct seeding of native trees and shrubs in coastal environments. *Journal of Coastal Research* **12**, 1006–1008.
- Barson MM, Calder DM (1981) The vegetation of the Victorian coast. *Proceedings of the Royal Society of Victoria* **92**, 55–65.

- Baskin CC, Baskin JM (1998) 'Seeds: ecology, biogeography, and evolution of dormancy and germination.' (Academic Press: San Diego)
- Baskin CC, Baskin JM (2004) Determining dormancy-breaking and germination requirements from the fewest seeds. In 'Ex situ plant conservation: supporting species survival in the wild.' (Eds EO Guerrant Jr., K Havens, M Maunder.) pp. 162–179. (Island Press: Washington, D.C)
- Batchelor JL, Ripple WJ, Wilson TM, Painter LE (2015) Restoration of riparian areas following the removal of cattle in the northwestern Great Basin. *Environmental Management* **55**, 930–942.
- Bechara FC, Dickens SJ, Farrer EC, Larios L, Spotswood EN, Mariotte P, Suding KN (2016) Neotropical rainforest restoration: comparing passive, plantation and nucleation approaches. *Biodiversity and Conservation* **25**, 2021–2034.
- Bednekoff PA, Houston AI (1994) Avian daily foraging patterns: effects of digestive constraints and variability. *Evolutionary Ecology* **8**, 36–52.
- Bell DT (1999) The process of germination in Australian species. *Australian Journal of Botany* **47**, 475–517.
- Bennett J, Hails J (1981) Sand movement in the coastal margin of the Coorong, South Australia. In 'Fifth Australian Conference on Coastal and Ocean Engineering, 1981: Offshore Structures. Perth'. pp. 155–161. (Institution of Engineers, Australia: Barton)
- Berg R (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* **23**, 475–508.
- Berger JJ (1993) Ecological restoration and nonindigenous plant species: a review. *Restoration Ecology* **1**, 74–82.
- Bewley JD, Bradford K, Hilhorst H, Nongaki H (2012) 'Seeds: physiology of development, germination and dormancy.' (Springer: New York)
- Bird P, Mutze G, Peacock D, Jennings S (2012) Damage caused by low-density exotic herbivore populations: the impact of introduced European rabbits on marsupial herbivores and *Allocasuarina* and *Bursaria* seedling survival in Australian coastal shrubland. *Biological Invasions* **14**, 743–755.
- Bitani N, Ehlers Smith DA, Ehlers Smith YC, Downs CT (2020) Functional traits vary among fleshy-fruited invasive plant species and their potential avian dispersers. *Acta Oecologica* **108**, e103651.

- Black JM (1952) 'Flora of South Australia. Part III. Callitrichaceae-Plumbaginaceae.' 2nd edn. (Government Printer: Adelaide)
- Blem CR, Blem LB (1993) Do swallows sunbathe to control ectoparasites? An experimental test. *The Condor* **95**, 728–730.
- Blignaut A, Milton SJ (2005) Effects of multispecies clumping on survival of three succulent plant species translocated onto mine spoil in the succulent Karoo Desert, South Africa. *Restoration Ecology* **13**, 15–19.
- Boege K, Barton KE, Dirzo R (2011) Influence of tree ontogeny on plant-herbivore interactions. In 'Size-and age-related changes in tree structure and function.' (Eds FC Meinzer, B Lachenbruch, TE Dawson.) pp. 193–214. (Springer: Dordrecht)
- Bourman R, Murray-Wallace C, Ryan D, Belperio A, Harvey N (2018) Geomorphological evolution of the River Murray Estuary, South Australia. In 'Natural history of the Coorong, Lower Lakes, and Murray Mouth region (Yarluwar-Ruwe).' (Eds L Mosley, Q Ye, S Shepherd, S Hemming, R Fitzpatrick.) pp. 71–102. (University of Adelaide Press: Adelaide)
- Brandle R (2002) A biological survey of the Murray Mouth Reserves, South Australia March 2002. Department for Environment and Heritage, Adelaide.
- Bustamante-Sánchez MA, Armesto JJ (2012) Seed limitation during early forest succession in a rural landscape on Chiloé Island, Chile: implications for temperate forest restoration. *Journal of Applied Ecology* **49**, 1103–1112.
- Butcher C, Rogers D (2013) Conservation planning in the CLLMM region. Phase I: a description of the landscapes of the CLLMM region. Department for Environment, Water and Natural Resources, Adelaide.
- Carlo TA, Morales JM (2016) Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. *Ecology* **97**, 1819–1831.
- Castillo-Escrivà A, López-Iborra GM, Cortina J, Tormo J (2019) The use of branch piles to assist in the restoration of degraded semiarid steppes. *Restoration Ecology* **27**, 102–108.
- Castley JG, Bruton J-S, Kerley GIH, McLachlan A (2001) The importance of seed dispersal in the Alexandria Coastal Dunefield, South Africa. *Journal of Coastal Conservation* **7**, 57–70.
- Caton B, Quinn J, Detmar S, Fotheringham D, Rubbo N, Royal M, Sandercock R, Laurence S (2011) Limestone Coast and Coorong coastal action plan and conservation priority



