Movement ecology of Australian arid-zone birds

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GIBSON, MICHELLE,RENE (2018) *Movement ecology of Australian arid-zone birds*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/12778/

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February 2018

Submitted for the degree of Doctor of Philosophy

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Michelle R. Gibson

February 2018

Author contributions

This thesis is based on research done by primarily by myself and co-authors. Author contributions to each chapter are stated below.

Chapter 1

Gibson, MR, Runge, CA, Fuller, RA, and SG Willis all contributed to writing and editing.

Chapter 2

Gibson, MR, Runge, CA, Fuller, RA, and SG Willis. *Monitoring Australian arid-zone birds using distance sampling*

RAF and SGW designed the study. MRG organized data and performed the analysis. SGW assisted with analysis. MRG wrote manuscript, all authors discussed the results and edited the manuscript.

Chapter 3

Gibson, MR, Runge, Fuller, RA, CA, Stephens, PA, and SG Willis. *Where nothing stands still: evidence of widespread fluctuations in Australian arid-zone birds*

MRG, PAS, SGW, and RAF conceived the ideas. MRG carried out the research and analysed the data with contributions from CAR, RAF, PAS, and SGW. MRG, SGW, RAF, and CAR contributed to writing the paper.

Chapter 4

Gibson, MR, McKinney, MR, Runge, CA, Fuller, RA and SG Willis. *The role of static and dynamic environmental conditions on site usage in an arid bird assemblage*

MRG, CAF, RAF, and MRM conceived the ideas. MRG prepared the data. MRG and MRM wrote the model and performed the analysis. MRG and MRM wrote manuscript, CAF, RAF, and SGW discussed the results and edited the manuscript.

Chapter 5

Gibson, MR, Runge, CA, Fuller, RA, Stephens, PA and SG Willis. *Quantifying the influence of rainfall on bird community flux in Australia's arid zone*

MRG, PAS, and SGW conceived the ideas. MRG carried out the research and analysed the data with contributions from CAR, RAF, PAS, and SGW. MRG, SGW, RAF, and CAR contributed to writing the paper.

Acknowledgements

This thesis is a collaborative work that would not be possible without the assistance and support of many people.

I would firstly like to thank my supervisors for their guidance and patience during the course of my PhD and I am fortunate to have their expertise guiding this piece of work. I would like to thank Durham Doctoral Scholarship funding scheme for financial support, the Durham Conservation Ecology group their for support and camaraderie, and the University of Queensland for allowing me to be part of their excellent Centre for Biodiversity and Conservation Science team, especially Kathleen McLeod and Dr. Richard Fuller. I owe particular thanks to my mentor and co-author, Dr. Claire Runge, for devoting a significant amount of her time to my research, contributing many brilliant ideas, and constructive feedback. I would also like to acknowledge Matthew McKinney for his enthusiasm for modeling and willingness to collaborate.

A huge thanks to those who have provided statistical and coding support, including Dr. David Baker, Dr. Philip Stephens, Dr. Naiara O'Mahony, Dr. Christine Howard, Dr. Alke Voskamp, Dr. Simone Blomberg, Dr. Matthew Holden, Jeffrey Hanson, Brendan Dillon, and Paloma Corvalan, and those who provided GIS support, including Scott Atkinson and Ruben Venegas-Li. A huge thanks to those that provided writing support, including Dr. Danielle Shanahan and the UQ Biology Shut Up and Write Group, particularly Carla Archibald and Rachel Friedman.

I am so thankful to have worked with so many wonderful volunteers during my time in the field. Thanks to Dr. Richard Seaton, Dr. Karen Mustin, Dr. Jeremy Ringma, Jasmine Lee, Russell Yong, Dr. Danielle Shanahan, Andrew Rogers, Carla Archibald, Eduardo Gallo-Cajiao, Ashwin Rudder, Dr. Robert Spencer, and to Dr. David Taggart for logistical support.

Finally, thanks to my friends and family for their unwavering support, near and far. I could not have finished this thesis without each and every one of you.

Abstract

The movements of nomadic species are poorly understood, being highly dynamic over time and space. There is an urgent need to better understand this group as current conservation approaches appear not to be providing adequate protection. In this thesis, I evaluate a survey method to monitor this dynamic group, assess environmental variables driving their movements over time, and explore how rainfall structures the overall avian community.

To date, no standardized, large-scale monitoring has been carried out for arid zone or nomadic species. In **Chapter 2**, I describe a protocol for surveying this group over five years using two survey methods. Detection probabilities and robust density estimates were generated for 64 species and showed the majority fluctuated markedly over time. Line transect surveys were more effective for species richness and abundance measures. This survey method provides the first standardized density estimates for this assemblage and can be easily repeated in future for this and other remote, arid biological communities.

The movement characteristics of species with unpredictable, aseasonal movements are very poorly understood and difficult to measure. In **Chapter 3**, I develop a method for quantifying extent of bird movement by analysing changes in species' site persistence and variability in inter-annual densities over time, and compare results with existing movement classifications. Continuous variation in extent of species movement indicated that a binary grouping of resident versus nomadic species is inappropriate. Existing movement classifications likely underestimate species movements within arid regions of their distribution, suggesting that caution is needed when using sweeping species-level classifications, especially for Australian birds whose movements can be heavily environment-dependent.

Unlike regular migration, which is triggered by seasonal cues such as day length and temperature, movement in nomads is thought to be triggered by less predictable environmental conditions. In **Chapter 4**, I explore the relative influence of dynamic and static environmental variables on species abundance. Dynamic variables were more important for nomadic versus resident species but static variables were equally important for nomadic and resident species. These findings suggest that habitat structure is important to consider in addition to dynamic environmental features for understanding nomadic species movements.

Pulse events are thought to be positively correlated with nomadic species movements and to play an important role in structuring arid biological communities. In **Chapter 5**, I investigate how structural changes observed in Australia's arid bird community relate to rainfall and vegetation greenness. The importance of rainfall was mediated through vegetation growth and the community is dynamic at a local level but exhibits stability at a landscape level, underscoring the importance of connectivity between suitable habitats within this landscape to enable species to reshuffle among sites.

In sum, my thesis highlights the importance of standardized data for enabling an empirical approach to understanding nomadic and arid-zone bird species. Findings will advance our understanding of these species' dynamics and lay groundwork for improving protection of this group by identifying further research priorities.

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1

General Introduction

1.1 Introduction

This thesis combines aspects of desert and movement ecology, and explores the latter with a focus on birds of Australia’s arid zone. The work seeks to develop a deeper understanding of the transient and resident birds whose populations are fundamentally tied to the ebb and flow of life-sustaining resources in one of the harshest, driest climates worldwide. What I hope emerges is a solid baseline for which arid bird surveys in the future can build upon and be continued annually, inspiration for others to invest in long-term monitoring of poorly understood biological communities, and a greater appreciation for the conservation importance of this vast landscape and of arid ecosystems globally.

In this thesis, I undertake and analyse structured surveys of Australia’s arid-zone birds to develop an objective understanding of extent of species’ movements, what environmental variables drive their movements in space and time, and how rainfall structures the overall avian community. There is a great need for this information because mobile species are a poorly understood group and are not adequately protected by current conservation approaches, which tend to consider species’ distributions as static. To manage highly mobile species effectively in the future, there is a need to quantify the nature of their movements and do so in relation to climatic and environmental variables. To introduce the research presented in my thesis, I provide background information on several relevant topics. Firstly, I list the main knowledge gaps that underpin the motivation for each of my thesis chapters. Then, I explore the importance of monitoring species abundance and occurrence, describe different categories of animal movement and current approaches to understanding movement patterns, and list the possible drivers of movement. I then review the dynamics of rainfall and resource pulses within arid ecosystems and introduce Australia as a case study. Following these sections, I go on to synthesize how material from each of my thesis chapters will contribute toward a body of knowledge that will improve the conservation of mobile species, with a particular focus on nomadic species. Finally, I conclude with my main research objectives.

1.2 Research gaps

Nomadic birds are an elusive and challenging group to study given their aseasonal and often wide-ranging movements. Unlike migratory species, nomads breed opportunistically in different locations when conditions are suitable and track resources that are patchy over space and time (Jonzén et al., 2011). While major knowledge gaps still exist for seasonal migrants, they are a comparatively well-studied group, and far less is known of species with irregular movements (Cottee-Jones et al., 2015). Much of the existing knowledge is compiled from anecdotal or opportunistic records (e.g. Handbook of Australian, New Zealand, and Antarctic Birds, Marchant & Higgins, 1990; del Hoyo et al., 2014), often only in portions of the species range.

To date, no standardized, large-scale monitoring has been carried out for arid zone or nomadic species. It is inherently difficult to study species whose location in any given season is essentially unknown; moreover, migratory species are found worldwide while the vast majority of nomads are found in arid and semi-arid regions of the southern hemisphere due to characteristically aseasonal rainfall patterns. This shortfall highlights a fundamental need for standardised occurrence and abundance data over an extended time-period. Without such information, the conservation needs of mobile arid zone species will remain poorly understood and an assessment of the geography of nomadism will not be possible. Another issue raised by this lack of empirical knowledge is the level of uncertainty over which species are actually nomadic. Current classifications of nomadic species could simply be an artefact of the amount of information available (Jonzén et al., 2011). In addition, nomadism is not necessarily a species-level attribute, and it is entirely possible that a species' movement strategy could vary in different parts of its geographic range depending on environmental conditions (Newton, 2012). This highlights the need to understand the influence of various environmental conditions on species' movement dynamics, which can elucidate which species might have more nomadic tendencies and help predict species' response to extreme weather episodes. Further uncertainty exists around how major rain events structure the arid bird community as whole. The period following such events can be critical for arid communities (Letnic & Dickman, 2006) and understanding the cumulative impacts of individual species on community-level structure can have important implications for conservation management strategies.

1.3 The importance of monitoring species abundance and occurrence

Species distribution and abundance data over time and space form the basis of ecology as a discipline and aids in understanding the drivers of temporal changes in biodiversity (Magurran et al., 2010). There remains a great need for long-term biodiversity time-series data in ecological research today, especially for understanding systems with complex phenomena that play out over prolonged periods (Lindenmayer et al., 2012). Long-term ecological datasets, such as the North American Breeding Bird Survey (Sauer et al., 2017), form the basis for hundreds of subsequent studies; however, bias toward populated areas and northern latitude (Chown et al., 2004; Boakes et al., 2010) is problematic and there is a critical need for ecological datasets that survey underrepresented and remote regions. Studies of temporal changes to communities across broad landscapes and multiple years often compile data from a variety of sources e.g. Peterson et al. (2015) and are limited by methodological inconsistencies among the original studies (Møller & Fiedler, 2010). An alternative approach is to collect field data using standardized repeated monitoring (e.g. Terrestrial Ecosystem Research Network; Lindenmayer et al., 2012); however, this is often resource intensive, logistically complex, and time consuming. To date, no standardized, large-scale monitoring has been carried out for nomadic birds. In **Chapter 2** of my thesis I describe a large-scale monitoring protocol for surveying arid-zone birds using standardized distance sampling methods and use this to generate robust species density estimates. Density estimates derived from distance sampling account for differences in detectability among individual species, whereas abundance data derived from e.g. counts or strip transects does not always account for detection error and so may only be an approximation of a species realized abundance (Buckland et al., 1993; Lee & Barnard, 2016).

1.4 Movement in animal populations

Animal movements create temporal changes in the abundance and occurrence of a species, and looking for patterns in these changes can yield insight into underlying movement strategies (Newton, 2006a; Webb et al., 2014). Establishing species movement patterns is important for informing conservation planning as the conservation needs of migratory species can be very different to those of non-migratory species (Runge et al., 2014). Mobility has been categorized into multiple broad types, ranging from regular to-and-fro movement to unpredictable and opportunistic long-distance dispersal. Migration is the most widely known and understood form of animal movement as it is the easiest to study due to largely predictable, seasonal movements. Migratory movements are generally thought to have evolved in species that are dependent on predictable, seasonally fluctuating resource availability (Holt & Fryxell, 2011) and are genetically controlled rather than learned behaviour (Berthold, 1991). Studies of the genetic basis for migratory instincts, however, suggest this behavior can be switched on and off multiple times over the evolution of taxonomic families due to changes in environmental conditions (Helbig, 2003); further, the phenomenon of partial migration, in which some populations within a species are resident while others are migratory (Chan, 2001), provides some evidence that the transition between migratory and resident life histories can be made easily and quickly via evolution processes (Berthold, 1999). Species are more likely to adopt a residential lifestyle when resources are consistently abundant and when severe annual environmental conditions are uncommon enough that at least some individuals survive to breed in future seasons (Chan, 2001). Nomadism is often considered a form of migration, but unlike migratory species, nomadic species display largely wandering movements without fixed breeding or non-breeding grounds (Dean, 2004; Runge et al., 2014). Nomadism is thought to be an evolutionary adaptation to cope with environmental extremes and competition for limited resources, thus most nomadic species exploit resources that are patchy in space and tend to occur in arid environments (Davies, 1984; Dean, 2004). Similarly, breeding occurs opportunistically rather than in fixed times and places. Nomadic species may become sedentary at certain times in their life-cycle, or under particular climatic conditions, reverting to nomadic movements as resource distributions start to change again (Runge et al., 2014). For example, species that are typically nomadic in the Gibson Desert of Australia displayed sedentary-resident and irruptive behaviour following drought-breaking heavy rainfall (Burbidge & Fuller, 2007). Other forms of facultative movement include irruption and dispersive migration (Cottee-Jones et al., 2015). Irruptive and dispersive species generally display more seasonality in their movements than nomadic species from year to year. Irruptive movements follow similar seasonal patterns year to year but the number of individuals performing the movement may vary, as well as the precise timing, direction and distance travelled (Cottee-Jones et al., 2015). Irruptions occur during years of markedly low or high resource abundance, such as seen in crossbills *Loxia* spp that track cone-masting patterns in conifer forests of North America and Europe (Newton, 2006a; Cornelius & Hahn, 2012). Dispersive species are those that have regular breeding grounds but display wandering foraging movements, as is seen in Australasian gannets *Morus serrator* for example (Pyk et al., 2013).

Recoveries or observations of birds fitted with uniquely identifiable markers can be used to learn about the movements of migratory species (Korner-Nievergelt et al., 2010) but are not especially useful for species with aseasonal movements that do not return to the same locations each year (e.g. Zann & Runciman, 1994). The movement characteristics of species with unpredictable, aseasonal movements are very poorly understood and methods that are frequently employed to understand the movement of species, including the use of various tracking devices, present major logistical challenges in such situations (Cottee-Jones et al., 2015). Because movement patterns are not necessarily a species-level attribute, with populations and even individuals exhibiting more or less mobility in different locations (Mueller & Fagan, 2008), movement classifications should thus be based on data collected comprehensively across a species' geographic range. Past studies have tended to rely on post-hoc anecdotal accounts of nomadic species occurrences to classify mobility type and are rarely based on empirical evidence (but see Roshier et al., 2008). Filling this knowledge gap is necessary for an objective assessment of nomadism as current classifications of resident and nomadic species could simply be an artefact of the amount of information available (Jonzén et al., 2011). In **Chapter 3** of my thesis, I explore the range in variation of occupancy and abundance of individual Australian arid zone species and provide likely movement categories. I then compare my results with existing movement classifications from a widely cited atlas as a critique of the current binary resident-nomad paradigm.

Drivers of individual nomadic species movements are poorly understood. Unlike regular migration, which is triggered by seasonal cues such as day length and temperature, movement in nomads is triggered by less predictable environmental conditions. General triggers of nomadic movements are major rainfall events, consequent formations of ephemeral waterbodies that cause long-distance movements of waterfowl (Pedler et al., 2014), growth of ephemeral grasses and seed production that attracts granivorous species (e.g. Budgerigar *Melopsittacus undulatus*, Wyndham, 1983; Zebra Finch *Taeniopygia guttata*, Zann et al., 1995) and causes rodent irruptions (Greenville et al., 2013), and nectar production that attracts nectarivores (e.g. Black Honeyeater *Sugomel niger*, Keast, 1968). In **Chapter 4**, I explore the importance of various environmental variables on species density, testing the hypothesis that nomadic species are more influenced by fluctuating conditions than sedentary species.

1.5 Resource dynamics in arid ecosystems

The impact of rain pulses on biotic communities can be influenced by the nature of the rain events themselves, such as amount and temporal connectivity of rain events (Nano & Pavey, 2013), by landscape features like soil type and vegetation structure (Pavey & Nano, 2009), and by species traits, such as feeding guild and interactions among predators and prey (Jaksic et al., 1997; Pavey & Nano, 2013). Nano and Pavey (2013) found that plant functional groups showed distinct responses to short (130mm) versus long (540mm) rain pulses in arid Australia, and that soil texture is important for how rainfall translates into plant productivity.

Resource pulses can be important bottom-up drivers of arid biological communities. A general pattern seen in arid ecosystems following extreme rainfall is an increase in vegetation growth and seed production, followed by an increase in primary consumers (e.g. rodents and insects), followed by an increase in predators that feed on the primary consumers (Ostfeld & Keesing, 2000). In Chile, Meserve et al. (1995) observed an increase in population growth by folivorous, granivorous and omnivorous rodents in response to increased growth and seed production in ephemeral desert plants. Similarly, populations of deer mice (*Peromyscus maniculatus*) increased markedly in the deserts of the south-western US following heavy rainfall as a result of a spike in vegetation productivity and heavy seed production (Mills et al., 1999). However, a study conducted in South Africa found that granivorous bird abundance was not correlated with seed abundance or rainfall and was only correlated with new plant growth and rainfall variability over longer periods (Dean & Milton, 2001). Further, a study in Australia found that fixed habitat parameters such as vegetation assemblage type were more important than food and water resource availability in influencing arid bird communities following extreme rain (Pavey & Nano, 2009).