- study. South East NRM Board and Department of Environment and Natural Resources, Adelaide.
- Cavallero L, Raffaele E, Aizen MA (2013) Birds as mediators of passive restoration during early post-fire recovery. *Biological Conservation* **158**, 342–350.
- Ceccon E, González EJ, Martorell C (2015) Is direct seeding a biologically viable strategy for restoring forest ecosystems? Evidences from a meta-analysis. *Land Degradation & Development* **27**, 511–520.
- Chladil M, Kirkpatrick JB (1989) A transect study of the sand dune vegetation at Bakers Beach, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **123**, 247–256.
- Choi YD (2017) Considering the future: anticipating the need for ecological restoration. In 'Routledge handbook of ecological and environmental restoration.' (Eds SK Allison, M S.D.) pp. 7–15. (Routledge: Abingdon)
- Clarke GM, Grosse S, Mathews M, Catling PC, Baker B, Hewitt CL, Crowther D, Sadler S (2000) State of the environment indicators for exotic environmental pest species. Environment Australia, Canberra.
- Clarke K, Gorley R (2015) 'Primer v7: User Manual/Tutorial. PRIMER-E, Plymouth, UK.'
- Cole RJ, Holl KD, Zahawi RA (2010) Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. *Ecological Applications* **20**, 1255–1269.
- Commander L (2008) Seed biology and rehabilitation in the arid zone: a study in the Shark Bay World Heritage Area, Western Australia. PhD thesis, University of Western Australia.
- Cooke BD (1987) The effects of rabbit grazing on regeneration of sheoaks, *Allocasuarina verticillata* and saltwater ti-trees, *Melaleuca halmaturorum*, in the Coorong National Park, South Australia. *Australian Journal of Ecology* **13**, 11–20.
- Cooke BD, McPhee SR (2007) Rabbits and native plant biodiversity. A report compiled for Australian Wool Innovation and Meat and Livestock Australia as part of the Invasive Animals Co-operative Research Centre Project. Project 7.T. 6: biodiversity impact of rabbits. Invasive Animals Co-operative Research Centre, Canberra.
- Corlett RT (2017) Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: an update. *Global Ecology and Conservation* **11**, 1–22.
- Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution* **23**, 104–112.

- Croft S, Pedler JA, Milne T (2006) 'Coastal vegetation communities of the Southern Mount Lofty Ranges.' (Nature Conservation Society of South Australia: Adelaide)
- Da Silva JMC, Uhl C, Murray G (1996) Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology* **10**, 491–503.
- Dardis C (2018) 'survMisc. R package version 0.5.5.'
- David P, Manakadan R, Ganesh T (2015) Frugivory and seed dispersal by birds and mammals in the coastal tropical dry evergreen forests of southern India: a review. *Tropical Ecology* **56**, 41–55.
- Davis NE, Coulson G, Forsyth DM (2008) Diets of native and introduced mammalian herbivores in shrub-encroached grassy woodland, south-eastern Australia *Wildlife Research* **35**, 684–694.
- de Almeida A, Marques MCM, Ceccon-Valente MdF, Vicente-Silva J, Mikich SB (2016) Limited effectiveness of artificial bird perches for the establishment of seedlings and the restoration of Brazil's Atlantic Forest. *Journal for Nature Conservation* **34**, 24–32.
- Debussche M, Isenmann P (1994) Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* **69**, 414–426.
- Department for Environment, Water and Natural Resources (2007) 'eFloraSA.' Available at <http://www.flora.sa.gov.au/index.html> [Accessed 25 November 2019].
- Dey D, Knapp B, Battaglia M, Deal R, Hart J, O'Hara K, Schweitzer C, Schuler T (2019) Barriers to natural regeneration in temperate forests across the USA. *New Forests* **50**, 11–40.
- Dixon KW, Roche S, Pate JS (1995) The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* **101**, 185–192.
- Duncan RS, Chapman CA (2002) Limitations of animal seed dispersal for enhancing forest succession on degraded lands. (Eds DJ Levey, WR Silva, M Galetti.) pp. 437–450. (CABI Publishing: Wallingford)
- Dunstan H, Florentine SK, Calviño-Cancela M, Westbrooke ME, Palmer GC (2013) Dietary characteristics of emus (*Dromaius novaehollandiae*) in semi-arid New South Wales, Australia, and dispersal and germination of ingested seeds. *Emu* **113**, 168–176.

- Elgar AT, Freebody K, Pohlman CL, Shoo LP, Catterall CP (2014) Overcoming barriers to seedling regeneration during forest restoration on tropical pasture land and the potential value of woody weeds. *Frontiers in Plant Science* **5**, 1–10.
- Elliott S, Blakesley D, Hardwick K (2013) 'Restoring tropical forests: a practical guide.' (Royal Botanic Gardens: Kew)
- Etikan İ, Bukirova K, Yuvalı M (2018) Choosing statistical tests for survival analysis. *Biometrics & Biostatistics International Journal* **7**, 477–481.
- Ferreira G, de Melo C (2016) Artificial roosts as seed dispersal nuclei in a cerrado area in Triângulo Mineiro, Brazil. *Bioscience Journal* **32**, 514–523.
- Forde N (1986) Relationships between birds and fruits in temperate Australia. In 'The dynamic partnership: birds and plants in southern Australia.' (Eds HA Ford, DC Paton.) pp. 42–58. (D. J. Woolman, Government Printer: Adelaide)
- Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. *BioScience* **53**, 77–88.
- Freeman AND, Freebody K, Montenero M, Moran C, Shoo LP, Catterall CP (2021) Enhancing bird-mediated seed dispersal to increase rainforest regeneration in disused pasture – a restoration experiment. *Forest Ecology and Management* **479**, e118536.
- French K (1991) Characteristics and abundance of vertebrate-dispersed fruits in temperate wet sclerophyll forest in southeastern Australia. *Australian Journal of Ecology* **16**, 1–13.
- French K (1996) The gut passage rate of silvereyes and its effect on seed viability. *Corella* **20**, 16–19.
- Gilbertson D, Foale MR (1977) 'The southern Coorong and lower Youngusband Peninsula of South Australia.' (Nature Conservation Society of South Australia: Adelaide)
- Gilbertson DD (1977) The off-road use of vehicles and aspects of the bio-physical systems of the lower Coorong region. In 'The southern Coorong and lower Youngusband Peninsula of South Australia.' (Eds DD Gilbertson, MR Foale.) pp. 71–91. (Nature Conservation Society of South Australia: Adelaide)
- Gilbertson DD (1981) The impact of past and present land use on a major coastal barrier system. *Applied Geography* **1**, 97–119.
- Gillham ME (1963) Some interactions of plants, rabbits and sea-birds on South African islands. *Journal of Ecology* **51**, 275–294.

- Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology* **97**, 1202–1214.
- Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL (2005) Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *Journal of Vegetation Science* **16**, 191–198.
- Gosper CR (1999) Plant food resources of birds in coastal dune communities in New South Wales. *Corella* **23**, 53–62.
- Gosper CR, Stansbury CD, Vivian-Smith G (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions* **11**, 549–558.
- Graham LLB, Page SE (2012) Artificial bird perches for the regeneration of degraded tropical peat swamp forest: a restoration tool with limited potential. *Restoration Ecology* **20**, 631–637.
- Guevara S, Laborde J (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio* **107**, 319–338.
- Guevara S, Purata SE, Maarel EVD (1986) The role of remnant forest trees in tropical secondary succession. *Vegetatio* **66**, 77–84.
- Guidetti BY, Amico GC, Dardanelli S, Rodriguez-Cabal MA (2016) Artificial perches promote vegetation restoration. *Plant Ecology* **217**, 935–942.
- Guja LK, Merritt D, Dixon K (2010) Buoyancy, salt tolerance and germination of coastal seeds: implications for oceanic hydrochorous dispersal. *Functional Plant Biology* **37**, 1175–1186.
- Haby NA, Brandle R (2018) Passive recovery of small vertebrates following livestock removal in the Australian rangelands. *Restoration Ecology* **26**, 174–182.
- Hannan L, Le Roux D, Milner R, Gibbons P (2019) Erecting dead trees and utility poles to offset the loss of mature trees. *Biological Conservation* **236**, 340–346.
- Hazard J, Parsons RF (1977) Size-class analysis of coastal scrub and woodland, Western Port, southern Australia. *Australian Journal of Ecology* **2**, 187–197.
- Heelemann S, Krug CB, Esler KJ, Reisch C, Poschlod P (2012) Pioneers and perches—promising restoration methods for degraded renosterveld habitats? *Restoration Ecology* **20**, 18–23.
- Herrera CM (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs* **54**, 2–23.

- Herrera CM (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* **68**, 511–538.
- Heyligers PC (2006) Primary vegetation development on the sand spit of Shallow Inlet, Wilsons Promontory, southern Victoria. *Cunninghamia* **9**, 571–595.
- Heyligers PC (2009) Formation of, and succession on, *Atriplex cinerea*-induced dune ridges in the Entrance Point Scientific Reference Area, Wilsons Promontory National Park, Victoria. *Cunninghamia* **11**, 1–26.
- Higgins PJ (1999) 'Handbook of Australian, New Zealand and Antarctic Birds. Volume 4: parrots to dollarbird.' (Oxford University Press: Melbourne)
- Higgins PJ, Davies SJJF (1996) 'Handbook of Australian, New Zealand and Antarctic birds. Volume 3: snipe to pigeons.' (Oxford University Press: Melbourne)
- Higgins PJ, Peter JM (2002) 'Handbook of Australian, New Zealand and Antarctic birds. Volume 6: pardalotes to shrike-thrushes.' (Oxford University Press: Melbourne)
- Higgins PJ, Peter JM, Cowling SJ (2006) 'Handbook of Australian, New Zealand and Antarctic birds. Volume 7: boatbill to starlings.' (Oxford University Press: Melbourne)
- Higgins PJ, Peter JM, Steele WK (2001) 'Handbook of Australian, New Zealand and Antarctic birds. Volume 5: tyrant-flycatchers to chats.' (Oxford University Press: Melbourne)
- Hobbs RJ, Atkins L (1991) Interactions between annuals and woody perennials in a Western Australian nature reserve. *Journal of Vegetation Science* **2**, 643–654.
- Hobbs RJ, Harris JA (2001) Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology* **9**, 239–246.
- Hobbs RJ, Walker LR, Walker J (2007) Integrating restoration and succession. In 'Linking restoration and ecological succession.' (Eds LR Walker, J Walker, RJ Hobbs.) pp. 168–179. (Springer: New York)
- Holl KD (1998) Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology* **6**, 253–261.
- Holl KD, Aide TM (2011) When and where to actively restore ecosystems? *Forest Ecology and Management* **261**, 1558–1563.
- Holl KD, Loik ME, Lin EHV, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* **8**, 339–349.

- Holl KD, Reid JL, Cole RJ, Oviedo-Brenes F, Rosales JA, Zahawi RA (2020) Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year study. *Journal of Applied Ecology* **57**, 2316–2328.
- Holl KD, Zahawi RA, Cole RJ, Ostertag R, Cordell S (2011) Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. *Restoration Ecology* **19**, 470–479.
- Horgan FG, Ramal AF, Villegas JM, Almazan MLP, Bernal CC, Jamoralin A, Pasang JM, Orboc G, Agreda V, Arroyo C (2016) Ecological engineering with high diversity vegetation patches enhances bird activity and ecosystem services in Philippine rice fields. *Regional Environmental Change* **17**, 1355–1367.
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecology, Evolution, and Systematics* **13**, 201–228.
- Hurt GC, Froliking S, Fearon M, Moore B, Shevliakova E, Malyshev S, Pacala S, Houghton R (2006) The underpinnings of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. *Global Change Biology* **12**, 1208–1229.
- Ireland KB, Rafter M, Kumaran N, Raghu S, Morin L (2019) Stakeholder survey reveals priorities for African boxthorn biocontrol research in Australia. *Biocontrol Science and Technology* **29**, 1123–1128.
- Izhaki I (2002) The role of fruit traits in determining fruit removal in east Mediterranean ecosystems. In 'Seed dispersal and frugivory: ecology, evolution, and conservation.' (Eds D Levey, W Silva, M Galetti.) pp. 161–175. (CABI Publishing: Wallingford)
- Izhaki I, Walton PB, Safriel UN (1991) Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *The Journal of Ecology* **79**, 575–590.
- Janzen DH (1988) Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanical Garden* **75**, 105–116.
- Jordano P (1987) Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology* **68**, 1711–1723.
- Jordano P (2000) Fruits and frugivory. In 'Seeds: the ecology of regeneration in plant communities.' (Ed. M Fenner.) pp. 125–166. (Commonwealth Agricultural Bureau International: Wallingford)
- Jordano P, García C, Godoy JA, García-Castaño JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences* **104**, 3278–3282.