Resource pulses in arid regions are not always a time of prosperity; they can also be critical “bust” periods as ephemeral resource oases attract temporarily high abundances of predators, leading to significant structural changes following major rain events (Ostfeld & Keesing, 2000; Letnic & Dickman, 2006, 2010). For example, in the deserts of Australia, irruption in rodent populations attracts high numbers of itinerant raptors and dingos, causing hyper-predation and subsequent declines in these primary consumers (Letnic & Dickman, 2006; Pavey & Nano, 2013). In South America, a resource pulse following heavy rains caused an increase in seed-eating rodents, followed by an increase in vertebrate predator abundance, though their response was delayed by nearly a year (Jaksic et al., 1997). The rate at which biotic communities respond to pulse events can depend on whether irruptions result from reproduction or dispersal processes and introduces various time lags into the system (Meserve et al., 1995; Pavey & Nano, 2013). Meserve et al. (1995) found that native seed-eating rodents responded anywhere from 1 week to over a year after a major rain event in Chile depending on life history traits. Rodent species irrupted six to nine months following an extreme rain in arid Australia, while raptor response times ranged from immediate in diurnal species to 9 months in rodent specialists (Pavey & Nano, 2013).

In arid Australia, the ecological “boom” phenomenon that results from resource pulses is pronounced as it has the highest annual rainfall variability of any desert globally (McMahon et al., 2008; Morton et al., 2011) and also has the highest proportion of opportunistic nomadic birds that can travel long distances to take advantage of sporadic resource surpluses (Burbidge & Fuller, 2007; Roshier et al., 2008). Pulse events are thought to be positively correlated with such nomadic species movements (Dean, 2004; Burbidge & Fuller, 2007) and to play an important role in structuring arid biological communities in general (Noy-Meir, 1973; Morton et al., 2011). However, the form of these relationships remains unclear (Dean & Milton, 2001; Pavey & Nano, 2009) and there has been no standardised analysis for an entire arid bird community over a large spatial extent. In **Chapter 5**, I explore structural changes observed in Australia’s largely nomadic arid bird community in relation to rainfall and vegetation greenness. Further, understanding the relative influence of weather and habitat features on species-level responses is an important consideration when predicting future responses to extreme climate scenarios.

1.5.1 Australia as a case study

The arid interior of Australia is characterised by irregular rainfall events that drive boom and bust ecosystem processes (Nano & Pavey, 2013) and by opportunistic species adapted to tracking and exploiting ephemeral resources (Davies, 1984). The vast majority of nomadic species are found in arid and semi-arid landscapes of the southern hemisphere, and a disproportionate number are found in Australia (up to 45% of Australia's breeding birds are nomadic; Dean, 2004; Newton, 2010). Many of Australia's nomadic birds are nectarivorous honeyeaters (Keast, 1968), granivorous finches and parrots, including Zebra Finch and Budgerigar (Wyndham, 1983; Zann et al., 1995), and raptors, such as Grey Falcon *Falco hypoleucos*, Letter-winged Kite *Elanus scriptus*, and Black Kite *Milvus migrans* (Pavey & Nano, 2013). The magnitude of en masse fluctuations of nomads into low productivity habitats has potentially lasting impacts as the region returns to a drier state.

Rainfall events in Australia are greatly influenced by the El Niño–Southern Oscillation. Both El Niño-driven drying in the western Pacific Ocean and rainfall increases in the central and eastern equatorial Pacific are predicted to intensify by the mid to late twenty-first century (Risbey et al., 2009; Power et al., 2013). Such events are likely to have a strong effect on nomadic species whose movements are driven in large part by "boom-bust" weather events (Burbidge & Fuller, 2007). Over the past two decades, Australia has experienced a series of extreme and unprecedented weather episodes and, most recently, the wettest 2-year period in recorded history caused by La Niña events (National Climate Centre, 2012). The La Niña event resulted in a globally relevant greening episode (Poulter et al., 2014) that presents a unique opportunity to study the effects of extreme weather events on the nomadic terrestrial bird species of Australia's interior. Previous studies have made some progress towards understanding the effect of rain on nomadic birds but often at the level of a single site or over a limited number of years (Burbidge & Fuller, 2007; Pavey & Nano, 2009; Tischler et al., 2013; Jordan et al., 2017). In this thesis, I assess community-wide changes in arid-zone birds over a five-year period following an extreme rain event in one of the most arid and climatically variable regions of the world- Australia’s Lake Eyre Basin (McMahon et al., 2008; Morton et al., 2011).

1.6 Conservation of mobile species

The conservation of mobile species in the arid zone requires data on species abundance and occurrence throughout their geographic range, temporal changes in numbers and distributions, and important environmental variables that influence species and community level structure. Conservation of mobile species is failing, with for example, more than 90% of the world’s migratory birds having one or more portions of their annual cycle inadequately covered by protected areas (Runge et al., 2015b).

With a rapidly changing climate and expansion of habitat loss and land use change, the need for information on the dynamic distributions for mobile species is high. In **Chapter 2**, I evaluate a method for collecting baseline biogeographic information for Australia’s arid zone birds, for which a multi-year, standardized dataset is lacking.

For nomadism to be maintained as a stable behaviour, extremes in environmental conditions must be frequent and unpredictable enough to maintain movement toward areas of high resource availability or maintain dispersal away from areas of low resource availability (Dean, 1997). Climate change is predicted to increase the frequency and unpredictability of extreme weather events (IPCC, 2013), and it is possible that nomadic species will be more resilient to climate change than other groups (Simmons et al., 2004). This has yet to be tested and it is necessary to understand how species are impacted by extreme weather events to predict future population responses to a more unpredictable and extreme climate. In **Chapter 4**, I quantify the importance of environmental drivers of arid bird species abundance, and in **Chapter 5** I measure changes in avian community structure in relation to rain and vegetation productivity.

Nomadic species distributions are dynamic in space and time, so identifying when and why they occur at certain locations is essential for management decisions such as protected area designations (Webb et al., 2014). Current approaches to protected area implementation are often based on the false assumption that species distributions are static (Runge et al., 2014).

For sedentary species it is of course advantageous to identify and then protect key areas but for dynamic species it might be better to adopt state- and time-dependent conservation actions, such as creating temporary habitat for migratory birds (Reynolds et al., 2017) or temporary spatial closures of fisheries to prevent seabird by-catch (Grantham et al., 2008). Ideally, all parts of mobile species distributions should receive some protection so that they are protected across the full annual cycle (Runge et al., 2015b). In **Chapter 3** and **Chapter 4** of my thesis, I quantify movement dynamics of arid bird species and environmental variables that influence species abundances from year to year.

1.7 Research objectives

The key gaps in existing knowledge of arid and nomadic avifauna that I have identified here raise four important issues that I address in my thesis. My main research objectives are to:

1) Evaluate a repeatable, standardized monitoring protocol to fill gaps in mobile species distributions (**Chapter 2**).
2) Develop a method for quantifying nomadism among the arid bird assemblage of the study region (**Chapter 3**).
3) Assess the relative influence of static and dynamic variables on changes in individual species abundance (**Chapter 4**).
4) Measure changes in the avian community over an environmentally dynamic period and attribute changes to rainfall and vegetation productivity (**Chapter 5**).

2

Monitoring Australian arid-zone birds using distance sampling

2.1 Abstract

The movements of nomadic and irruptive species are poorly understood in comparison with migratory species. The challenge of studying this group lies in their unpredictable movements over time and space, understanding the role of environmental variables in such movements, and the remote arid landscapes they often inhabit. Here, I introduce a standardized sampling protocol over multiple years and over an extensive, remote region to collect abundance and habitat data for the terrestrial bird assemblage of arid Australia, which contains one of the highest proportions of nomadic species globally. In this chapter, I use this dataset to (i) evaluate the effectiveness of line and point transects, and (ii) present detection functions and density estimates for individual species in the assemblage. The relationship between species abundance data and environmental variables is analysed in Chapters 4 and 5. Line transect and point count surveys were conducted each winter between 2012 and 2016 by teams of trained surveyors using distance sampling methods, whereby species detection probabilities are modelled as a function of distance from the observer at the moment of first detection. By accounting for differences in detectability among species, I generate robust density estimates for 64 individual species. Results show that line transects detected 14% more species, 36% more individuals of species, and 4 times more unique species than point counts and so appear to be more effective for generating accurate density estimates. However, point counts detected a handful of cryptic species not detected on line transects, perhaps because the observer was still and silent while standing at a point location, so this survey method still contributed to a more complete list of species for the region, and seems worth retaining in the survey design. Probability of detection was low (< 0.30) for 40 out of 64 species, and abundance fluctuated significantly between at least one pair of consecutive years for 42 species and remained fairly stable for 22 species. This study confirms the utility of this repeatable protocol for generating reliable detection probabilities and density estimates for arid bird species, thus facilitating effective monitoring of arid bird abundances over time. This protocol can be adopted for other taxa to assess large-scale changes in arid biological communities over a relatively short period of time.

2.2 Introduction

The movements, distributions, and population sizes of nomadic and irruptive species are poorly understood in comparison with their migratory counterparts (Jonzén et al., 2011; Cottee-Jones et al., 2015). Without foundational biogeographical knowledge, it is difficult to develop reliable assessments of species population trends and conservation status, and to design an appropriate suite of management options. Nomadic and irruptive species are difficult to study due to the aseasonal nature of their movements and current knowledge of nomadic bird movements is largely based on anecdotal and opportunistic evidence, or inference (Griffioen & Clarke, 2002; Newton, 2010). To date, no standardised time series of large-scale patterns of abundance and occupancy for nomadic species exists. Here, I seek to fill this gap by evaluating a large-scale monitoring protocol focused on a mobile, nomadic species assemblage over multiple years.

Nomadic and irruptive species are characterized by facultative, aseasonal movements, distributional ranges that fluctuate greatly from year to year, and are not restricted to specific breeding grounds (Dean, 2004; Newton, 2006b). Moreover, such species can be sedentary in some years when conditions are favourable and disperse when they become locally scarce or can disperse in part of their range where environmental conditions are less predictable, while remaining sedentary elsewhere (Clulow et al., 2011; Newton, 2012). Nomads and irruptive species can travel long distances in short periods (Newton, 2006a; Roshier et al., 2008). Conventional extinction risk assessment and protected area approaches often make the simplifying assumption that species distributions are static or at least seasonally predictable in the case of migratory species. Neither is true for nomadic and irruptive species, thus these species require different protection strategies than resident or migratory species (Runge et al., 2014). Conserving facultatively mobile species is therefore a major challenge and highlights the need to understand where such species occur, and when.

There is presently rather little empirical understanding of nomadic and irruptive species occupancy or movement patterns and few field studies have focused on this group over a large scale (Table 2.1). Reserve-scale studies have revealed that nomadic and irruptive birds tend to appear in an area in large numbers following rainfall and leave during dry conditions (Burbidge & Fuller, 2007; Tischler et al., 2013). Detailed species-level studies found that the nomadic Swift Parrot *Lathamus discolor* distribution, abundance and nesting activity shifted significantly from year to year with food availability over a large area (Stojanovic et al., 2015). Multiple years of aerial surveys in Australia's interior wetlands measured changes in abundance of mobile waterbirds and found differential responses to wetting and drying (Roshier et al., 2002). Equivalent detailed studies conducted on multiple species or on-foot surveys of terrestrial birds would require an inordinate amount of resources and time. Evidence of species movements can be obtained from ringing records for migratory species but this approach is less useful for species with little or no site fidelity, and very few studies have tracked nomadic species movements with satellite tags (but see Roshier et al., 2008). For a multi-species, multi-year, large-scale survey of highly mobile species to be feasible, easy access to fixed sites and rapid surveying by trained observers is required (see Webb et al., 2014).

All previous field studies on arid-zone irruptive and nomadic birds use a conventional count approach (Table 2.1) to assess species' abundances, which may lead to an underestimate if not all individuals are detected. Robust estimates of animal abundance should account for factors affecting detectability of a species, such as observer bias, species' behaviour, and habitat type (Bibby et al., 1998). A widely used method that accounts for such factors is distance sampling (Buckland et al., 1993). Distance sampling uses distances at which an animal is detected from the observation line or point and generates a detection probability value under four assumptions: 1.) lines or points are placed randomly with respect to the distribution of animals; 2.) animals on the survey point or line are detected with 100% probability; 3.) animals are detected at their initial location prior to movement in response to the observer; 4.) exact distances are measured to the animal from the survey line or point (Buckland et al., 1993). This approach allows direct comparisons of density between species and between the same species in different habitats (Bibby et al., 1998). Line transects and point counts are the two main methods of collecting distance sampling data. Line transects are better suited for surveying lower density, more mobile species in even habitats and record more birds than point counts. Point counts are better suited for habitats with denser vegetation and rough terrain that is difficult to

Table 2.1 Table summarizing details and main findings of all studies of dry-zone irruptive and nomadic birds within Australia and other southern hemisphere referenced in this thesis.

Study	Location	Study species	Spatial extent	Temporal extent	Survey method/ Data type	Main findings
Burbidge & Fuller 2007	Gibson desert, Western Australia	54 species of Australian arid birds	8 km^2	1988-1992; multi-season	Random walks/ Abundance (count)	Sedentary-resident species declined with drought; irruptive species responded immediately to heavy rain; some nomads behaved as resident and irruptive
Dean & Milton 2001	Southern Karoo, arid South Africa	46 species of arid South African birds	~20000 km^2	1988-1990; multi-season	Point count/ Abundance (count)	New plant growth, but not rainfall, influenced local abundance of birds; no correlation between seed and granivore abundance
Jordan et al., 2017	Newhaven Wildlife Sancturary, arid central Australia	115 species of Australian arid birds	2610 km^2	2008-2013; autumn	Random walks/ Abundance (count)	Bird abundance and species richness was influenced by rainfall; common species persisted in dry periods
Lloyd 1999	Arid Northern Cape, South Africa	11 species of arid-zone terrestrial birds	100 km^2	1993-1996; early summer	Nest searching via random cycling/Breeding activity	Rainfall influenced clutch size
Pavey & Nano 2009	Finke Bioregion, arid Northern Terrority, Australia	106 species of Australian arid birds	54292 km^2	Mar-Nov 2001	Line transect/ Abundance (count)	Arid bird assemblage patterns driven by vegetation and not resource variables

Pedler et al., 2014	Wetlands of arid-zone Australia and coast of western Australia	Banded Stilt *Cladorhynchus leucocephalus*, 21 individuals	Extensive sections of western and central Australia (measured as vectors rather than area)	2012-2014; tracked daily for mean of 192 days	Tracking, satellite telemetry	Rapid continent-wide movements in response to unpredictable ephemeral resource pulses, including directed, ranging, and regular (returning to starting locations) movements
Roshier et al., 2002	Wetlands of arid New South Wales, Australia	43 species of Australian waterbird	~60000 km^2	1987-1990, 1993; multi-season	Aircraft transects/ Abundance (count)	Wetting and drying of large temporary wetlands and magnitude of the change influence abundance of waterbirds
Roshier et al., 2008	Agricultural wetlands of eastern Australia and arid wetlands of central Australia	Grey Teal *Anas gracilis*	Extensive sections of eastern and central Australia (measured as vectors rather than area)	2003-2005; tracked daily from 39-879 days	Tracking, satellite telemetry	Some long-distance movements are directed by rainfall and flooding, some are ranging, i.e. independent of environmental cues
Tischler et al., 2013	Simpson desert, central Australia	83 species of Australian arid birds	4485 km^2	2006-2008; multi-season	Point count/ Abundance (count)	Granivores and nomadic species were most abundant after heavy rains
Zann et al., 1995	Alice Springs, arid central Australia	Zebra Finch *Taeniopygia guttata*	0.15 km^2	1986-1992; multi-season	Trapping/ Breeding activity, diet, aging	Rainfall over previous 1-4 months influenced intensity and length of breeding activity
Wiens 1991	Great Basin, USA and arid New South Wales	Arid bird communities of North America and Australia	~ 3.5 km^2 (USA), 2 km^2 (Aus)	1977-1979 (USA), 1984-1985 (Aus); summer	Line transect/Abundance (count)	Densities of Australian species were half that of N. American; Australian species had longer breeding season, more breeding attempts, sedentary/nomadic rather than seasonal migrants

navigate (Bibby et al., 1998). Therefore, I used line transect data to generate species density estimates and used point count and line transect data to generate estimates of species richness (Chapter 5) and analyse inter-annual occupancy patterns (see Chapter 4).

Australia contains an unusually high number of nomadic and irruptive bird species (Newton, 2010), with up to one third of the breeding bird assemblage thought to be capable of nomadic movements (Dean, 2004). In Australia, bird movements fluctuate in response to the highly variable climate conditions of the vast arid interior. Granivores, nectarivores, and rodent-specialist raptors track seed, nectar and prey resources resulting from heavy rain during ecological “boom” times (Keast, 1968; Wyndham, 1983; Pavey & Nano, 2013). One such pulse occurred in 2010 and 2011, when Australia experienced rainfall on a scale and intensity that is unprecedented in recorded history, driven by the strongest La Niña weather pattern since 1917. The rainfall event abruptly came to an end, opening up access to large parts of the Australian interior at a time of ecological boom and presenting a unique research opportunity. These unfolding events provide the opportunity to study what happens to the nomadic terrestrial bird species of the interior during such periods.

Here, I outline a standardized monitoring protocol designed to measure species abundance of a largely nomadic and irruptive assemblage over a relatively short time period and with low operating costs. Surveys also involved collection of habitat data at the local scale, which is used in analyses exploring environmental drivers of species abundances (Chapter 4) and community metrics (Chapter 5). The surveys take place over three long-distance (800km+) dirt tracks that provide access to a remote, and otherwise unreachable section of the arid Lake Eyre Basin region of South Australia and Queensland (see Methods). Surveys are conducted during the same season each year over a five-year period and over a large spatial scale, utilizing both point and line transect distance sampling methods to account for differences in species detectability. My research objectives are:

1.) To systematically collect bird abundance and habitat data along a series of transects following a period of unprecedented rainfall
2.) To generate detection functions and annual density estimates for individual species, and broadly assess inter-annual variation of species’ densities

3.) To verify a survey strategy that can be repeated and continued in the future to detect the impacts of weather changes on both short- and long-term population dynamics in nomadic and irruptive species

2.3 Methods

2.3.1 Study site

The study region occurs within inland Australia's Lake Eyre Basin and spans an area of approximately 160,000 km^2 in size (Fig. 2.1). Eighty-three percent of land in the region is grazed, with 15% managed for nature conservation (Land Use of Australia, Version 4, 2005–2006; http://data.daff.gov.au/anrdl/metadata_files/pa_luav4g9abl07811a00.xml), and artifical boreholes provide year-round water on pastoral leases. Vegetation primarily consists of chenopod shrublands, samphire shrublands and forblands (47% of sites; National Vegetation Information System (NVIS)—Major Vegetation Groups version 4.2; Table 2.2). The remainder of the study sites contain tussock grassland (29% of sites), and eucalypt and acacia woodland (10% of sites combined), hummock grassland (6% of sites), acacia shrubland (5% of sites), aquatic, naturally bare, and other shrublands and grasslands (3% of sites combined). The climate is characterized by extended periods of drought interspersed with brief and irregular rainfall events and is known for having the greatest rainfall variability of any arid region globally (McMahon et al., 2008; Morton et al., 2011). Mean annual temperatures range from 14.5 °C (minimum) to 29.5 °C (maximum) and mean annual rainfall is 186mm, with an average intra-annual rainfall coefficient of variation (CV) of 1.5 and an average inter-annual CV of 0.56. Long-term weather averages were calculated by averaging conditions from three representative weather stations (Birdsville Police Station, Marree, and Oodnadatta Airport) from the 1961-1990 reference period used by the Australian Bureau of Meteorology (www.bom.gov.au/climate/data).

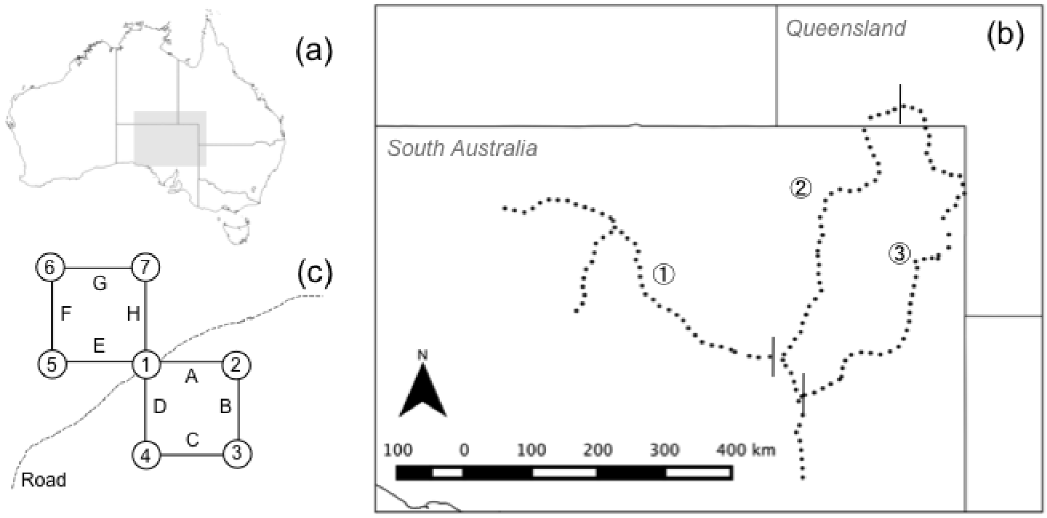


Figure 2.1. (a) Study region (shaded rectangle) within Australia. (b) Census stops (dots) along three driveable tracks: [1] Oodnadatta track; [2] Birdsville track; [3] Strzelecki track. Vertical lines indicate where tracks begin or end. c) Orientation of the eight 400m survey transects (letters) and seven survey points (numbers) at each census stop relative to the road.

Table 2.2. Mean percent cover of Major Vegetation Groups within a 2-kilometer radius of the 150 monitoring sites.

Major Vegetation Group	% cover
Acacia Open Woodlands	3.8
Acacia Shrublands	4.8
Chenopod Shrublands, Samphire Shrublands and Forblands	47.3
Cleared, non-native vegetation, buildings	< 0.1
Eucalypt Woodlands	5.8
Hummock Grasslands	6.3
Inland aquatic - freshwater, salt lakes, lagoons	1.1
Naturally bare - sand, rock, claypan, mudflat	0.1
Other Grasslands, Herblands, Sedgelands and Rushlands	0.7
Other Shrublands	1.6
Tussock Grasslands	28.5
Unclassified native vegetation	< 0.1
Unknown/no data	< 0.1

2.3.2 Study design

Three long-distance transect routes were established, each of approximately 800 kilometres in length along the Oodnadatta, Birdsville, and Strzelecki tracks of arid South Australia and Queensland and surveyed during each winter (between June and September) from 2012 to 2016. A survey team comprised of three people surveyed each of these transects over approximately 10 days. At least two of the three surveyors were fully trained in Australian bird identification and all were briefed on survey methods prior to commencing surveys. Each team travelled an average of 80 kilometres per day along each route, making a pre-determined census stop every ~16 kilometres to undertake spatially independent surveys while also surveying a sufficient number of sites within the survey season. A census stop forms a central point from which a series of line transect and point count survey replicates radiate (in a ‘figure-8’ orientation- see Fig. 2.1c) to thoroughly cover the surrounding habitat and to provide spatial replicates of bird counts. The locations of all census stops were provided as GPS waypoints. A survey (line) transect is a 400-metre transect carried out near to the census stop, and a survey point (count) is the location of a point survey near to the census stop (Fig. 2.1).

Upon arriving at a census stop, all three surveyors navigated to the GPS coordinates of the first census stop north of the road and broke into two groups. Both groups noted the census stop number, surveyor initials, date, and any conditions that may have affected the bird survey (wind, rain, presence of cattle, dingoes, etc.) in the survey notebook. Using a GPS unit to guide them, one group walked 400 metres due east (survey transect A) and the other group walked 400 metres due west (survey transect D), conducting the line transect method as they went (see method below under *2b: Line transect method*). Once each group reached the end of their survey transect, they conducted a 5-minute point count at survey points 2 and 5, respectively (see method below under *2a: Point count method*). Each team continued in this fashion following the scheme in Figure 2.1 until all survey transects and points were complete. Whichever group finished their surveys and returned to survey point 1 first completed this point count at the end. The survey teams aimed to complete all the surveys for each census stop within 60 minutes, although this varied a little according to terrain and the number of birds present.

2.3.3 Point count method

During the bird survey, surveyors stood at the survey point and looked intensively for birds for 5 minutes, timed on a stopwatch. For each individual or group of birds seen, observers noted: (i) the species; (ii) the number of birds in the group; (iii) the distance to the birds at the moment initially detected, measured with a laser rangefinder or estimated where use of the rangefinder was not possible; (iv) whether the bird was seen and/or heard; and (iv) whether the birds were flying or perched. Birds disturbed by observers walking toward the nearest survey point just prior to the survey (and distance from survey point) were included in the survey. There was no maximum distance for recording birds such that every audible or visible bird was recorded. Bird age, sex, any signs of breeding or feeding activity, and any animals recorded on multiple surveys (double counts) were written in the notes column of the survey booklet but did not significantly delay the survey.

Survey teams collected baseline vegetation data to rapidly assess local habitat structure and composition in ways that might influence bird species abundances, e.g., tree and shrub density, and type of vegetation cover. Within a 100-metre radius, each survey group noted the approximate proportion of main habitat types in the area: grass, bare ground, rock/gibber, chenopod, water, or herb. Survey groups recorded the presence of standing water or flowers anywhere in the greater survey area (i.e. beyond the 100m radius), noting the extent (e.g. small puddle versus a large lake or wetland) and proximity (> 1 kilometre away or within the survey area) where it was appropriate. To obtain estimates of tree and shrub density, surveyors recorded approximate distance to the nearest tree and shrub within four cardinal directional quadrants (northeast, southeast, southwest, northwest), as well as tree or shrub type if known (e.g. *Eucalyptus*, *Acacia*, *Eremophila*, chenopod, saltbush, etc).

2.3.4 Line transect method

Surveyors walked along the transect line looking and listening for birds, keeping an even, averaged, slow pace throughout the survey. For each individual or group of birds seen, surveyors noted: (i) the species, (ii) the number of birds in the group; (iii) the perpendicular distance between the bird and the transect line at the moment initially detected, measured with a laser rangefinder or estimated where it was not possible; (iv) whether the bird was seen and/or heard; and (v) whether the birds were flying or perched. Any animals detected on multiple surveys were marked ‘double’ in the notes section of the survey booklet. As with point counts, there was no maximum distance for recording birds and every bird was recorded. However, for line transects, observers did not record birds beyond the end or before the beginning of the transect line. Bird age, sex, any signs of breeding or feeding activity, and any animals recorded on multiple surveys (double counts) were recorded in the survey booklet but did not significantly delay the survey.

2.3.5 Distance sampling

I estimated densities for 64 species in total, which comprised 96% of all observations and 98% of all individual birds detected from 2012 to 2016. Individual species densities (birds/ha) were estimated using distance sampling methods, which model detection probability as a function of distance (Buckland et al., 2001). The detection probability is used to estimate the proportion of birds that were undetected. This is important as individual species are detected differently as a result of e.g. size, calling rate, behaviour and habitat preferences. Conventional distance sampling models make three core assumptions: (1) all objects at zero distance are detected; (2) objects do not move or are detected at their initial location; and (3) exact distances are measured (Thomas et al., 2010). Based on these assumptions, a detection probability is generated to estimate the likelihood that a bird is detected based on its distance from the transect line, and it is then possible to estimate the number of individuals that were undetected, and hence the density of birds in the area (Buckland et al., 1993). All density analyses were performed using the ‘Distance’ package in R (Miller, 2015; R Core Team, 2016).

2.3.6 Density estimation

Density is an abundance measure derived over a certain unit of area. For arid birds, I estimated density as the number of individual birds of a species per hectare using the formula (Buckland et al., 2001):

$$D = \frac{n}{2wLP_a}$$

where n is the detected number of individual birds of a species, w is the distance from the line within which individuals are detected (equivalent to the truncation distance), L is the transect length, and P_a is species' detection probability (derived from detection function models- see below). I estimated densities for individual species at each site in each year by pooling line transect counts and effort at a site, using three different approaches depending on whether a species had a sufficient number of observations. I estimated densities for 51 species with the minimum number of observations required for robust estimates (60; Buckland et al., 2001) by fitting detection functions to distance sampling data (Miller, 2015). I estimated densities for 13 species considered non-rare (present at >10% of sites) but that fell short of 60 observations using one of two approaches. A "surrogate species" approach was used for 9 species whereby the detection probability of the less common species is assumed to be similar to a more common surrogate species that has similar detection characteristics (Alldredge et al., 2007a; Fuller et al., 2008). I used a pooling approach for four species that lacked a surrogate equivalent by combining observations of two less common species with similar detection characteristics to generate one detection probability, which can then be applied to density estimation of each species individually (Alldredge et al., 2007). To obtain detection probabilities, I evaluated the fit of hazard rate and half normal detection function models, as recommended by Thomas et al. (2010), and included observer team as a covariate in each species' detection function model to account for potential differences in observer bias and ability. Since species detectabilities might vary with time of day, I ran an additional model for all species that included time of day as an additional covariate. I treated time of day as a discrete (factor) variable, with three levels depending on when an observation period commenced: 'AM' = before 11:00; 'MD' = 11:00 to 15:00; 'PM' = 15:00 onwards. If the model with time of day as a covariate had substantial support compared with the model without time of day as a covariate (i.e. had a lower AIC and ΔAIC > 2; Burnham & Anderson, 2002), this indicates that time of day affected the detection probability of these species. Distances at which birds were observed were grouped into intervals with cut-points selected such that distances favoured for rounding (e.g. 10m, 20m, etc.) fell midway between cut-points to avoid a heaping effect. Detections beyond 145 meters were excluded for density estimation of smaller-bodied (body mass < 150g; Table 2.3) species as at this distance detection probabilities for such species tended to fall below a suggested 15% threshold (Buckland et al., 2001). Similarly, I excluded detections beyond 505 meters for larger-bodied (body mass > 300 g) species.

Species with an average flock size of >4 within the relevant truncation distance were tested for cluster-size bias, as larger clusters of individuals are sometimes more easily detected at greater distance. Potential cluster bias was assessed by regressing log-transformed group size against scaled detection probability (Buckland et al., 2001). If cluster-size bias was present (as indicated by a significant regression), group size was included as an additional covariate in the detection function model. For each species or species-group (using the pooling method discussed previously), detection function model selection was performed using Akaike's Information Criterion, and model fit was assessed visually by checking detection function plots.

Table 2.3. Species mean body mass values from Garnett et al. 2015.

Species	Body mass (g)
Australasian Pipit	25.7
Australian Magpie	280
Australian Raven	593
Banded Lapwing	186
Banded Whiteface	10.5
Black Honeyeater	9.3
Black Kite	847
Black-faced Cuckoo-shrike	115
Black-faced Woodswallow	35.3
Black-shouldered Kite	275
Brown Falcon	574
Brown Songlark	53.2
Budgerigar	28.8
Chirruping Wedgebill	40.8
Cinnamon Quail-thrush	56.1
Cockatiel	92.4
Crested Bellbird	63.4
Crested Pigeon	192
Crimson Chat	10.7
Diamond Dove	32.1
Emu	35500
Fairy Martin	10.8

Flock Bronzewing	289
Galah	306
Gibberbird	17.5
Horsfield's Bronze-cuckoo	23.2
Inland Dotterel	79.2
Little Button-quail	45
Little Corella	497
Little Crow	396
Little Eagle	832
Magpie-lark	88
Masked Woodswallow	34.7
Mistletoebird	8.8
Nankeen Kestrel	179
Orange Chat	10.5
Pallid Cuckoo	87.6
Pied Honeyeater	26.4
Red-backed Kingfisher	51.7
Red-browed Pardalote	10.1
Red-capped Robin	8.7
Rufous Fieldwren	14.5
Rufous Songlark	29.7
Rufous Whistler	23.5
Singing Honeyeater	24.3
Southern Whiteface	12.4
Spiny-cheeked Honeyeater	44.7
Spotted Harrier	568
Striated Pardalote	11.1
Stubble Quail	101
Thick-billed Grasswren	19.3
Tree Martin	16.6
Variegated Fairy-wren	8
Wedge-tailed Eagle	3630
Whistling Kite	769
White-backed Swallow	14
White-browed Woodswallow	35.3
White-fronted Honeyeater	17.2

White-plumed Honeyeater	18.3
White-winged Fairy-wren	7.5
White-winged Triller	25.5
Willie Wagtail	20.7
Yellow-throated Miner	57.4
Zebra Finch	11.1

2.4 Results

The majority of species for which detection functions were generated (Fig. 2.2) and for which density was estimated (64%) showed significant fluctuations in inter-annual densities from 2012 to 2016 (Table 2.4; Fig. 2.3). Species detection probabilities ranged from 0.02 for Little Corella to 0.70 for Chirruping Wedgebill (Table 2.4) with a median of 0.22. Detection functions of most species showed a monotonically decreasing curve, indicating that detection probabilities were highest near the survey line or point and decreased with increasing distance (Fig. 2.2).