- Kanowski J, Catterall CP, Neilan W (2008) Potential value of weedy regrowth for rainforest restoration. *Ecological Management & Restoration* **9**, 88–99.
- Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* **53**, 457–481.
- Kassambara A, Kosinski M, Przemyslaw B, Scheipl F (2018) 'survminer. R package version 0.4.3.'
- Kay BJ, Twigg LE, Korn TJ, Nicol HI (1994) The use of artificial perches to increase predation on house mice (*mus domesticus*) by raptors. *Wildlife Research* **21**, 95–105.
- Kelsall Y (2015) Foreshore and hinterland vegetation management plan. Practical Ecology, Preston.
- Kirkpatrick J, Harris S (1999) Coastal, heath and wetland vegetation. In 'Vegetation of Tasmania.' (Eds JB Reid, RS Hill, MK Brown, MJ Hovenden.) pp. 304–332. (Australian Biological Resources Study: Canberra)
- Knight A, Beale P, Dalton G (1997) Direct seeding of native trees and shrubs in low rainfall areas and on non-wetting sands in South Australia. *Agroforestry Systems* **39**, 225–239.
- La Mantia T, Rühl J, Massa B, Pipitone S, Lo Verde G, Bueno RS (2019) Vertebrate-mediated seed rain and artificial perches contribute to overcome seed dispersal limitation in a Mediterranean old field. *Restoration Ecology* **27**, 1393–1400.
- Ladd BM, Facelli JM (2005) Effects of competition, resource availability and invertebrates on tree seedling establishment. *Journal of Ecology* **93**, 968–977.
- Lea AM, Gray JT (1935a) The food of Australian birds: an analysis of the stomach contents. Part II. *Emu* **35**, 63–98.
- Lea AM, Gray JT (1935b) The food of Australian birds: an analysis of the stomach contents. Part III. *Emu* **35**, 145–178.
- Lenz TI, Facelli JM (2005) The role of seed limitation and resource availability in the recruitment of native perennial grasses and exotics in a South Australian grassland. *Austral Ecology* **30**, 684–694.
- Lenz TI, Moyle-Croft JL, Facelli JM (2003) Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. *Austral Ecology* **28**, 23–32.
- Levey DJ (1986) Methods of seed processing by birds and seed deposition patterns. In 'Frugivores and seed dispersal.' (Eds A Estrada, TH Fleming.) pp. 147–158. (Junk: Dordrecht)

- Liney J (2011) A natural vegetation regeneration event. *Australasian Plant Conservation* **20**, 17–18.
- Liu Z-J, Chen L-J, Liu K-W, Li L-Q, Rao W-H, Zhang Y-T, Tang G-D, Huang L-Q (2013) Adding perches for cross-pollination ensures the reproduction of a self-incompatible orchid. *PLoS ONE* **8**, e53695.
- Logan DP, Xu X (2006) Germination of kiwifruit, *Actinidia chinensis*, after passage through Silvereeyes, *Zosterops lateralis*. *New Zealand Journal of Ecology* **30**, 407–411.
- Marchant S, Higgins PJ (1993) 'Handbook of Australian, New Zealand and Antarctic birds. Volume 2: raptors to lapwings.' (Oxford University Press: Melbourne)
- Martin GR, Twigg LE, Zampichelli L (2007) Seasonal changes in the diet of the European rabbit (*Oryctolagus cuniculus*) from three different Mediterranean habitats in southwestern Australia. *Wildlife Research* **34**, 25–42.
- Martínez-López V, Zapata V, De la Rúa P, Robledano F (2019) Uncovering mechanisms of bird seed dispersal in semiarid environments to help to restore them. *Ecosphere* **10**, e02673.
- McClanahan TR, Wolfe RW (1987) Dispersal of ornithochorous seeds from forest edges in central Florida. *Vegetatio* **71**, 107–112.
- McClanahan TR, Wolfe RW (1993) Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology* **7**, 279–288.
- McDonnell MJ (1986) Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bulletin of the Torrey Botanical Club* **113**, 6–11.
- McDonnell MJ, Stiles EW (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* **56**, 109–116.
- McIver J, Starr L (2001) Restoration of degraded lands in the interior Columbia River basin: passive vs. active approaches. *Forest Ecology and Management* **153**, 15–28.
- McLaughlin JF (2013) Engaging birds in vegetation restoration after Elwha dam removal. *Ecological Restoration* **31**, 46–56.
- McNair JN, Sunkara A, Frobish D (2012) How to analyse seed germination data using statistical time-to-event analysis: non-parametric and semi-parametric methods. *Seed Science Research* **22**, 77–95.
- Mellor JW (1931) Bird notes. *South Australian Ornithologist* **11**, 104–106.
- Merritt D (2014) Seed longevity of Australian species. *Australasian Plant Conservation: Journal of the Australian Network for Plant Conservation* **22**, 8–10.