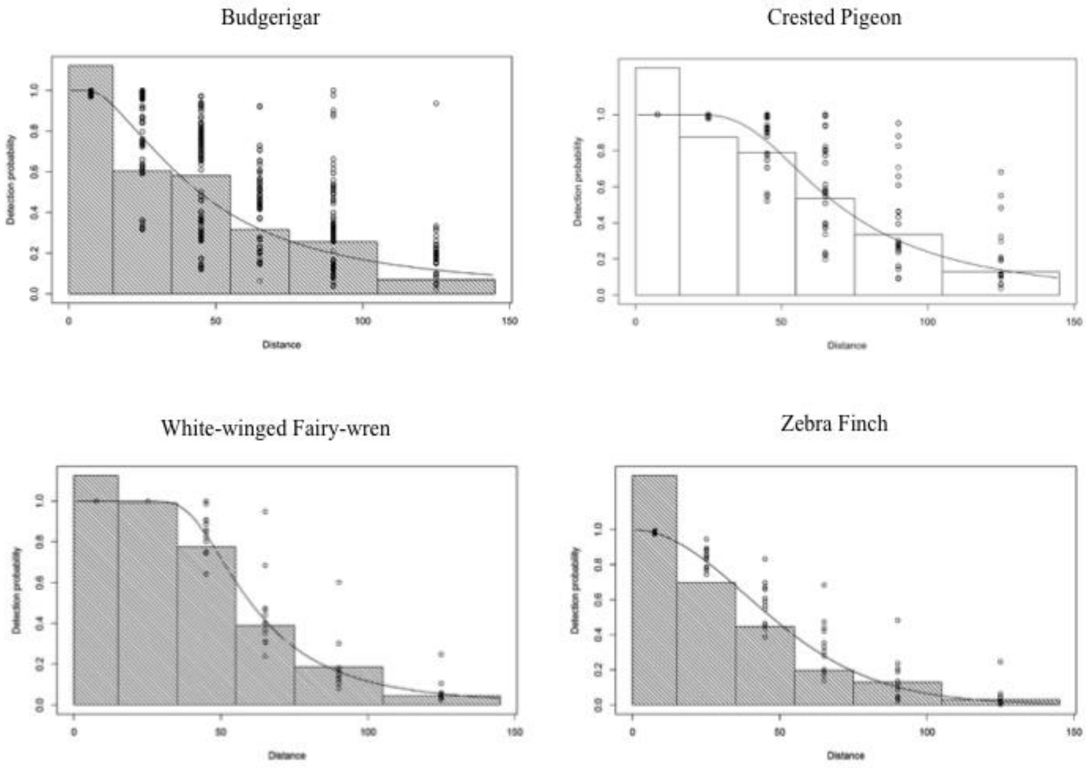


Figure 2.2. Species detection functions that model detection probability of species and species' composites (from Table

2.4) as a function of distance from the transect line. Observer team was included as a covariate to account for variable detection abilities among teams (open circles); a best fit detection function line is shown that best fits the variable team detections. Detection functions are shown for four example species here. See Fig. S1 (Appendices) for detection functions for all species.

Table 2.4. Species mean annual density estimates (± standard error) averaged across sites and years, results from Kruskal-Wallis rank sum test measuring whether species inter-annual densities varied significantly over the five-year period, and detection probabilities generated from detection function models. Densities for species with less than 60 observations in total were estimated using either a surrogate species or a pooling approach (see Methods).

Species	*Mean annual density (birds/km^2)*	*Kruskal-Wallis rank sum test (chi-sq; df; p-value)*	*Detection probability*	*Surrogate species (*)/species group (**)*
Australasian Pipit	3.9 ± 0.29	77.5; 4; 5.88E-16	0.31	
Australian Magpie	0.3 ± 0.04	17.7; 4; 0.001	0.33	
Australian Raven	1.2 ± 0.12	13.4; 4; 0.009	0.31	
Banded Lapwing	1.8 ± 0.66	2.2; 4; 0.695	0.10	Wader**
Banded Whiteface	0.4 ± 0.07	3.3; 4; 0.503	0.25	
Black Honeyeater	0.2 ± 0.06	6.3; 4; 0.18	0.30	Pied Honeyeater*
Black Kite	2 ± 0.82	157.1; 4; < 2.2e-16	0.11	
Black-faced Cuckoo-shrike	0.8 ± 0.44	3.8; 4; 0.428	0.09	
Black-faced Woodswallow	4.5 ± 0.63	19.9; 4; 0.001	0.20	
Black-shouldered Kite	0.1 ± 0.01	32.2; 4; 1.73E-06	0.38	
Brown Falcon	0.3 ± 0.04	87.4; 4; < 2.2e-16	0.29	
Brown Songlark	1.2 ± 0.14	17.1; 4; 0.002	0.62	
Budgerigar	34.1 ± 4.49	213.1; 4; < 2.2e-16	0.05	
Chirruping Wedgebill	1.2 ± 0.15	7.7; 4; 0.104	0.70	
Cinnamon Quail-thrush	1.7 ± 0.13	20.5; 4; 0.004	0.51	
Cockatiel	1.3 ± 0.39	22.4; 4; 0.0002	0.06	
Crested Bellbird	0.1 ± 0.04	2.1; 4; 0.709	0.42	
Crested Pigeon	3.7 ± 0.62	12.9; 4; 0.019	0.21	
Crimson Chat	3.4 ± 0.65	24.8; 4; 0.00006	0.09	
Diamond Dove	7.2 ± 4.81	61.3; 4; 1.5E-12	0.08	
Emu	0.2 ± 0.05	12.4; 4; 0.014	0.11	
Fairy Martin	2.5 ± 0.88	47.9; 4; 9.98E-10	0.35	
Galah	5.2 ± 1.42	26; 4; 0.00003	0.04	
Gibberbird	1.4 ± 0.89	16.2; 4; 0.003	0.22	
Hooded Robin	0.2 ± 0.05	4.2; 4; 0.376	0.22	Red-capped Robin*
Horsfield's Bronze-cuckoo	0.3 ± 0.13	37; 4; 1.84E-07	0.29	

Inland Dotterel	2.8 ± 0.76	11.8; 4; 0.019	0.10	Wader**
Little Button-quail	1.9 ± 0.43	33.7; 4; 8.73E-07	0.04	Ground flusher**
Little Corella	6.1 ± 2.2	6.3; 4; 0.179	0.02	
Little Crow	1 ± 0.14	26.3; 4; 0.00003	0.17	
Little Eagle	0.02 ± 0.006	8.8; 4; 0.066	0.41	Whistling Kite*
Magpie-lark	0.2 ± 0.04	8.7; 4; 0.069	0.51	
Masked Woodswallow	6.8 ± 2.45	22.3; 4; 0.0002	0.03	
Mistletoebird	0.3 ± 0.08	6.8; 4; 0.148	0.30	
Nankeen Kestrel	0.6 ± 0.05	74.1; 4; 3.10E-15	0.37	
Orange Chat	6.3 ± 0.59	62.6; 4; 8.07E-13	0.14	
Pallid Cuckoo	0.5 ± 0.19	12; 4; 0.018	0.09	Black-faced Cuckoo-shrike*
Pied Honeyeater	0.9 ± 0.26	32.4; 4; 1.61E-06	0.30	
Red-backed Kingfisher	0.2 ± 0.04	47.2; 4; 1.4E-09	0.45	
Red-browed Pardalote	0.1 ± 0.03	3.8; 4; 0.434	0.60	
Red-capped Robin	0.9 ± 0.19	15.3; 4; 0.004	0.22	
Rufous Fieldwren	1.6 ± 0.82	14.5; 4; 0.006	0.19	
Rufous Songlark	0.7 ± 0.19	41.6; 4; 2.03E-08	0.38	
Rufous Whistler	0.4 ± 0.1	7; 4; 0.134	0.22	White-winged Triller*
Singing Honeyeater	3.6 ± 0.28	24.6; 4; 0.00006	0.41	
Southern Whiteface	0.4 ± 0.1	2.8; 4; 0.584	0.25	Banded Whiteface*
Spiny-cheeked Honeyeater	1.1 ± 0.22	8; 4; 0.092	0.36	
Spotted Harrier	0.2 ± 0.03	32.3; 4; 1.66E-06	0.11	Black Kite*
Striated Pardalote	0.3 ± 0.07	4.4; 4; 0.36	0.23	
Stubble Quail	1 ± 0.26	35.2; 4; 4.18E-07	0.04	Ground flusher**
Thick-billed Grasswren	0.7 ± 0.18	8.8; 4; 0.066	0.17	
Tree Martin	6.4 ± 3.36	13.6; 4; 0.009	0.03	
Variegated Fairy-wren	2.8 ± 0.65	5.7; 4; 0.222	0.08	
Wedge-tailed Eagle	0.1 ± 0.02	7.8; 4; 0.099	0.35	
Whistling Kite	0.1 ± 0.02	19; 4; 0.008	0.41	
White-backed Swallow	2.6 ± 0.79	10.8; 4; 0.029	0.07	
White-browed Woodswallow	5.9 ± 3.42	5.2; 4; 0.271	0.03	Masked Woodswallow*
White-fronted Honeyeater	0.4 ± 0.15	17.7; 4; 0.001	0.36	Spiny-cheeked Honeyeater*

White-plumed Honeyeater	3.2 ± 0.51	0.2; 4; 0.996	0.20
White-winged Fairy-wren	19.5 ± 1.01	58.2; 4; 6.89E-12	0.21
White-winged Triller	0.4 ± 0.12	24.7; 4; 0.00006	0.22
Willie Wagtail	1.7 ± 0.15	9.3; 4; 0.054	0.37
Yellow-throated Miner	1.3 ± 0.32	4.2; 4; 0.38	0.17
Zebra Finch	52.9 ± 4.83	68.7; 4; 4.18E-14	0.07

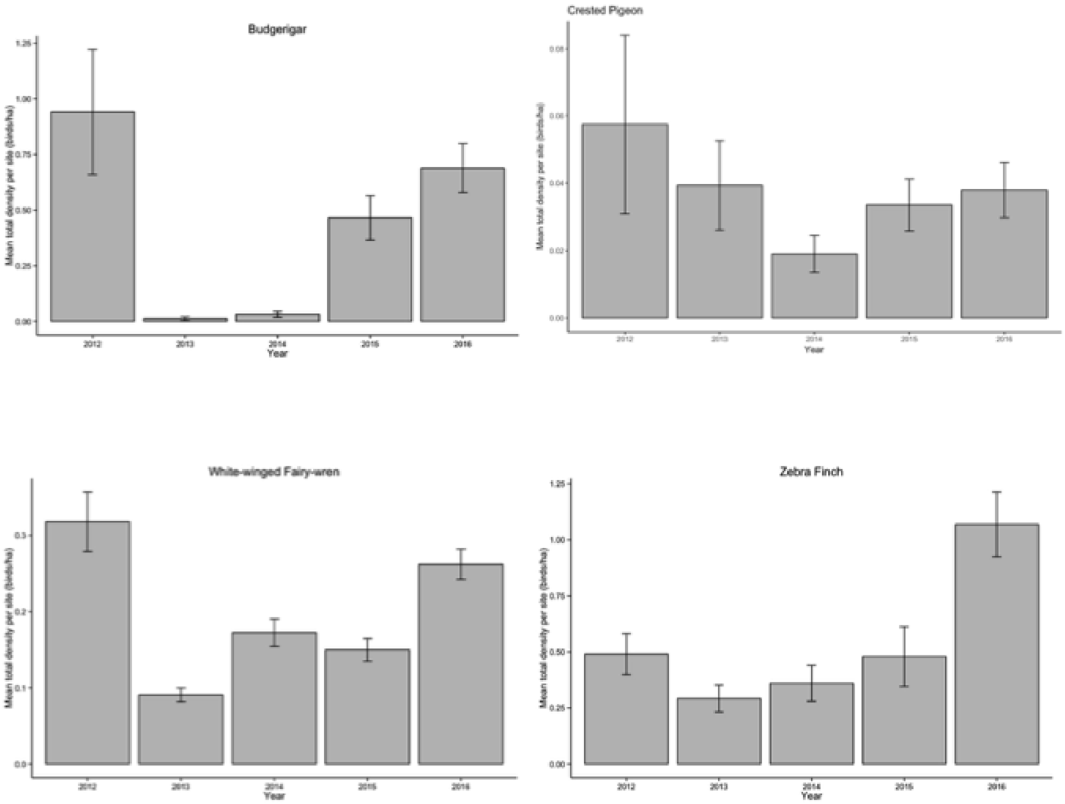


Figure 2.3. Species mean annual densities averaged across sites ± standard error. Densities are shown for four example species here. See Fig. S2 (Appendices) for densities for all species.

The species detected most frequently during line and point surveys were Zebra Finch and White-winged Fairy-wren, which consistently had the highest numbers of observations across all survey years (Table 2.5). These species also had the highest mean annual densities along with Budgerigar, with 19.5 ± 1.01 birds/km^2 for White-winged Fairy-wren, 34.1 ± 4.49 birds/km^2 for Budgerigar, and 52.9 ± 4.83 birds/km^2 for Zebra Finch (Table 2.4). Twenty-eight species (18%) were detected in only one survey year, and 50 species

(32%) were detected on five or fewer occasions (Table 2.5). The least abundant species with enough observations for a robust density estimate was Little Eagle, with a mean annual density of 0.02 ± 0.006 birds/km^2 (Table 2.4). The most widespread species found at the most number of sites was Australian Raven, followed by White-winged Fairy-wren, Nankeen Kestrel, Zebra Finch, and Australasian Pipit (Table 2.5). The least widespread species found at five or less sites accounted for 38% of all species detected and included Chestnut-breasted Whiteface, Blue-winged Parrot, Letter-winged Kite, Red-tailed Black-cockatoo, Australian Bustard, and Black and Grey Falcon (Table 2.5). Time of day significantly improved detection model fit for seven species and six pooled detection function group species– Australian Magpie, Banded Lapwing, Black-faced Cuckoo-shrike, Cinnamon Quail-thrush, Crested Pigeon, Diamond Dove, Inland Dotterel, Little Crow, Little Eagle, Pallid Cuckoo, Rufous Songlark, Whistling Kite, and Willie Wagtail (Fig. S1).

Table 2.5. Total number of observations made for individual species at line transect and point counts and total number of sites each species at which each species was detected.

Species	*2012*	*2013*	*2014*	*2015*	*2016*	*# sites (out of 156)*
Australasian Darter	5	0	0	0	0	1
Australasian Grebe	2	0	0	1	2	3
Australasian Pipit	162	83	151	220	360	138
Australian Bustard	1	1	0	0	1	3
Australian Hobby	8	2	3	1	3	11
Australian Magpie	143	99	53	65	61	84
Australian Owlet-nightjar	1	0	1	0	0	2
Australian Pelican	1	4	0	0	4	6
Australian Pratincole	0	0	0	3	26	7
Australian Raven	336	282	261	324	211	147
Australian Reed-Warbler	3	0	0	0	1	1
Australian Ringneck	15	4	7	3	3	10
Australian Wood Duck	2	0	0	0	0	1
Banded Lapwing	7	18	11	14	17	28
Banded Whiteface	23	13	14	23	12	32
Barn Owl	3	0	0	0	0	3
Black Falcon	2	1	0	0	1	4
Black Honeyeater	4	8	4	16	15	21
Black Kite	257	7	25	54	379	110
Black Swan	3	0	0	1	0	2
Black-breasted Buzzard	4	1	0	3	11	11
Black-eared Cuckoo	0	0	1	1	3	3
Black-faced Cuckoo-shrike	22	10	11	30	13	26
Black-faced Woodswallow	189	125	116	237	213	117

Black-fronted Dotterel	4	0	1	1	4	6
Black-shouldered Kite	48	4	2	2	11	26
Black-tailed Native-hen	0	0	2	3	0	3
Blue Bonnet	14	15	6	2	9	7
Blue-winged Parrot	0	0	0	1	1	2
Bourke's Parrot	4	5	8	8	3	12
Brolga	11	3	0	2	1	9
Brown Falcon	163	14	47	33	63	110
Brown Goshawk	1	0	0	0	1	2
Brown Songlark	131	111	87	216	174	103
Budgerigar	203	22	60	338	682	130
Caspian Tern	0	0	0	3	5	4
Chestnut-breasted Whiteface	0	0	1	0	0	1
Chestnut-crowned Babbler	1	4	2	6	13	11
Chestnut-rumped Thornbill	6	2	1	8	6	9
Chiming Wedgebill	2	4	2	9	9	4
Chirruping Wedgebill	239	169	144	163	214	80
Cinnamon Quail-thrush	129	181	132	182	272	113
Cockatiel	3	17	2	15	44	29
Collared Sparrowhawk	1	0	0	1	1	3
Common Bronzewing	2	0	0	0	0	2
Common Starling	0	1	0	0	0	1
Crested Bellbird	21	26	22	26	11	21
Crested Pigeon	177	141	113	151	156	99
Crimson Chat	37	16	17	97	57	63
Diamond Dove	22	9	8	29	107	45
Dusky Woodswallow	0	1	2	0	2	4
Elegant Parrot	11	1	2	7	14	10
Emu	4	31	14	7	36	31
European Starling	0	0	0	0	3	1
Eyrean Grasswren	1	7	1	1	25	10
Fairy Martin	1	0	8	0	60	20
Fantail Cuckoo	0	0	0	0	1	1
Flock Bronzewing	13	13	1	1	0	16
Galah	96	94	110	151	206	94
Gibberbird	9	10	9	19	55	32
Grey Butcherbird	3	1	14	4	1	5
Grey Falcon	1	1	1	1	0	4
Grey Fantail	1	0	1	2	5	6
Grey Shrike-thrush	5	0	1	8	3	7
Grey Teal	3	0	0	3	5	8
Ground Cuckoo-shrike	2	0	0	0	0	2
Gull-billed Tern	0	0	0	0	3	3
Hardhead	1	0	0	0	0	1
Hoary-headed Grebe	0	0	2	0	0	1
Hooded Robin	11	5	4	11	4	14

Horsfield's Bronze-cuckoo	8	10	28	36	73	63
Horsfield's Bushlark	5	3	2	7	7	15
House Sparrow	8	1	3	2	5	4
Inland Dotterel	10	9	6	18	24	32
Inland Thornbill	0	1	0	1	0	2
Jacky Winter	3	0	2	7	1	10
Letter-winged Kite	0	3	0	0	3	2
Little Black Cormorant	0	0	0	0	1	1
Little Button-quail	13	1	0	2	17	24
Little Corella	38	90	60	73	120	77
Little Crow	201	90	99	44	146	96
Little Eagle	2	2	6	11	7	17
Little Grassbird	2	0	0	3	1	3
Little Pied Cormorant	2	0	0	0	0	1
Little Raven	4	8	0	0	4	6
Magpie-lark	25	4	13	19	29	25
Masked Lapwing	2	1	4	3	1	3
Masked Woodswallow	4	5	130	46	46	49
Mistletoebird	26	35	9	15	18	27
Mulga Parrot	4	1	0	4	11	11
Nankeen Kestrel	346	121	99	196	171	145
Orange Chat	154	34	65	228	185	114
Pacific Black Duck	2	0	0	0	5	7
Painted Honeyeater	0	0	1	0	0	1
Pallid Cuckoo	6	1	1	16	13	14
Peaceful Dove	3	0	1	0	0	3
Peregrine Falcon	1	1	1	3	1	6
Pied Butcherbird	8	8	2	0	2	4
Pied Cormorant	0	1	0	0	0	1
Pied Honeyeater	18	6	11	143	57	55
Pink-eared Duck	0	0	1	2	0	2
Plains-wanderer	1	0	0	0	0	1
Plumed Whistling Duck	0	0	0	0	1	1
Rainbow Bee-eater	0	0	1	0	10	7
Red-backed Kingfisher	7	2	2	9	79	36
Red-browed Pardalote	3	23	12	23	24	19
Red-capped Plover	5	0	0	2	0	5
Red-capped Robin	59	25	23	34	23	45
Red-rumped Parrot	0	0	2	2	1	4
Red-tailed Black-Cockatoo	0	0	1	4	0	2
Redthroat	7	4	0	1	3	8
Restless Flycatcher	0	0	0	1	1	2
Rufous Fieldwren	33	68	58	68	112	48
Rufous Songlark	12	14	17	46	126	48
Rufous Whistler	14	4	16	6	26	23
Sacred Kingfisher	0	0	0	0	1	1

Silver Gull	0	0	0	0	1	1
Silvereye	0	0	1	0	0	1
Singing Honeyeater	395	259	281	312	315	124
Southern Boobook	0	0	2	0	0	2
Southern Whiteface	10	7	12	13	7	19
Spangled Drongo	0	0	1	0	0	1
Spiny-cheeked Honeyeater	121	95	42	51	46	51
Splendid Fairy-wren	2	4	15	11	8	7
Spotted Harrier	28	6	2	4	21	32
Spotted Nightjar	0	0	0	1	0	1
Spotted Pardalote	3	0	0	0	0	2
Straw-necked Ibis	4	0	0	0	17	9
Striated Pardalote	41	12	12	12	15	14
Striated Thornbill	0	0	0	0	1	1
Stubble Quail	13	3	0	1	3	17
Sulphur-crested Cockatoo	0	0	1	0	0	1
Swamp Harrier	0	0	0	1	0	1
Thick-billed Grasswren	30	6	22	19	14	31
Tree Martin	45	30	23	47	53	45
Variegated Fairy-wren	30	26	23	41	37	58
Wedge-tailed Eagle	119	106	75	59	67	122
Weebill	11	1	4	0	2	8
Welcome Swallow	9	2	4	5	9	14
Whistling Kite	51	11	7	31	34	52
White-backed Swallow	35	42	22	54	40	55
White-breasted Woodswallow	0	0	2	0	3	3
White-browed Babbler	4	2	0	3	2	7
White-browed Woodswallow	9	5	8	11	7	20
White-faced Heron	2	2	0	0	1	3
White-fronted Chat	0	2	0	1	2	4
White-fronted Honeyeater	17	3	3	27	2	17
White-necked Heron	11	0	1	3	8	11
White-plumed Honeyeater	68	112	80	81	78	41
White-winged Fairy-wren	591	435	466	490	788	145
White-winged Triller	5	5	3	21	41	24
Willie Wagtail	155	103	78	142	106	100
Yellow-throated Miner	53	50	38	27	42	32
Zebra Finch	457	331	391	444	776	142

Over the five-year survey period, survey teams conducted 715 site-surveys over 156 sites in total (additional sites were created when original sites were inaccessible), with 126 of the 150 sites visited in all years due to flood and access-related logistic difficulties. Each of the three tracks were surveyed over a ~16-day period and total field costs were $16500 on average each year (see Table S1 for details). Teams completed 5716 line transects and 5005 point counts that covered 2290 kilometres and 417 hours, respectively. In total, 21955 observations of 89764 individual birds were made at line transects and 13145 observations of 65914 individual birds were made at point counts. Surveyors detected 145 species along line transects and 127 species during point counts, with 24 species unique to line transects and six species unique to point counts. In each survey year, more observations were made and more individual birds and species were detected along line transects than at point counts (Table 2.6). Line transects also consistently detected more unique species than point counts (Table 2.6).

Table 2.6. Summary of completed line transect and point count surveys, and number of species observations, individual birds, and species detected for each survey type. Total numbers are reported across all sites and medians, minima, and maxima are reported at the site-level for each survey year. N = number of sites surveyed; IQR = inter-quartile range.

	2012		2013		2014		2015		2016	
Time of year	Jul		Jun, Jul		Jul		Jul, Aug		Aug, Sep	
# Observers	10		9		6		8		7	
Census stops	N = 132		N = 148		N = 150		N = 150		N = 135	
Surveys	*Line*	*Point*	*Line*	*Point*	*Line*	*Point*	*Line*	*Point*	*Line*	*Point*
Total	1056	924	1182	1036	1198	1050	1200	1050	1080	945
Observations										
Total	5132	2746	2906	2104	2839	1970	4608	2550	6470	3775
Median per site ± IQR	28.5 ± 35.8	17 ± 20	13 ± 21.8	11 ± 15	13.5 ± 19	11 ± 12	20.5 ± 29.3	14 ± 14.8	44 ± 34.5	27 ± 18.5
Range	1–194	1–68	0–131	0–60	0–107	0–46	0–182	0–68	4–164	2–82
Individual birds										
Total	22515	14171	17757	16121	15050	13255	16205	10921	18237	11446
Median per site ± IQR	82.5 ± 144	45 ± 77.8	30 ± 57.3	20.5 ± 34.3	27.5 ± 60	20.5 ± 46	50.5 ± 102.3	28.5 ± 58.5	100 ± 117.5	56 ± 65
Range	1–1789	1–1542	0–8451	0–10047	0–6033	0–4019	1–1742	0–2552	3–687	2–1063
Species richness										
Total	116	97	90	81	90	84	105	86	115	102
Median per site ± IQR	12 ± 9	8.5 ± 7	6 ± 6	5.5 ± 5	6 ± 6	6 ± 5.8	9 ± 8.5	7.5 ± 5	12 ± 8	11 ± 6.5
Range	1–37	1–25	0–23	0–17	0–28	0–20	0–41	0–30	3–37	2–29
Species unique to survey type	22	3	16	7	19	13	24	4	20	7

2.5 Discussion

To obtain unbiased, representative abundance estimates of arid Australian bird species across a large portion of their range, a standardized distance sampling monitoring protocol was developed. This approach yielded the first ever estimates of detection probabilities and robust density estimates across 126 repeatedly visited sites over the five-year survey period for much of Australia's arid-zone bird assemblage. Vegetation surveys yielded data on local environmental conditions that are used as covariates in models of site-level species abundance in Chapter 4. Line transects detected more species and more individuals of species than point counts but each approach detected unique species not detected by the other survey type (Table 2.6). Similarly, other studies found that line transects were more efficient in terms of precision of density estimates in open habitats (Buckland, 2006), and in terms of time- and cost-effectiveness (Cassey et al., 2007). Line transects are better for covering more ground, detecting more birds, preferable for less dense populations of more mobile and conspicuous species, and result in less serious errors compared with point counts (Bibby et al., 1998; Gregory et al., 2004). Species counts from line transects are thus more appropriate for generating accurate density estimates in this study than from point counts. However, species records from point counts combined with records from line transects give a more complete species list for the study region and contribute data toward species occurrence patterns. While line transects are better for recording more species of bird overall, a strength of the point count method is that it is better for detecting cryptic and skulking species (Bibby et al., 1998; Gregory et al., 2004). Surprisingly, only two other studies of arid birds used line transects to survey species abundance (Table 2.1; Wiens, 1991; Pavey & Nano, 2009); the majority of previous studies used random walks while two used point counts (Dean & Milton, 2001; Tischler et al., 2013). As point counts are conducted contemporaneously with the vegetation surveys in order to relate species detections with habitat features (Bibby et al., 1998), the amount of time saved by discontinuing point counts would likely be minimal, therefore it is worthwhile continuing both survey methods. Probability of detection was fairly low for all species, indicating that many individuals went undetected by observers, and abundance fluctuated significantly between years for 42 species and remained fairly stable for 22 species.

Previous studies that have measured arid bird abundance found densities comparable to this study, with generally low species abundance compared to other arid regions (Wiens, 1991). Jordan et al. (2017) measured species abundances at a reserve within central Australia's Great Sandy Desert bioregion over a six-year period. Species abundances were similar to density estimates for many species in this study, but densities for some of the most abundant species were much higher in this study, such as Budgerigar (x6), Black Kite (x130), and Galah (x70). Jordan et al used bird counts from random walks to measure abundance rather than distance sampling, which accounts for missed individuals, and their surveys were conducted in autumn, thus their abundance estimates are likely underestimated. Wiens (1991) conducted surveys over just a year period in summer in arid shrublands of New South Wales and found similar densities of Zebra Finch to this study when averaged over three different plots. Burbidge and Fuller (2007) reported bird counts from a reserve in Western Australia's Gibson Desert Bioregion over a five-year period for 54 species. Many of the most common species in this study were also common in these studies, including Budgerigar, Masked Woodswallow, White-winged Fairy-wren, and Zebra Finch. While these studies used standardized survey methods, they did not account for different detectabilities among species and consequent observer detection error and were conducted at relatively limited spatial or temporal scales. Jordan et al conducted surveys across 66 sites at Newhaven Wildlife Sanctuary—a region 2,600 square kilometres in area—in comparison to the 126 sites surveyed over approximately 160,000 square kilometres in the study area. Wiens' survey was conducted at four 2km^2 plots in arid New South Wales, and Burbidge and Fuller surveyed four paired 1-square kilometre quadrats over an 18,900-square kilometre reserve. Thus, extrapolating species' abundances from limited spatial areas or over limited time scales is likely to be less accurate than a study done over a large area and over multiple years.

This methodology is a snapshot approach to surveying as it only takes place in austral winter. This season is arguably the most active time for Australia's arid bird assemblage as it receives more rain and has lower temperatures than other times of year (Morton et al., 2011), allowing for optimal breeding and foraging conditions (Burbidge & Fuller, 2007). However, bird activity at census stops the remainder of the year is unknown. Birds could be dying, breeding, or moving in between sites during the period of time between winter surveys. Surveying during other seasons is one option, although maximum summer temperatures in the study region can reach dangerously high levels (mean highest temperature in January for Birdsville, Queensland is 45 °C), and surveying during this period would require avoiding the hottest times of the day to ensure surveyor safety, substantially lengthening the period of the entire field trip. Bird activity during the middle of the day is also likely to be negligible. Surveying during spring and autumn would be more feasible, with spring coinciding with the breeding period of many species and the arrival and departure of migratory species. Other options include remote surveying, such as the deployment of acoustic sensors that can remain in place year-round.

Other improvements that could be made to this survey, pending logistical and financial limitations, would be conducting a more rigorous assessment of plant groups and species at the site level. As this survey relies on a rapid assessment of bird numbers at a site, less time is given to describing vegetation communities, which undoubtedly influence the species and numbers of birds present at the time of surveying. Continued monitoring of survey sites over a long-term period (10+ years) would capture sporadic weather events such as flooding and droughts and give important insight into longer-term population trends. Monitoring the breeding success of resident species at sites would give further insight into species reproductive rates in relation to fluctuating weather and would enable attributing changes in species inter-annual abundance to demographic versus movement processes.

Line transects and point counts were used to monitor a highly mobile avian community over a vast and remote arid region. Line transects were more effective at detecting species and numbers of birds, but point counts still contributed unique species detections. A distance sampling approach allowed for missed individuals to be incorporated into individual species detection probabilities, providing improved and robust measures of abundance compared with previous studies of arid-zone birds. I have shown the survey approach outlined in this chapter is a cost- and time-effective way to perform a standardized survey across years that yields reliable abundance estimates for a suite of data-poor species.

Arid-zone birds are a little-studied group due to logistical challenges associated with accessing remote locations, harsh climate conditions, and naturally low densities of animals, which necessitates an increased survey effort to sample a statistically sufficient number of individuals. Where publicly accessible roads provide adequate geographic coverage of an arid region, the survey methodology outlined here can be applied to gather data on multiple species. Many forms of bias can lead to underestimated species counts and densities, underscoring the importance for implementing survey methods that account for such factors. Distance sampling is an ideal solution that allows for abundance estimates adjusted for various detection biases and that can be compared between different species and habitats. I show that the bird community of arid Australia has densities much higher than previous studies found using unadjusted species count data. Obtaining precise abundance measures of poorly understood groups is critical to assess population declines and related threats especially in relation to habitat and climatic factors, to assess serious threats and extinction risk.

3

Where nothing stands still: evidence of widespread fluctuations in Australian arid-zone birds

3.1 Abstract

In arid regions of the southern hemisphere, nomadism is a dominant form of movement for many species in response to irregular climate-driven fluctuations in resources. Bird communities of Australia's arid interior contain one of the highest proportions of presumed nomadic bird species worldwide. However, because of limited survey data, our understanding of spatial and temporal changes in avian occurrence and abundance remains very poor. Here I make a first attempt to quantify nomadism among an entire bird assemblage, identify which species undertake nomadic movements, the extent to which they perform such movements, and whether there are clear nomadic and non-nomadic strategists in the assemblage. I then use results to critique the existing paradigm of species movement classifications. Repeat annual bird surveys were undertaken at 150 points spread along three long-distance (800km+) transects through the interior of southeast and central Australia from 2012-2016 using distance sampling techniques. I measured how many years each species was present at a site, and calculated inter-annual variability in species density, using both to infer movement patterns of this arid-zone bird assemblage. I compare my results with movement classifications from an authoritative monograph of Australian birds. Eighteen and 10 species were classified as nomadic and resident, respectively, while the majority (34) fell somewhere in between based on inter-annual patterns of occurrence and abundance. Extent of movement varied along a gradual continuum with no evidence of distinct nomadic and non-nomadic groups. In comparison to existing classifications, I found the extent of species movements was underestimated for over half of the arid bird assemblage. Results indicate that much of Australia's arid bird assemblage is considerably more mobile than existing classifications suggest. Such findings have important implications for how to best protect these dynamic species as a traditional static protected area approach is likely inadequate. I advise that caution is needed when using sweeping species-level classifications, especially for Australian birds whose movements can be heavily environment-dependent.

3.2 Introduction

Mobile species can be classified into one of four groups based on differing strategies for acquiring resources: residents inhabit a given locality year to year by having broad dietary niches and/or moving locally; migrants display predictable to-and-fro movement each year, relocating wholesale to areas with consistently available seasonal resources; irruptive species can exhibit resident behaviour in years when resources are abundant and undertake long-distance movements outside of their normal range in years of low resource availability; and nomadic species move with little or no seasonal regularity, tracking resources that fluctuate over space and time (Jonzén et al., 2011; Newton, 2012; Runge et al., 2014; Cottee-Jones et al., 2015). Nomadism represents the most extreme example of spatially and temporally dynamic distributions (Jonzén et al., 2011; Cornelius & Hahn, 2012; Cottee-Jones et al., 2015), functioning to buffer species against extreme environmental variation (Lloyd, 1999; Dean, 2004), and is the dominant form of movement for many southern hemisphere species (Dean, 2004). It is found across a wide range of feeding guilds, from granivores and nectarivores tracking seed and nectar production (Keast, 1968; Wyndham, 1983; Eby et al., 1999), to herbivores (Singh et al., 2012) and raptors tracking irruptions of prey populations (Pavey & Nano, 2013). Resource pulses often follow rainfall events and can also lead to opportunistic breeding; for example, the swift parrot (*Lathamus discolor*) tracks ephemeral, nectar-producing flowers and breeds where they are most abundant (Stojanovic et al., 2015). Information on arid bird breeding response to rainfall and newly available resources is lacking. There is some evidence of breeding activity within a couple months of rainfall for certain species (Burbidge & Fuller, 2007) and a study on Zebra Finch found peak breeding activity four months following heavy rainfall (Zann et al., 1995). The possibility of breeding contributing to an increase in population rather than movement cannot be ruled out for arid species, especially following significant rain events.

Very little is known about the movements of nomadic species despite the fact that many are threatened (Cottee-Jones et al., 2015), challenging the development of effective conservation strategies for these species. Most conventional conservation approaches assume species distributions to be static and envision protected areas as the primary tool to protect species. This can lead to inadequate management strategies, for species with dynamic distributions such as nomads (Runge et al., 2014; Cottee-Jones et al., 2015). Alternative approaches that incorporate dynamic species distributions include state- and time-dependent actions, such as creating temporary habitat for migratory species (Reynolds et al., 2017), or altering human activities to mitigate negative impacts on migratory animals and their habitats (Drewitt & Langston, 2006; Grantham et al., 2008). Furthermore, treating species geographic range size as a fixed attribute when assessing extinction risk or as a proxy for their typical distribution may underestimate extinction risk in nomadic species if range size is estimated by pooling occurrences over time (Runge et al., 2015a). Indeed, spatial prioritization of protected areas can vary enormously depending on movement patterns of species, thus improving our understanding of movement patterns is an essential first step toward making informed conservation decisions (Runge et al., 2016).