- Milne T (2015) Floristic survey of remnant vegetation and revegetation in the Coorong, Lower Lakes and Murray Mouth region. Department for Environment, Water and Natural Resources, Adelaide.
- Moran C (2007) Consequences of rainforest fragmentation for frugivorous vertebrates and seed dispersal. PhD thesis, Griffith University.
- Moulton MAB, Hesp PA, Miot da Silva G, Bouchez C, Lavy M, Fernandez GB (2018) Changes in vegetation cover on the Youngusband Peninsula transgressive dunefields (Australia) 1949–2017. *Earth Surface Processes and Landforms* **44**, 459–470.
- Mowling FA, Taylor SG (1977) Vegetation. In 'The southern Coorong and lower Youngusband Peninsula of South Australia.' (Eds DD Gilbertson, MR Foale.) pp. 19–24. (The Nature Conservation Society of South Australia: Adelaide)
- Münzbergová Z (2012) Seed density significantly affects species richness and composition in experimental plant communities. *PLoS ONE* **7**, e46704.
- Mutze G, Bird P, Cooke B, Henzell R (2008) Geographic and seasonal variation in the impact of rabbit haemorrhagic disease on European rabbits, *Oryctolagus cuniculus*, and rabbit damage in Australia. In 'Lagomorph biology: evolution, ecology and conservation.' (Eds P Alves, N Ferrand, K Hackländer.) pp. 279–293. (Springer: Heidelberg)
- Mutze G, Bird P, Jennings S, Peacock D, De Preu N, Kovaliski J, Cooke B, Capucci L (2014) Recovery of South Australian rabbit populations from the impact of rabbit haemorrhagic disease. *Wildlife Research* **41**, 552–559.
- Mutze G, Cooke B, Jennings S (2016) Density-dependent grazing impacts of introduced European rabbits and sympatric kangaroos on Australian native pastures. *Biological Invasions* **18**, 2365–2376.
- Neilan W, Catterall CP, Kanowski J, McKenna S (2006) Do frugivorous birds assist rainforest succession in weed dominated oldfield regrowth of subtropical Australia? *Biological Conservation* **129**, 393–407.
- Nichols P, Yates R, Loo C, Wintle B, Stevens J, Titterington J, Moore G, Dixon K, Barrett-Lennard E (2014) Direct seeding of chenopod shrubs for saltland and rangeland environments. Future Farm Industries CRC, Crawley.
- Nield AP, Enright NJ, Ladd PG (2015) Study of seed dispersal by emu *Dromaius novaehollandiae* in the Jarrah *Eucalyptus marginata* forests of south-western Australia through satellite telemetry. *Emu* **115**, 29–34.

- Noble M, Adair R (2014) African boxthorn (*Lycium ferocissimum*) and its vertebrate relationships in Australia. *Plant Protection Quarterly* **29**, 80–84.
- Noble MR, Rose MC, Balnaves J (2013) African boxthorn national best practice manual: managing African boxthorn (*Lycium ferocissimum*) in Australia. Tasmanian Department of Primary Industries, Parks, Water and Environment, Devenport.
- Nogales M, Hernández EC, Valdés F (1999) Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago). *Ecoscience* **6**, 56–61.
- Odendaal LJ, Haupt TM, Griffiths CL (2008) The alien invasive land snail *Theba pisana* in the West Coast National Park: is there cause for concern? *Koedoe* **50**, 93–98.
- Oliveira AKM, Bocchese RA, Pereira KRF, Carvalho TD (2018) Seed deposition by birds on artificial perches at different distances from a gallery forest in the Cerrado area. *Floresta* **48**, 363–372.
- Onofri A, Gresta F, Tei F (2010) A new method for the analysis of germination and emergence data of weed species. *Weed Research* **50**, 187–198.
- Ooi MK, Auld TD, Whelan RJ (2007) Distinguishing between persistence and dormancy in soil seed banks of three shrub species from fire-prone southeastern Australia. *Journal of Vegetation Science* **18**, 405–412.
- Oppermann AM (1999) 'A biological survey of the South Australian coastal dune and cliff-top vegetation, 1996-1998.' (Coast and Marine Section, Environment Protection Agency: Adelaide)
- Osunkjoya OO, Ash JE, Hopkins MS, Graham AW (1992) Factors affecting survival of tree seedlings in North Queensland rainforests. *Oecologia* **91**, 569–578.
- Palma AC, Laurance SGW (2015) A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? *Applied Vegetation Science* **18**, 561–568.
- Palmer MA, Zedler JB, Falk DA (2016) Ecological theory and restoration ecology. In 'Foundations of restoration ecology.' (Eds MA Palmer, JB Zedler, DA Falk.) pp. 3–26. (Island Press: Washington, D.C)
- Paton DC (2010) 'At the end of the river: the Coorong and lower lakes.' (ATF Press: Adelaide)
- Paton JB (1977) Historical notes on the Coorong. In 'The southern Coorong and lower Younghusband Peninsula of South Australia.' (Eds DD Gilbertson, MR Foale.) pp. 99–105. (Nature Conservation Society of South Australia: Adelaide)

- Pérez HE, Kettner K (2013) Characterizing *Ipomopsis rubra* (Polemoniaceae) germination under various thermal scenarios with non-parametric and semi-parametric statistical methods. *Planta* **238**, 771–784.
- Pias KE, Welch ZC, Kitchens WM (2012) An artificial perch to help snail kites handle an exotic apple snail. *Waterbirds* **35**, 347–351.
- Pillatt N, Pillatt N, Franco ETH, Coelho GC (2010) Dry artificial perches and the seed rain in a subtropical riparian forest. *Brazilian Journal of Biosciences* **8**, 246–252.
- Possingham HP, Bode M, Klein CJ (2015) Optimal conservation outcomes require both restoration and protection. *PLoS Biology* **13**, e1002052.
- Prather CM, Huynh A, Pennings SC (2017) Woody structure facilitates invasion of woody plants by providing perches for birds. *Ecology and evolution* **7**, 8032–8039.
- Prieto I, Padilla FM, Armas C, Pugnaire FI (2011) The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics* **13**, 181–187.
- Pyke DA, Brooks ML, D'Antonio C (2010) Fire as a restoration tool: a decision framework for predicting the control or enhancement of plants using fire. *Restoration Ecology* **18**, 274–284.
- R Core Team (2018) 'R: a language and environment for statistical computing.' (R Foundation for Statistical Computing: Vienna, Austria)
- Ramankutty N, Foley JA (1999) Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles* **13**, 997–1027.
- Ramaswami G, Kaushik M, Prasad S, Sukumar R, Westcott D (2016) Dispersal by generalist frugivores affects management of an invasive plant. *Biotropica* **48**, 638–644.
- Rawsthorne J, Watson DM, Roshier DA (2011) Implications of movement patterns of a dietary generalist for mistletoe seed dispersal. *Austral Ecology* **36**, 650–655.
- Read CF, Duncan DH, Vesk PA, Elith J (2011) Surprisingly fast recovery of biological soil crusts following livestock removal in southern Australia. *Journal of Vegetation Science* **22**, 905–916.
- Reid JL, Holl KD (2013) Arrival  $\neq$  survival. *Restoration Ecology* **21**, 153–155.
- Reid N (1986) Pollination and seed dispersal of mistletoes (Loranthaceae) by birds in southern Australia. In 'The dynamic partnership: birds and plants in southern Australia.' (Eds HA Ford, DC Paton.) pp. 64–84. (D. J. Woolman, Government Printer: Adelaide)