The arid interior of Australia contains one of the highest proportions of nomadic bird species worldwide, with 30 to 46% of the continent's breeding species considered at least partially nomadic (Dean, 2004). Irregular rainfall events in the region result in resource pulses (Nano & Pavey, 2013) that trigger an influx of nomadic species, some flying thousands of kilometres in a matter of days (Pedler et al., 2014). The remainder of the arid bird assemblage is thought to comprise mainly residents (Dean, 2004; Burbidge & Fuller, 2007), which are more arid-adapted and able to persist through harsh periods. This movement dichotomy has become conventional wisdom (Davies, 1984), but it remain uncertain as to whether there are nomadic versus non-nomadic strategists or whether species vary along a continuum of movement types from fully resident to fully nomadic. Further, the classification of species as nomadic has been largely based on incidental historical records and expert opinion (e.g. Keast, 1968; Schodde, 1982; Pavey & Nano, 2009) and there have been few attempts to quantify extent of species movements (Griffioen & Clarke, 2002; Webb et al., 2014; Jordan et al., 2017). Existing data collected by citizen scientists and field biologists have progressed understanding of arid bird species distributions and movements (Reside et al., 2012; Runge et al., 2015a) and response to rain (Burbidge & Fuller, 2007; Pavey & Nano, 2009; Tischler et al., 2013; Jordan et al., 2017). However, strong spatial and temporal biases in survey effort, for instance toward coastal areas or during cooler periods of the year, result in sparse and localized data. Moreover, field studies are often done at smaller spatial or temporal scales than that at which mobile species and weather dynamics typically operate. Repeated, systematic surveys across a broad area are needed to generate data on movement patterns that are comparable among species.

For the first time, I use empirical time series data to assess avian movement patterns across one of the most arid regions of central Australia following an extreme rainfall event. I (i) quantify inter-annual variation in occupancy and abundance among a majority of species in the arid-zone assemblage, (ii) determine whether their movement patterns fall into two distinct groups of nomads and residents, and (iii) compare my measures of nomadism with existing classifications of bird movement strategies. I measure variation in mean annual density for 63 species ('CV of density'), and explore persistence of individual species at each site over the five-year survey period ('site persistence'). Because an increase in species abundance alone could be due to demographic processes (births and deaths), I consider change in abundance and change in occupancy together as a measure of species nomadism versus residency. I expect that previously-identified nomadic species will display highly variable abundance and low site persistence as they are thought to track rain and resources that are unpredictable in space and time (Davies, 1984; Burbidge & Fuller, 2007). Conversely, I expect resident species will show less variable inter-annual abundance and high site persistence.

3.3 Methods

3.3.1 Study Region

The study area is located in the Lake Eyre Basin, a region of approximately 1.2 million km^2 (16% of the continent) of arid inland Australia and which has the greatest annual rainfall variability of any arid region globally. About 83% of land in the region is grazed, with 15% managed for nature conservation (Land Use of Australia, Version 4, 2005–2006; http://data.daff.gov.au/anrdl/metadata_files/pa_luav4g9abl07811a00.xml). Artifical boreholes provide year-round water on pastoral leases, and vegetation is dominated by chenopod shrublands, samphire shrublands and forblands, and tussock grassland as defined by the Australian Government's National Vegetation Information System (NVIS 4.2, Australian Government Department of Environment and Energy; Table 2.2). The area experiences extended periods of drought interspersed with brief and irregular rainfall events (McMahon et al., 2008; Morton et al., 2011). Long-term weather averages for the region are taken from three representative weather stations (Fig. 3.1) from the 1961-1990 reference period used by the Australian Bureau of Meteorology (www.bom.gov.au/climate/data). Mean annual temperatures range from 14.5 °C (minimum) to 29.5 °C (maximum) and mean annual rainfall is 186mm, with an average intra-annual rainfall coefficient of variation (CV) of 1.5 and an average inter-annual CV of 0.56. Intra-annual rainfall CV was calculated for each year (1961-1990) as the standard deviation of total monthly rainfall divided by the average total monthly rainfall, which was then averaged across the three weather stations. Inter-annual rainfall CV was calculated as the standard deviation of total annual rainfall across years divided by the average total annual rainfall across years. In 2010 and 2011, back-to-back rainfall events that greatly exceeded long-term averages occurred over much of central Australia, marking both the wettest two-year period and the end of the longest dry period in Australia's recorded history (National Climate Centre, 2012).

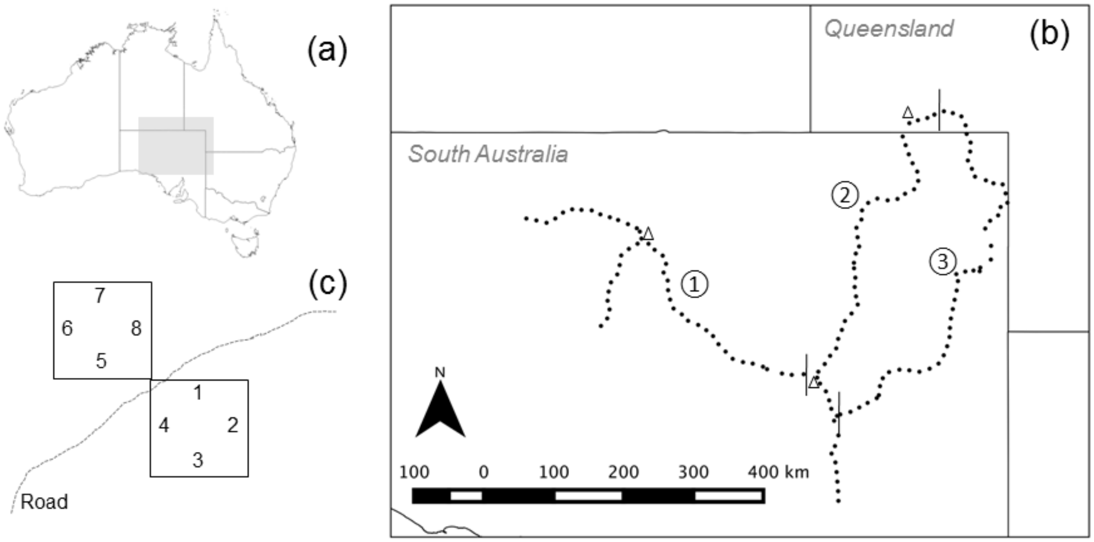


Figure 3.1. (a) Study region (shaded rectangle) within Australia. (b) Survey sites (dots) along three driveable tracks ([1] Oodnadatta track, [2] Birdsville track [3] Strzelecki track). Triangles indicate weather stations (clockwise from far left: Oodnadatta airport; Birdsville Police Station; Marree) and vertical lines indicate where tracks begin or end. c) Orientation of the eight 400m line transects at each census stop relative to the road.

3.3.2 Bird surveys

One hundred and fifty sites, located an average of 16 kilometres apart, were each surveyed once annually from 2012 to 2016 inclusive during winter (July-September) along the Birdsville, Oodnadatta, and Strzelecki tracks of South Australia and Queensland (Fig.

3.1b). Due to track closures resulting from flooding in years with heavy rain, only 125 sites were surveyed in all five years. Eight 400-metre line transect surveys and seven five-minute point counts were conducted at each site between sunrise and sunset (Fig. 3.1c) using distance sampling techniques to account for undetected individuals (Buckland et al., 2001). Observers walked the transect line at a moderate, consistent pace (85% of surveys were between 3 and 15 minutes in length and recorded: the identity and group size of all birds detected by sight or sound between the start and stop points of the transect, and the perpendicular distance of a bird/group from the transect line at the initial moment of detection. Survey teams also recorded the presence or absence of woodland, and percentage ground cover (in the classes: Chenopodiaceae-type shrubs and herbs, grass, water, rock/gibber or other bare ground). A laser range finder was used whenever possible to record distances from observers to birds (Bushnell Yardage Pro Sport 450). Survey teams comprised highly experienced ornithologists trained in the identification by sight and sound of all local species, and followed a strict survey protocol.

3.3.3 Density estimation

Individual species densities (birds/ha) were estimated using distance sampling methods, which model detection probability as a function of distance (Buckland et al., 2001). I obtained density estimates for each species at each site in each year by pooling line transect counts and effort (i.e. transect length) at a site. Records of nocturnal and aquatic species were excluded from analyses, as the survey was not designed to estimate their density. I define an observation as a single detection event where at least one individual of a species is detected, and in the case of a flock includes multiple individuals of the same species.

To ensure robust density estimates, detection functions were calculated only for species with at least 60 observations (n= 51 species), following Buckland et al. (2001). For eight species with fewer than 60 observations but that were not considered rare (present at >10% of sites), the detection probability of ‘surrogate’ species with similar detection characteristics was used to calculate density (Alldredge et al., 2007; Fuller et al., 2008; Runge et al., 2015a; see Table 2.4). Detection probabilities for four species that lacked a surrogate equivalent were calculated by pooling observations of species with similar detection characteristics (Alldredge et al., 2007b). Consequently, densities were estimated for 63 species in total, which comprised 96% of all observations and 98% of all individual birds detected in surveys. Using the 'Distance' package in R (Miller, 2015; R Core Team, 2016), I evaluated the fit of hazard rate and half normal detection function models, as recommended by Thomas et al. (2010). Observer team was included as a covariate in the detection function model for each species (to account for potential differences in observer ability) and time of day was included as an additional covariate (because a species' detectability may vary throughout the course of a day) when it improved detection model fit as indicated by AIC (see Chapter 2 Methods for details). Distances were grouped into intervals with cut-points selected such that distances favoured for rounding (e.g. 10m, 20m, etc.) fell midway between cut-points to avoid 'heaping' effects (Buckland et al., 2001). I excluded detections beyond 145 metres for most smaller-bodied (body mass < 300g; Table 2.3) species as at this distance detection probabilities tended to fall below the suggested minima of 15% required for robust density estimations (Buckland et al., 2001). Similarly, I excluded detections beyond 505 metres for most larger-bodied (>300 g) species. Species with an average flock size of >4 within the relevant truncation distance were tested for cluster-size bias, as larger clusters of species are sometimes more easily detected at longer distance. Potential cluster bias was assessed by regressing log-transformed group size against scaled detection probability (Buckland et al., 2001). If cluster-size bias was present (as indicated by a significant regression), group size was included as an additional covariate in the detection function model. For each species or species-group (using the pooling method discussed previously), detection function model selection was performed using Akaike's Information Criterion, and model fit was assessed visually by checking detection function plots.

3.3.4 Estimating inter-annual distribution variability

To explore inter-annual variability of each species' overall abundance across the region I first calculated the mean density of each species in each year across all sites, so that each species had five annual density estimates across sites ($\mu_{i,y}$):

$$\mu_{i,y} = \frac{1}{n_s} \sum_{s=1}^{n_s} x_{i,y,s}$$

where $x_{i,y,s}$ is the density at site *s* in year *y* for species *i*, and n_s is the number of sites. Then I calculated the coefficient of variation (CV) of each species' annual density estimates (hereafter referred to as 'CV of density'; CV_i) by dividing the standard deviation of annual density estimates by the average of annual density estimates:

$$CV_i = \frac{\sigma_i}{\mu_i}$$

$$CV_i = \frac{\sqrt{\sum_{i=1}^{n_y}(\mu_{i,y} - \mu_i)^2}}{\mu_i}$$

where σ_i is the standard deviation of annual densities of species *i* across sites, n_y is number of years, and μ_i is the mean density of species *i* across sites and years:

$$\mu_i = \frac{1}{n_y\ n_s}\sum_{s=1}^{n_s}\left[\sum_{y=1}^{n_y} x_{i,y,s}\right]$$

To explore how the density of a species varied at the site level across years, I first calculated the CV of density at each site ($CV_{i,s}$) by dividing the standard deviation of annual site-level density estimates by the 5-year average of site-level density:

$$CV_{i,s} = \frac{\sigma_{i,s}}{\mu_{i,s}}$$

where $\sigma_{i,s}$ is the standard deviation of annual densities of species *i* at site *s*, and

$$\mu_{i,s} = \frac{1}{n_y}\sum_{y=1}^{n_y} x_{i,y,s}$$

I then calculated the mean of these site CVs (hereafter 'site-level CV of density'; $\overline{CV_{\iota,s}}$):

$$\overline{CV_{\iota,s}} = \frac{1}{n_s}\sum_{s=1}^{n_s} CV_{i,s}$$

Species persistence at a site ('site persistence') was calculated for species detected at >10% of those sites that were surveyed in all years (64 species and 125 sites in total, respectively) using line transect and point count data. Site persistence was calculated for each species as the number of years a species was detected at a site and then averaged across all sites so that each species had one mean site persistence value (theoretically ranging from 0 to 5; SP_i):

$$SP_i = \frac{1}{n_s} \sum_{s=1}^{n_s} y_{i,s}$$

where $y_{i,s}$ is the number of years species i is detected at site s. Because species' site persistence may be influenced by an observer's ability to detect a bird if it's present and by the size of a species' home range, I tested for relationships between species' site persistence and detection probability (values generated from detection function models), site persistence and body mass (as an indicator of range size; Garnett et al., 2015), and detection probability and my movement classifications (see Results) using univariate generalized models. Detection probability and body mass values can be found in Tables 2.3 and 2.4 (Chapter 2). To explore variability of species persistence among sites, the CV was calculated by dividing the standard deviation of site persistence across sites by the species' average site persistence across sites. Species detected at the same site in less than half of the survey period (≤ 2.5 years) on average were considered to have lower site persistence and more dynamic distributions, and species with CV of density greater than one were considered to have high inter-annual abundance. Species that met both criteria were considered nomadic as these species are characterised by dynamic inter-annual distributions and abundances. Species that did not meet either criterion were considered resident as these species are characterised by more sedentary distributions and more stable inter-annual abundances than nomadic species. Because these surveys are conducted in the same season each year, I cannot assess species as migratory using this data. Some partial migrants exhibit residency while some exhibit seasonal movements, thus depending on when surveys fell relative to migratory movements, a partially migratory species could appear as resident or nomadic.

3.3.5 Existing movement classifications

I compared my results with species mobility classifications from Garnett et al. (2015), which compiled and adapted data from the Handbook of Australian, New Zealand and Antarctic Birds (Marchant & Higgins, 1990) and the Handbook of the Birds of the World (del Hoyo et al., 2014). Garnett et al. (2015) assigned binary scores (0/1) to species in one or more categories: local dispersal; partial migrant; total migrant; nomadic or opportunistic; and irruptive. I adapted this scheme so that each species was classified into a single movement category. I considered nomadic species those whose movements are described by Garnett et al. (2015) as nomadic, irruptive, and/or opportunistic with no local dispersal. Species with only local dispersal were classified as resident (n = 19), and those described as having local and nomadic, irruptive, or opportunistic dispersal were classified as resident/nomadic (n = 16). Species described as complete (n = 1) or partial migrants (n=16) were classified as migratory (n = 17). The inclusion of migratory species to which compare this data functions to see where they fall relative to species with more resident or nomadic tendencies rather than as a critique. Further, existing classifications for most migratory species are supported by banding records and/or seasonal changes in occurrence or abundance (Marchant & Higgins, 1990; del Hoyo et al., 2014).

3.4 Results

3.4.1 Variation in density and site persistence

Over the five years of annual bird surveys (2012 to 2016), 715 site-surveys were conducted, with 125 of the 150 sites visited in all years. Teams surveyed 5,713 400m line transects and detected 122 terrestrial species. Variability of inter-annual species densities (CV of density) spanned a wide range of values, from 0.19 for Wedge-tailed Eagle to 2.2 for Fairy Martin (Fig. 3.2). Most species (44 of 63 species for which I could estimate densities) showed low CV of density (CV < 1) and 19 showed high CV of density (> 1), although there was continuous variation among the species, rather than two groups representing nomads and non-nomads. Variation in species densities spanned a range of existing movement classifications, but on average, resident species (blue bars) had lower CV values (16/19 residents had CV < 1), nomadic species (red bars) had higher CV values (10/11 nomads had CV > 0.8), and resident/nomadic (grey bars) and migratory species (green bars) were spread evenly throughout (Fig. 3.2). Variation of site-level densities (site-level CV of density) was high for all species across years, ranging from 0.99 in White-winged Fairy-wren to 2.2 in Stubble Quail (Fig. 3.3), suggesting widespread species fluctuations in species abundance at a local level. Species classified by Garnett et al. as resident tended to have relatively lower site-level CV values (13/19 residents are in the lower 50th percentile), those classified as nomadic had relatively higher CV values (10/11 nomads are in the upper 50th percentile), and species classified as migratory and resident/nomadic had CV values spread evenly throughout.

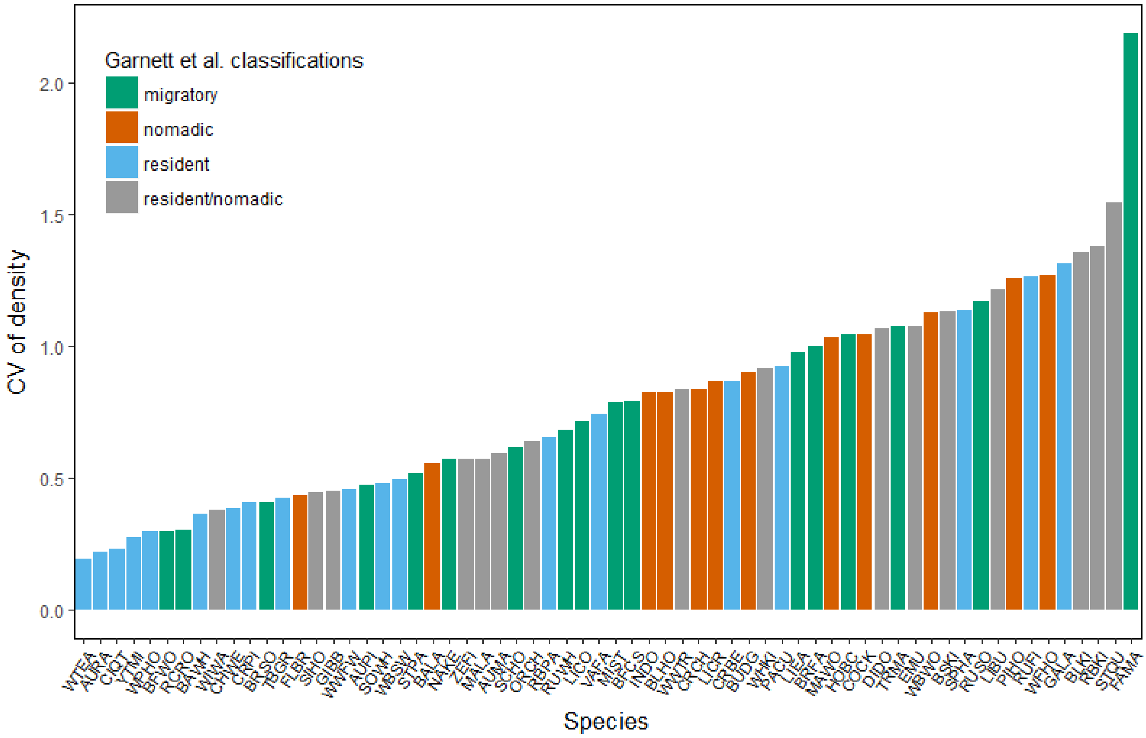


Figure 3.2. Overall variation in density across the entire study area between years ('CV of density') from 2012 to 2016 for 63 species. Colors represent existing movement classifications from Garnett et al. (2015). Species codes can be found in Table S2.

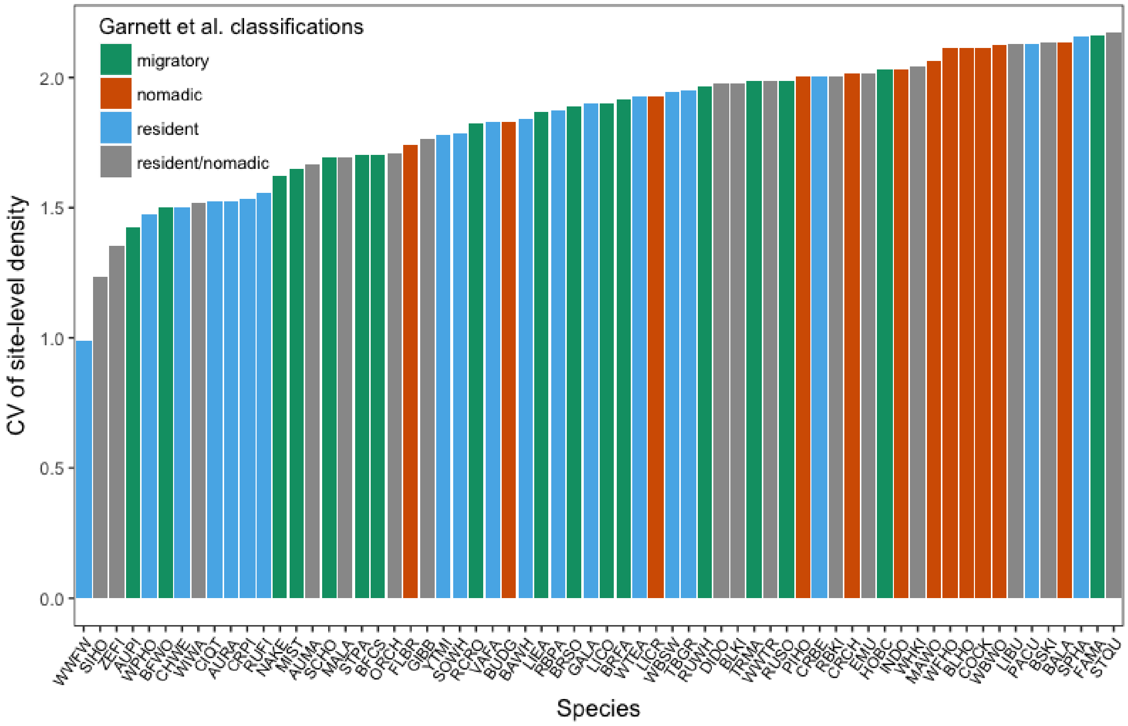


Figure 3.3. Coefficient of variation of species site-level densities from 2012 to 2016. Colors represent existing movement classifications from Garnett et al. (2015). Species codes can be found in Table S2.

The number of years a species was detected at the same site (‘site persistence’) was tallied and the mean of this value calculated across all sites where a species occurred for each of the 63 species for which I could estimate densities (excluding those found at less than 10% of sites). This ranged from 1 for Flock Bronzewing to 4.2 for White-winged Fairy-wren (out of a maximum 5 years; Fig. 3.4). Overall apparent site persistence was low among species, with a majority of species (53 of 64 species) detected at the same site in less than half of the survey years and only 11 detected at the same site in more than half of the survey years on average. Site persistence followed a gradual continuum, with the exception of three species for which it was markedly higher than for the rest of the bird assemblage: Singing Honeyeater, Zebra Finch, and White-winged Fairy-wren (Fig. 3.4). Among-site variation in site persistence was low (CV’s less than 1; error bars in Fig. 3.4), indicating that these estimates are robust to variations in the set of sites surveyed.

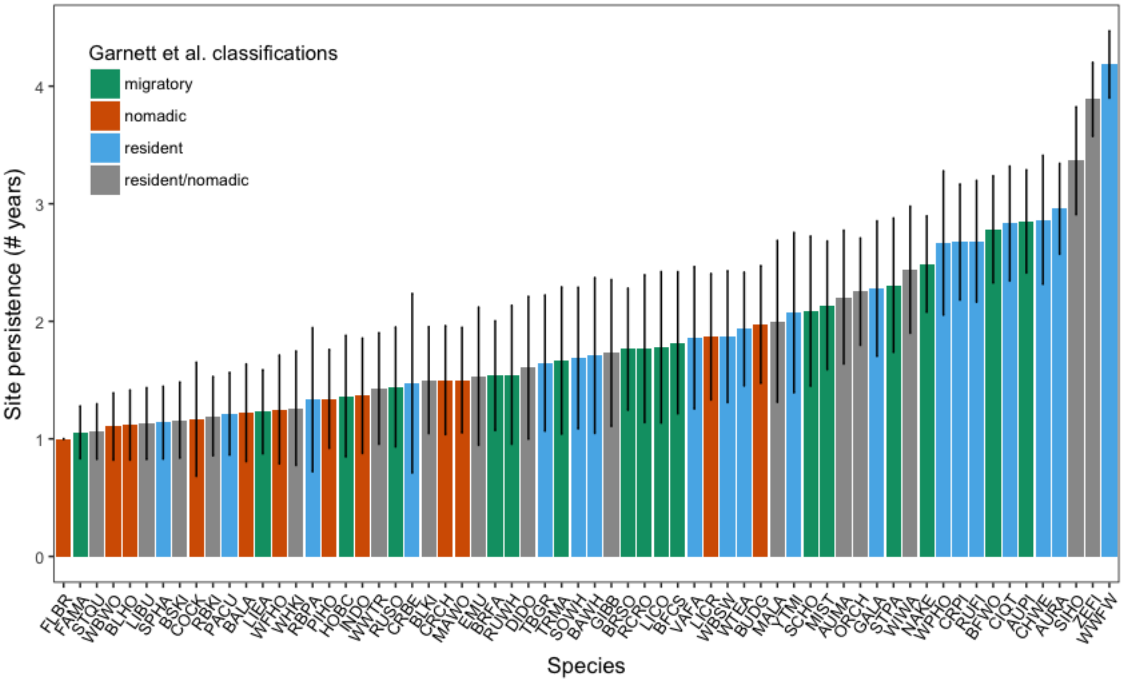


Figure 3.4. The mean number of years each species was detected at the same site (‘site persistence’) from 2012 to 2016. Black bars are coefficient of variation. Species present at less than 10% of sites were excluded. Colors represent existing movement classifications from Garnett et al. 2015.

3.4.2 Movement classifications

Eighteen species showed clear evidence of nomadism, with low site persistence (present at the same site in less than half the survey period) and highly variable inter-annual density (CV of density > 1; Fig. 3.5). Ten species showed clear evidence of residency, with high site persistence and generally consistent inter-annual density (CV < 1). Most species (34 of 63 species) had low site persistence and low inter-annual variation in density (lower left quadrant of Fig. 3.5), which I termed ‘intermediate nomads’ (Table 3.1). One species—Rufous Fieldwren—showed both high site fidelity across 47 sites and high CV of mean site density across years, which I termed ‘dynamic resident’.

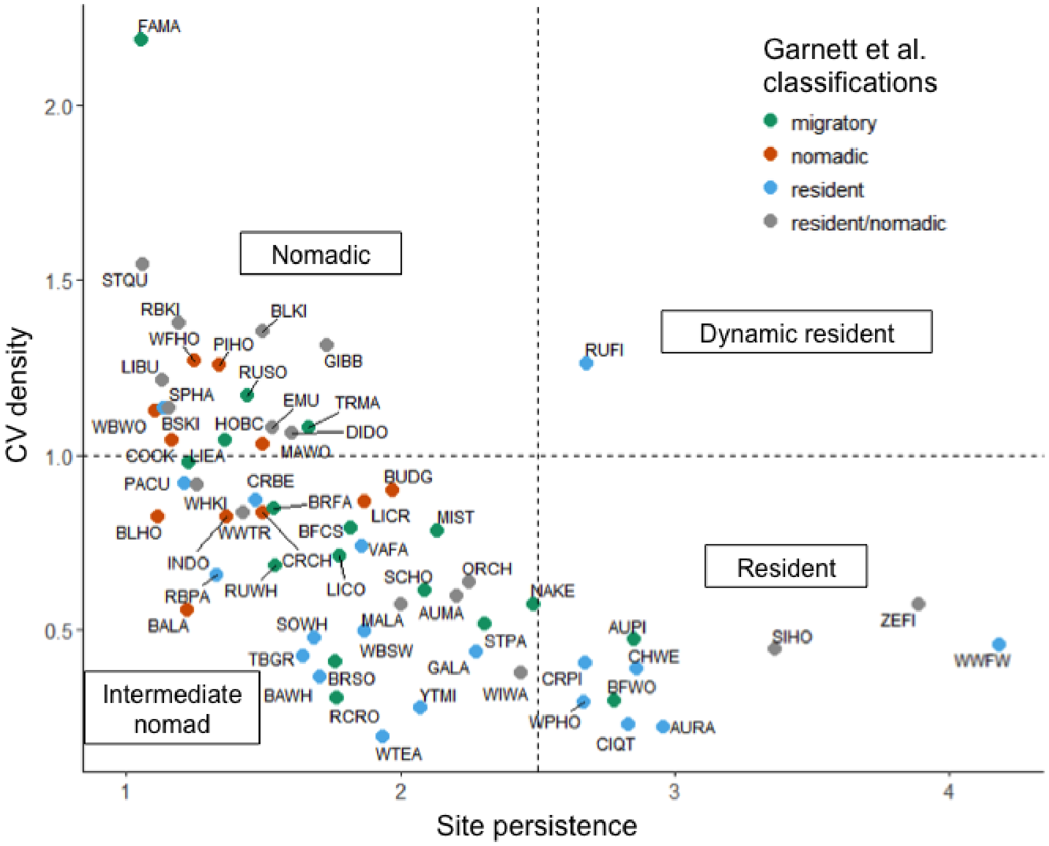


Figure 3.5. Scatterplot of site persistence (from Fig. 3.4) versus variability of species’ mean annual densities (CV of density from Fig. 3.2). Dotted lines indicate the half-way cut-off point in survey years and CV value of 1, above which is considered high variation. Quadrants are labelled according to revised movement groupings based on my results. Species present at less than 10% of sites were excluded. Species codes can be found in Table S2.

Table 3.1. Movement classifications from this study based on site persistence and CV of density values (see Methods), existing movement classifications derived from Garnett et al. 2015, species site persistence (measured as # years a species was present across years, averaged across sites), and CV of density values. Classification agreements are in bold.

Gibson et al. movement category	Garnett et al. 2015 movement category	Species	Site persistence (# years)	CV of density
Resident	Migratory	Australasian Pipit	2.9	0.47
	Resident	**Australian Raven**	3	0.22
	Migratory	Black-faced Woodswallow	2.8	0.3
	Resident	**Chirruping Wedgebill**	2.9	0.39
	Resident	**Cinnamon Quail-thrush**	2.8	0.23
	Resident	**Crested Pigeon**	2.7	0.4
	Resident/Nomadic	Singing Honeyeater	3.4	0.44
	Resident	**White-plumed Honeyeater**	2.7	0.29
	Resident	**White-winged Fairy-wren**	4.2	0.46
	Resident/Nomadic	Zebra Finch	3.9	0.57
Nomadic	Resident/Nomadic	Black Kite	1.5	1.36
	Resident/Nomadic	Black-shouldered Kite	1.2	1.13
	Nomadic	**Cockatiel**	1.2	1.04
	Resident/Nomadic	Diamond Dove	1.6	1.06
	Resident/Nomadic	Emu	1.5	1.08
	Migratory	Fairy Martin	1.1	2.19
	Resident/Nomadic	Gibberbird	1.7	1.31
	Migratory	Horsfield's Bronze-cuckoo	1.4	1.04
	Resident/Nomadic	Little Button-quail	1.1	1.22
	Nomadic	**Masked Woodswallow**	1.5	1.03
	Nomadic	**Pied Honeyeater**	1.3	1.26
	Resident/Nomadic	Red-backed Kingfisher	1.2	1.38
	Migratory	Rufous Songlark	1.4	1.17
	Resident	Spotted Harrier	1.1	1.13
	Resident/Nomadic	Stubble Quail	1.1	1.54
	Migratory	Tree Martin	1.7	1.08
	Nomadic	**White-browed Woodswallow**	1.1	1.13
	Nomadic	**White-fronted Honeyeater**	1.3	1.27
Intermediate nomad	Resident/Nomadic	Australian Magpie	2.2	0.6
	Nomadic	Banded Lapwing	1.2	0.55
	Resident	Banded Whiteface	1.7	0.36
	Nomadic	Black Honeyeater	1.1	0.82

	Migratory	Black-faced Cuckoo-shrike	1.8	0.79
	Migratory	Brown Falcon	1.5	0.85
	Migratory	Brown Songlark	1.8	0.41
	Nomadic	Budgerigar	2	0.9
	Resident	Crested Bellbird	1.5	0.87
	Nomadic	Crimson Chat	1.5	0.84
	Resident	Galah	2.3	0.43
	Nomadic	Inland Dotterel	1.4	0.82
	Migratory	Little Corella	1.8	0.71
	Nomadic	Little Crow	1.9	0.87
	Migratory	Little Eagle	1.2	0.98
	Resident/Nomadic	Magpie-lark	2	0.57
	Migratory	Mistletoebird	2.1	0.78
	Migratory	Nankeen Kestrel	2.5	0.57
	Resident/Nomadic	Orange Chat	2.3	0.64
	Resident	Pallid Cuckoo	1.2	0.92
	Resident	Red-browed Pardalote	1.3	0.66
	Migratory	Red-capped Robin	1.8	0.3
	Migratory	Rufous Whistler	1.5	0.68
	Resident	Southern Whiteface	1.7	0.48
	Migratory	Spiny-cheeked Honeyeater	2.1	0.61
	Migratory	Striated Pardalote	2.3	0.52
	Resident	Thick-billed Grasswren	1.6	0.42
	Resident	Variegated Fairy-wren	1.9	0.74
	Resident	Wedge-tailed Eagle	1.9	0.19
	Resident/Nomadic	Whistling Kite	1.3	0.92
	Resident	White-backed Swallow	1.9	0.49
	Resident/Nomadic	White-winged Triller	1.4	0.84
	Resident/Nomadic	Willie Wagtail	2.4	0.38
	Resident	Yellow-throated Miner	2.1	0.28
Dynamic resident	Resident	Rufous Fieldwren	2.7	1.26

I found moderate to poor support for my movement classifications of resident and nomadic species, respectively, compared with those of Garnett et al. Six out of the 10 species I proposed as resident were in complete agreement with Garnett et al. (lower right quadrant of Fig. 3.5; Table 3.1); two species were classified as migratory, and two species were classified as resident/nomadic. Five out of the 18 species I proposed as nomadic were also classified as nomadic by Garnett et al. (upper left quadrant of Fig. 3.5; Table 3.1); of the remaining 13 species, eight were resident/nomadic, four were migratory, and one was considered resident. Of the 34 species I classified as intermediate nomads, 11 species were classified by Garnett et al. as migratory, six as nomadic, 11 as resident, and six as resident/nomadic. Not accounting for migratory species in this study (n = 16), and assuming that resident/nomadic species are more likely to behave as nomads in the survey given that nomadic movement is associated with arid regions and irregular weather conditions (i.e. extreme rainfall; Chan, 2001), only 19 species behaved as predicted by Garnett et al. out of 47 non-migratory species.