- Reid N, Yan Y (2000) Mistletoes and other phanerogams parasitic on eucalypts. In 'Diseases and pathogens of eucalypts.' (Eds PJ Keane, GA Kile, FD Podger, BN Brown.) pp. 353–383. (CSIRO Publishing: Collingwood)
- Reis A, Bechara FC, Tres DR (2010) Nucleation in tropical ecological restoration. *Scientia Agricola* **67**, 244–250.
- Renne IJ, Barrow Jr WC, Johnson Randall LA, Bridges Jr WC (2002) Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Diversity and Distributions* **8**, 285–295.
- Rey Benayas JM, Bullock JM, Newton AC (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment* **6**, 329–336.
- Robinson AC, Cauty PD, Fotheringham D (2008) Investigator Group expedition 2006: flora and vegetation. *Transactions of The Royal Society of South Australia* **132**, 173–220.
- Rodríguez-Pérez J, Riera N, Traveset A (2005) Effect of seed passage through birds and lizards on emergence rate of mediterranean species: differences between natural and controlled conditions. *Functional Ecology* **19**, 699–706.
- Rose AB (1999) Notes on the diet of some passerines in New South Wales II: butcherbirds to starlings. *Australian Bird Watcher* **18**, 164–178.
- Rudduck P (1982) European heritage of the Coorong: a general survey of the sites of early European heritage of the area now comprising the Coorong National Park and Coorong Game Reserve. National Parks and Wildlife Service, Adelaide.
- Samuels I, Levey D (2005) Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology* **19**, 365–368.
- Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* **107**, 15–29.
- Scott R, Pattanakaew P, Maxwell J, Elliott S, Gale G (2000) The effect of artificial perches and local vegetation on bird-dispersed seed deposition into regenerating sites. In 'Forest restoration for wildlife conservation.' (Eds S Elliott, J Kerby, D Blakesley, K Hardwick, K Woods, V Anusarnsunthorn.) pp. 327–337. (International Tropical Timber Organisation and The Forest Restoration Research Unit, Chiang Mai University: Chiang Mai)
- Shiels AB, Walker LR (2003) Bird perches increase forest seeds on Puerto Rican landslides. *Restoration Ecology* **11**, 457–465.

- Shono K, Cadaweng EA, Durst PB (2007) Application of assisted natural regeneration to restore degraded tropical forestlands. *Restoration Ecology* **15**, 620–626.
- Shoo LP, Catterall CP (2013) Stimulating natural regeneration of tropical forest on degraded land: approaches, outcomes, and information gaps. *Restoration Ecology* **21**, 670–677.
- Shumway SW (2000) Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia* **124**, 138–148.
- Slocum M, Horvitz C (2000) Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecology* **149**, 51–62.
- Smith GG (1973) 'A guide to the coastal flora of south-western Australia.' (Western Australian Naturalists' Club: Perth)
- South Australian Seed Conservation Centre (2016) Coorong, Lower Lakes and Murray Mouth recovery project – vegetation program seed germination and propagation research project. Department for Environment, Water and Natural Resources, Adelaide.
- South Australian Seed Conservation Centre (2020) 'Seeds of South Australia.' Available at <https://spapps.environment.sa.gov.au/SeedsOfSA/home.html> [Accessed 24 March 2021].
- South East Natural Resources Management Board (2018) 2016-17 annual report. South East Natural Resources Management Board, Mount Gambier.
- Standish RJ, Cramer VA, Hobbs RJ (2008) Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. *Journal of Applied Ecology* **45**, 1576–1583.
- Standish RJ, Cramer VA, Wild SL, Hobbs RJ (2007) Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia. *Journal of Applied Ecology* **44**, 435–445.
- Stanley MC, Lill A (2001) Accessibility as a factor influencing frugivory by silvereyes *Zosterops lateralis*: field comparisons with aviary experiments. *Australian Journal of Zoology* **49**, 171–182.
- Stanley MC, Lill A (2002) Avian fruit consumption and seed dispersal in a temperate Australian woodland. *Austral Ecology* **27**, 137–148.
- Stansbury C, Vivian-Smith G (2003) Interactions between frugivorous birds and weeds in Queensland as determined from a survey of birders. *Plant Protection Quarterly* **18**, 157–164.

- Stansbury CD (1996) Observations of birds feeding on bridal creeper (*Asparagus asparagoides*) fruits within Yanchep National Park, Western Australia. *Plant Protection Quarterly* **11**, 59–60.
- Stansbury CD (2001) Dispersal of the environmental weed bridal creeper, *Asparagus asparagoides*, by silvereeyes, *Zosterops lateralis*, in south-western Australia. *Emu* **101**, 39–45.
- Stiles EW, White DW (1986) Seed deposition patterns: influence of season, nutrients, and vegetation structure. In 'Frugivores and seed dispersal.' (Eds A Estrada, TH Fleming.) pp. 45–54. (Junk: Dordrecht)
- Suding KN (2011) Toward an era of restoration in ecology: successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics* **42**, 465–487.
- Summers DM, Bryan BA, Nolan M, Hobbs TJ (2015) The costs of reforestation: a spatial model of the costs of establishing environmental and carbon plantings. *Land Use Policy* **44**, 110–121.
- Sweedman L, Merritt D (2006) 'Australian seeds: a guide to their collection, identification and biology.' (CSIRO Publishing: Melbourne)
- Tiver F, Boland J, McArthur L, Rosenberg K, Watson I, Auld T, Denham A, Palisetty R, Stokes A, Farroway L (2008) Projecting the effects of grazing and drought on populations of shrubs and trees in the Australian rangelands. Desert Knowledge Cooperative Research Centre, Alice Springs.
- Toh I, Gillespie M, Lamb D (1999) The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecology* **7**, 288–297.
- Tomazi AL, Castellani TT (2016) Artificial perches and solarization for forest restoration: assessment of their value. *Tropical Conservation Science* **9**, 809–831.
- Traveset A (1998) Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* **1**, 151–190.
- Traveset A, Riera N, Mas R (2001) Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology* **15**, 669–675.
- Traveset A, Robertson AW, Rodríguez Pérez J (2007) A review on the role of endozoochory in seed germination. In 'Seed dispersal: theory and its application in a

- changing world.' (Eds A Dennis, R Green, EW Schupp.) pp. 78–103. (Cabi Publishing: Wallingford)
- Valiela I (2006) 'Global coastal change.' (Blackwell Publishing: Malden)
- van Elden S, Miranda NAF, Perissinotto R, Adams JB (2015) Plant selection and grazing activity of the invasive snail *Theba pisana* in coastal Algoa Bay, South Africa. *African Zoology* **50**, 227–231.
- Verdú M, Traveset A (2004) Bridging meta-analysis and the comparative method: a test of seed size effect on germination after frugivores' gut passage. *Oecologia* **138**, 414–418.
- Vicente R, Martins R, Zocche JJ, Harter-Marques B (2010) Seed dispersal by birds on artificial perches in reclaimed areas after surface coal mining in Siderópolis municipality, Santa Catarina State, Brazil. *Brazilian Journal of Biosciences* **8**, 14–23.
- Vogel HF, McCarron VEA, Zocche JJ (2018) Use of artificial perches by birds in ecological restoration areas of the Cerrado and Atlantic Forest biomes in Brazil. *Neotropical Biology and Conservation* **13**, 24–36.
- Vogel HF, Spotswood E, Campos JB, Bechara FC (2016) Annual changes in a bird assembly on artificial perches: implications for ecological restoration in a subtropical agroecosystem. *Biota Neotropica* **16**, e0069.
- Weber E (2017) 'Invasive plant species of the world: a reference guide to environmental weeds.' (Cabi: Wallingford)
- Williams PA, Karl BJ (1996) Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology* **20**, 127–145.
- Willson MF, Crome FHJ (1989) Patterns of seed rain at the edge of a tropical Queensland rain forest. *Journal of Tropical Ecology* **5**, 301–308.
- Willson MF, Graff DA, Whelan CJ (1990) Color preferences of frugivorous birds in relation to the colors of fleshy fruits. *The Condor* **92**, 545–555.
- Willson MF, Irvine A, Walsh NG (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* **21**, 133–147.
- Wilson PJ, Aebischer NJ (1995) The distribution of dicotyledonous arable weeds in relation to distance from the field edge. *Journal of Applied Ecology* **32**, 295–310.

- Wunderle JM (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* **99**, 223–235.
- Yates CJ, Hobbs RJ, Atkins L (2000) Establishment of perennial shrub and tree species in degraded *Eucalyptus salmonophloia* (salmon gum) remnant woodlands: effects of restoration treatments. *Restoration Ecology* **8**, 135–143.
- Young EK (1981) An evaluation of avian use of fresh surface water sources in the southern Coorong National Park: implications for management programmes. Masters thesis, The University of Adelaide.
- Young TP (2000) Restoration ecology and conservation biology. *Biological Conservation* **92**, 73–83.
- Zahawi R, Augspurger C (2006) Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. *Ecological Applications* **16**, 464–478.
- Zahawi RA, Holl KD, Cole RJ, Reid JL (2013) Testing applied nucleation as a strategy to facilitate tropical forest recovery. *Journal of Applied Ecology* **50**, 88–96.
- Zahawi RA, Reid JL, Holl KD (2014) Hidden costs of passive restoration. *Restoration Ecology* **22**, 284–287.
- Zanini L, Ganade G (2005) Restoration of *Araucaria* forest: the role of perches, pioneer vegetation, and soil fertility. *Restoration Ecology* **13**, 507–514.
- Zimmerman JK, Pascarella JB, Aide TM (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* **8**, 350–360.
- Zwiener VP, Cardoso FCG, Padial AA, Marques MCM (2014) Disentangling the effects of facilitation on restoration of the Atlantic Forest. *Basic and Applied Ecology* **15**, 34–41.



## Appendices

### Appendix 1

Total days that each artificial perch was monitored by a remote camera in the paddocks of Cantara in the months between December 2016 and May 2017. Two complex and six simple perches were monitored. The placement of each of these perches at Cantara can be found in Fig. 3.1.

	Complex perch number		Simple perch number					
	1	2	1	2	3	6	11	12
<b>Summer</b>								
December	7	9	12	12	8	12	6	8
January	17	1	31	31	17	31	11	27
February	28	3	28	28	28	28	3	28
Total	52	13	71	71	54	71	20	63
<b>Autumn</b>								
March	31	1	31	31	31	31	15	31
April	1	0	30	30	30	30	0	7
May	0	0	14	14	14	14	0	0
Total	32	1	75	75	75	75	15	37
Overall total	84	14	146	146	129	146	35	100

## Appendix 2

Total number of individuals captured and total number of faecal samples containing seed collected from three bird species caught in mistnets across five sites in the Coorong National Park in January 2015 and January 2016 (i.e. mid-summer). The sites were Salt Creek (36°07'S, 139°38'E), Tommy's Track (36°08'S, 139°38'E), Tea Tree Crossing (36°11'S, 139°39'E), 4 km south of Tea Tree Crossing and 42 Mile Crossing (36°17'S, 139°42'E).

	Silvereye		Singing honeyeater		Spiny-cheeked honeyeater	
	Captures	Faecal samples	Captures	Faecal samples	Captures	Faecal samples
<b>2015</b>						
Salt Creek	368	289	10	6	6	3
Tommy's Track	193	142	35	15	43	31
Tea Tree Crossing	153	134	7	8	0	0
4 km South of Tea Tree Crossing	107	74	3	2	4	3
42 Mile Crossing	153	115	6	5	1	1
<b>2016</b>						
Salt Creek	249	91	44	22	13	4
Tommy's Track	25	14	13	5	30	14
Tea Tree Crossing	132	89	3	3	3	1
4 km South of Tea Tree Crossing	175	89	3	1	3	1
42 Mile Crossing	153	13	7	2	4	0

### Appendix 3

The abundances of species (mean seed/m<sup>2</sup>/year ± SE) deposited beneath the artificial perches ( $n = 12$ ), into the open paddock ( $n = 25$ ), beneath paddock shrubs ( $n = 4$  shrub species, 10 shrubs per species) and beneath dune shrubs ( $n = 4$  shrub species, 10 shrubs per species) at Cantara during a 12-month period, between September 2015 and August 2016. Shrub species comprised of *Acacia sophorae* (AS), *Leucopogon parviflorus* (LP), *Lycium ferocissimum* (LF) and *Myoporum insulare* (MI). \* = introduced species.

Species	Artificial perches	Open paddock	Paddock shrubs				Dune shrubs			
			AS	LP	LF	MI	AS	LP	LF	MI
<i>Acacia sophorae</i>	82.3 ± 28.6	0	19.7 ± 5.3	0.1 ± 0.1	82.6 ± 46.4	12.1 ± 3.0	19.3 ± 7.6	0	17.4 ± 17.0	2.4 ± 1.1
<i>Alyxia buxifolia</i>	11.7 ± 5.9	0	1.9 ± 1.1	0.6 ± 0.5	1.6 ± 0.6	1.5 ± 1.0	0.5 ± 0.3	0.5 ± 0.4	2.5 ± 1.0	2.5 ± 1.3
<i>Amyema melaleuca</i>	51.0 ± 30.8	0	4.7 ± 3.1	0	0	17.4 ± 11.3	0.2 ± 0.2	0	0	2.7 ± 2.1
<i>Asparagus asparagoides</i> *	1.6 ± 0.5	0	1.1 ± 0.5	0.8 ± 0.6	0.4 ± 0.2	0.8 ± 0.3	0	2.0 ± 1.1	0	0.5 ± 0.3
<i>Billardiera cymosa</i>	0	0	1.5 ± 1.5	0	0.1 ± 0.1	0	0	0.3 ± 0.3	0	0
<i>Dianella revoluta</i>	7.6 ± 3.9	0	5.0 ± 4.4	1.6 ± 0.7	1.7 ± 0.6	0.9 ± 0.5	0.4 ± 0.3	1.2 ± 0.6	2.3 ± 0.6	5.3 ± 1.4
<i>Enchylaena tomentosa</i>	93.8 ± 36.4	0.04 ± 0.04	22.9 ± 9.2	0.3 ± 0.2	29.2 ± 15.0	37.9 ± 17.9	1.6 ± 0.8	3.1 ± 1.2	0.8 ± 0.3	1.9 ± 1.1
<i>Exocarpos syrticola</i>	26.2 ± 10.4	0	1.5 ± 0.9	2.2 ± 0.9	2.0 ± 0.7	3.2 ± 2.8	0	6.3 ± 5.3	1.2 ± 0.9	1.2 ± 0.7
<i>Leucopogon parviflorus</i>	181.8 ± 88.8	0	38.3 ± 12.2	175.3 ± 56.5	28.4 ± 9.8	34.3 ± 10.3	19.1 ± 6.5	102.0 ± 24.6	39.2 ± 22.3	65.7 ± 19.1
<i>Lycium ferocissimum</i> *	1031.0 ± 298.8	0.08 ± 0.08	8.6 ± 3.7	73.3 ± 52.8	411.8 ± 158.6	54.3 ± 33.1	2.7 ± 1.6	6.2 ± 3.0	76.5 ± 44.8	18.0 ± 14.6
<i>Muehlenbeckia gunnii</i>	80.1 ± 21.6	0	55.2 ± 20.0	53.7 ± 16.4	26.9 ± 9.5	35.1 ± 13.2	25.2 ± 7.6	48.5 ± 28.6	12.1 ± 2.9	31.2 ± 11.0
<i>Myoporum insulare</i>	198.7 ± 59.6	0.04 ± 0.04	36.3 ± 8.2	64.2 ± 17.1	71.2 ± 33.6	97.2 ± 23.1	15.5 ± 3.5	31.9 ± 20.0	23.1 ± 15.5	44.7 ± 9.7
<i>Rhagodia candolleana</i>	248.9 ± 84.2	0.2 ± 0.2	125.5 ± 46.7	20.2 ± 7.9	54.6 ± 17.0	120.4 ± 41.2	18.2 ± 11.4	4.4 ± 2.2	4.3 ± 1.4	16.8 ± 11.2
<i>Scaevola calendulacea</i>	0.9 ± 0.8	0	0	0	0	0	0	0	0	0
<i>Tetragonia implexicoma</i>	48.7 ± 28.8	0	74.9 ± 34.6	12.4 ± 8.1	7.3 ± 3.1	1.5 ± 0.6	5.2 ± 2.4	2.0 ± 0.1	1.6 ± 0.7	2.2 ± 1.0
<i>Threlkeldia diffusa</i>	96.9 ± 4.5	0	4.7 ± 3.2	7.7 ± 3.0	20.9 ± 11.1	3.4 ± 1.2	0.4 ± 0.3	23.0 ± 1.1	2.1 ± 0.8	4.2 ± 2.3
Average seeds/m <sup>2</sup> /year	2161.2 ± 578.5	0.32 ± 0.18	401.9 ± 86.4	412.4 ± 84.2	738.7 ± 236.1	420.0 ± 113.8	108.3 ± 16.2	224.2 ± 74.6	183.1 ± 65.7	199.3 ± 68.2