I did not find significant relationships between species detection probability and site persistence (GLM: $t = 0.51$; $p = 0.62$) or species body mass and site persistence ($t = -1.4$; $p = 0.16$), or between my movement classifications and detection probability (intermediate nomad: $z = 0.2$; $p = 0.85$; nomadic: $z = 0.01$; $p = 0.99$; resident: $z = 0.24$; $p = 0.81$).

3.5 Discussion

This study took an empirical approach to assess movement patterns of an entire assemblage, testing the notion that Australian arid-zone species can be classified into two groups of either resident or nomadic. The data suggest that the movement patterns of arid-zone birds span a continuum of strategies rather than simply fitting a binary classification of either resident or nomadic, and that most species are moderately nomadic in the study region as evidenced by variation in occurrence and abundance. Many species typically classified as resident showed variation in abundance and site persistence comparable to species usually classified as nomadic.

Most existing studies of arid Australian birds use *a priori* movement classifications or expert opinion, with few assessing mobility and persistence based solely on patterns in occurrence or abundance data (Burbidge & Fuller, 2007; Pavey & Nano, 2009; Tischler et al., 2013) but see (Wyndham, 1983; Griffioen & Clarke, 2002). A recent study by Jordan et al. (2017) conducted at a reserve in arid central Australia characterized temporal patterns of arid Australian birds as stable or fluctuating, based on the proportion of surveyed sites in which a species was recorded (frequency of occurrence). Of the 33 species that I classified and which were also included in Jordan et al. (2017), I found broad agreement in our classifications. All species that I considered nomadic were classified as extremely or moderately irruptive by their study (100%) based on frequency of occurrence at 66 sites over six years, and all but one (Zebra Finch) of the species I classified as resident were considered stable by Jordan et al. (83%). However, over half of the species I classified as intermediate nomads were classified by Jordan et al. as resident (56%). This difference could be attributable to the inclusion of site-level persistence as a measure of nomadism rather than variation in occurrence over a general study region as done by Jordan et al. Thus, species considered resident by Jordan et al. could still exhibit local movements beyond the site level whereas this study measures residency as a species persisting at the same site more than half the time on average. In addition to measuring species occurrence, this study incorporated fluctuating density as measure of nomadism, which was not used by Jordan et al. Because nomadic species are known to respond en masse to shifts in resource availability, changes in abundance and occurrence are both important indicators of movement.

Over the five-year survey period, I found that most species showed at least moderate fluctuations in their distribution and abundance (lower left quadrant, Fig. 3.5) and did not fit the criteria as strictly nomadic or resident. In contrast, Garnett et al. (2015) classified many of these species as nomadic (n = 6) or as resident (n = 11). Disagreements could be due to the phenomenon of partial nomadism—whereby populations or individuals within a species display nomadic movements while some remain resident (Chan, 2001). In this study region of the Lake Eyre Basin, the most arid region in Australia, species must evolve flexible life history strategies that enable them to adapt to harsh conditions. Thus, species previously reported as resident from less arid regions might be more likely to behave as nomads in this study. This disagreement highlights that movement strategy is not a species-level attribute, but rather an interaction between species and place – a species can be nomadic in some places and resident in others. A banding study of Zebra Finch in southeastern Australia found species regularly dispersed but between permanent nesting areas (Zann & Runciman, 1994). Therefore, at the population level, species were resident but at the individual level, species were mobile/nomadic. This would corroborate both my and Garnett et al's movement classifications of this species as resident and resident-nomadic, respectively, depending on scale. Species reported as nomadic by Garnett et al. (2015) that I classified as intermediate nomads may have fluctuated less in this study depending on the timing of surveys relative to extreme climatic events or which part of their distribution is surveyed. For example, a study on Budgerigars involving banding over multiple years found underlying seasonal patterns of movement that broadly followed seasons of pasture growth within distinct bioclimatic zones across their range, while a lack of recaptured individuals at breeding sites suggests non-regular movements at the level of individual birds (Wyndham, 1983). Thus, individuals may behave as nomads, lending support to Garnett et al's classification, while at the population level species may appear less nomadic. In some cases, movement classifications are based on case studies in only part of a species range—for example, the Black-faced Woodswallow, which is reported to have known seasonal movements in the northern part of its range (Marchant & Higgins, 1990). Much of the existing classifications are not corroborated by robust empirical evidence; at best, banding records and season changes in occurrence or abundance validate species movement patterns, usually for migrants, but many current classifications are based on general consensus and expert opinion. All but one (Brown Songlark) of the migratory species detected in this study were considered partial (rather than complete) migrants by Garnett et al. (2015), indicating that in some part of their range these species also act as residents. This could explain why two species classified as migratory by Garnett et al. were found to behave as residents in this study; species classified as migratory by Garnett et al. that I classified as nomadic could have underlying seasonal movements but nomadic local movements (e.g. Budgerigar, Wyndham 1982).

I cannot definitively attribute changes in species abundance to movement (immigration/emigration) or demographic processes (births/deaths). However, some studies have documented nomadic species arrival to an area where they were previously absent, or population increases within periods too short to attribute to a breeding response (Burbidge & Fuller, 2007; Tischler et al., 2013; Jordan et al., 2017). Nonetheless, a conservative interpretation is necessary until demographic processes can be more convincingly ruled out. Thus, I acknowledge that site persistence and variability in abundance, based on single annual surveys in the non-breeding season, are merely indicators of species movement.

Despite surveying in mostly open habitats, imperfect detection can result in false absences, which could lead to underestimation of site persistence and potentially labelling a species as more nomadic than it actually is. This is more likely for species that are difficult to detect or have a lower likelihood of being encountered by the observer, such as cryptic species, rare species, or species with large home ranges. However, very few species used in my analyses fit either of these profiles. Species that were detected at 12 or fewer sites (10% of all sites) were excluded from analyses, and all but two of the remaining species used in my analysis were likely to be consistently detected by site and/or by sound. These were Stubble Quail and Little Button-quail, which were only detected when flushed by observers close to or on the transect line (see species detection functions: Fig. S1). Five of the study species had large range sizes as indicated by markedly greater body mass (four raptors and Emu). Larger ranging species are inherently less likely to be present at the site-level given the scale of their territories, thus I cannot rule out that they may consistently occupy a territory and so may be less nomadic than indicated by my approach. Inaccurate site persistence measures can also occur if all individuals of a species at a site are missed by observers- I argue that the likelihood of this occurring is very low for widespread species given the spatial extent of the survey design and that surveys were conducted by multiple trained birders in predominantly open, flat habitats with low-density, short vegetation. Although distance sampling methods do not account for false absences, they do account for missed individuals at sites where a species is detected and thus result in more accurate species density estimates. A limitation of this study is the ability to detect hyper-nomadic species. Such species include Flock Bronzewing, Grey Falcon and Letter-winged Kite; species that are characterized by large-scale, extremely patchy occurrence and that are too few to measure changes in inter-annual abundance or occurrence. Understanding the movement of such species requires targeted surveys in preferred habitat type and potentially the deployment of tracking devices that do not necessitate recapturing individuals.

I show that, in contrast to much of the available literature, there is no clear evidence for a binary resident-nomad paradigm, but rather my results suggest a range of continuous variation in movement strategies for Australian arid-zone birds. I further show that within-species mobility strategies are flexible and encourage further work to assess variation in movement patterns across the geographic range of species. In the case of to-and-fro migration, there are a number of cases where some species populations are migratory and others are sedentary (Lack, 1943; Chan, 2001) – and I would expect the same thing for nomads. This suggests care is needed in sweeping species-level classifications and that perhaps such groupings are not very useful if they are heavily environment-dependent. Further, the use of *a priori* movement categories hinders objective assessment of arid bird dynamics by restricting the interpretation of species ecologies through an unnecessarily narrow lens. I hope my findings encourage further objective approaches when classifying supposed facultative mobile species, as differing interpretations can lead to very different conclusions and conservation actions.

4

The role of static and dynamic environmental conditions on site usage in an arid bird assemblage

4.1 Abstract

Changing environmental conditions are thought to be important drivers of nomadic movements, but this has yet to be empirically tested at the community level. Here, I aim to quantify the importance of environmental drivers of a largely nomadic assemblage of birds and hypothesize that nomadic species are most influenced by dynamic weather conditions than static habitat variables. I apply a state-space model with automatic variable selection techniques to five years of distance-sampled bird abundance data from transects across arid inland Australia. I then rank species by the magnitude of influence of selected environmental variables on site usage and attribute importance to three dynamic (proportion grass cover, maximum monthly rainfall and enhanced vegetation index—EVI) and four static (extent of gibber and woodland, shrub and tree density) environmental covariates. Site usage was not able to be predicted for the majority of species using the environmental variables chosen. For the minority of species whose models worked, dynamic environmental conditions were more important predictors of nomadic species' site usage relative to resident species, and static conditions were equally influential of nomadic and static species' site usage. I did not find conclusive evidence that nomadic and resident species employ distinct site usage patterns but rather that nomads use sites based on a combination of dynamic and static conditions while residents are more restricted in their site use patterns. My results can provide support for re-considering some bird species whose status as a resident / nomad is in doubt or data-deficient. Importantly, my results contradict the commonly held idea that resource availability and relative habitat quality are strong predictors of nomadic species distributions. Thus, caution is needed when assuming resource-driven distributions for Australia's arid bird assemblage.

4.2 Introduction

Nomadic species are a unique but little-known group of organisms whose movements are thought to be driven by highly variable environmental conditions (Jonzén et al., 2011) rather than seasonally predictable factors as seen in regular migrants (Chan, 2001). However, the drivers of landscape-scale nomadic movements have yet to be established for multiple species. Conventional wisdom describes nomadic species as having seasonally random movements that are driven by extreme, erratic weather events and ensuing resource pulses, with breeding occurring in different locations from year to year (Dean, 2004). Of the few empirical studies conducted, some have shown that certain species thought to be nomadic actually exhibit underlying structured directional movements, with local nomadic movements along the way (e.g. Budgerigar *Melopsittacus undulatus*, Wyndham, 1983; Regent honeyeater *Anthochaera phrygia*, Franklin et al., 1989). In contrast, a study tracking nomadic Grey Teal *Anas gracilis* in Australia found that long-distant movement in some individuals coincided with rainfall-induced flooding in arid inland regions but movements in most took place without any obvious environmental cue (Roshier et al., 2008). The term "nomadic" thus encompasses a variety of movement behaviours, with different triggers and physiological responses. Teasing out the environmental triggers of movement is a first step in improving this understanding. In this chapter, I investigate environmental drivers of landscape-scale dynamics for a largely nomadic arid bird assemblage over a five-year period, seeking to disentangle the relative influence of fluctuating versus static environmental triggers of species' site usage. Operating under the assumption that nomadic and resident species differ in their movements with respect to fluctuating resources, I ask whether nomadic species are actively selecting sites based on resource availability and, by association, relative suitability.

Nomadism is defined in a number of ways, ranging from continual wandering movements (Chan, 2001), to occupation of different breeding grounds each year but with some seasonal directionality to their movement (Dean, 2004). Distinguishing nomadism from similar facultative movements, such as irruption, is challenging as irruptive species can behave as residents in some years and undertake wandering movements in search of resources in others (Jonzén et al., 2011). Further, the term "irruptive migrant" is used to describe species that fall somewhere between regular migrants and nomads, but is closer to the latter (Newton, 2006b). Clarifying this terminology for research purposes is important because the definition of nomadism also defines the type of data needed to identify nomadic species. For example, if nomadism is defined based on frequency, magnitude, and direction of movement, then detailed individual-based movement data–VHF radio-tracking data at minimum–are needed. Here, I adhere to the broad definition of nomadism as described by Dean (2004) that species are found in different locales each year. Considering that the resources required to collect more detailed data for characterizing an entire assemblage are usually prohibitive at present, collecting standardized survey data at repeated sites is the next best option.

Beyond defining nomadism, further challenges exist in applying typical ecological modelling techniques to nomadic species data. Ecological surveys to estimate changing animal abundances often revisit sites and count unmarked individuals (e.g. Jordan et al., 2017; Webb et al., 2017). Subsequent inference regarding habitat use and population size of resident species assumes that the same population is being repeatedly observed (e.g. Royle et al., 2007). Nomadic species do not meet the common assumption of population closure for typical species population models, i.e. a population in which neither immigration nor emigration occurs (Royle, 2004). Individual or flock movement is unpredictable, and flock size is likewise unpredictable; birds may travel great distances or entirely exit the system before returning, with no predictable breeding sites. Because of the non-closure assumption, the change in the number of individuals of a potentially nomadic species in a location is a function of (i) the demographic response of individuals persisting between observations, and (ii) the effect of nomadic movement into or out of that location. In arid areas, both demographic response and nomadism could be driven in part by the same set of environmental conditions (Burbidge & Fuller, 2007). Therefore, it is difficult to propose a mathematical model to distinguish between the effects of nomadism and demography on the change in abundance at a surveyed site. Furthermore, because nomads are not tied to a single site or territory, and have at minimum the opportunity to select sites based on relative suitability, a net decrease in suitability at a single site between years could conceivably represent a net increase in relative suitability, or vice versa, depending on conditions at alternate sites. Therefore, the appropriate modelling technique and data structure must be able to explicitly incorporate high uncertainty and also preserve flexibility. I incorporate ideas from standard logistic growth with open-population models (Dail & Madsen, 2010; Hostetler & Chandler, 2015) in a Bayesian framework to model changes in bird species abundance against a suite of variables representing dynamic and static environmental conditions. Using this model, I then estimate the variation in changing abundance (hereafter ‘site usage’) attributable to dynamic and static variables for each species in this study. I applied this method to 64 bird species of a largely nomadic assemblage in arid Australia.

Nomadic species have the capability to move large distances, whereas sedentary or resident species more often display limited, local movement. As environmental conditions change, the relative suitability of a particular site may increase or decrease for a particular species with fluctuating environmental conditions, which, nomadic species have theoretically evolved to track (Dean, 2004; Jonzén et al., 2011). I therefore hypothesize that nomads and residents respond differently to fluctuating and static environmental conditions. I use a combination of dynamic (rainfall, vegetation productivity, grass cover) and static (shrub and tree density, and extent of gibber and woodland) environmental variables known to be important for arid species movements and breeding to model how relative site suitability influences species site usage. Rainfall has high inter-annual variability and is thought to directly influence arid species activity (e.g. breeding, Burbidge & Fuller, 2007) and nomadic movements (Roshier et al., 2008). Vegetation productivity has been positively related to bird abundance in arid regions (Mcfarland et al., 2012) and is used in our study as an indicator of foraging and nesting resource availability. Grass seeds are important for many granivorous nomadic species, such as Budgerigars (Wyndham, 1983) and Zebra Finch (Zann et al., 1995), and static conditions, such as gross structural components like tree density and substrate type have been found to be important for arid bird assemblage patterns (Pavey & Nano, 2009).

My hypothesis presents two predictions – the first prediction, which I term the "strong" prediction, is that nomadic species will respond primarily to variables representing fluctuating resources, while sedentary species will respond primarily to variables representing static resources. This prediction follows the theory that nomads evolved to track fluctuating resources (Jonzén et al., 2011) while resident species are able to cope with harsh conditions rather than disperse to new areas. The second prediction, which I term the "relaxed" prediction, is that nomadic species will respond to variables representing fluctuating resources, while there will be no difference between the two species groups in their response to static resources. This prediction adheres to the idea that fixed habitat parameters important for breeding and foraging ability, such as vegetation type, have a greater effect on arid dwelling species than fluctuating resources (Pavey & Nano, 2009). The null alternative to my hypothesis is that nomads are randomly searching for good conditions, and may or may not find them. To test my hypothesis, I used five years of distance sampling bird survey data from arid Australia to model how both static and fluctuating environmental conditions relate to bird species' site usage, and I analytically generated two lists of species: one list of species whose abundance was influenced by fluctuating conditions, and another list of species whose abundance was influenced by static conditions. I then used existing movement classifications from the literature to categorize species in the lists as nomadic or resident, and checked the lists against my predictions.

4.3 Methods

4.3.1 Site Description

The study area is located within the Lake Eyre Basin region, an area with some of the greatest rainfall variability of any arid region globally (McMahon et al., 2008). Between 1961 and 1990, total annual rainfall across the region ranged from 23 mm to 496 mm, and average monthly temperatures range from 14.5 °C to 29.5 °C (Australian Bureau of Meteorology). Vegetation is characterised primarily by chenopod shrublands, samphire shrublands and forblands, and tussock grassland, with scattered eucalypt and acacia woodland. For more details about the study region, refer to Chapter 2.

4.3.2 Bird Surveys

During the months of July through September from 2012 to 2016, teams of trained volunteers performed annual surveys at 150 sites located every 16 kilometres along the Birdsville, Oodnadatta, and Strzelecki tracks of South Australia and Queensland. At each site, teams surveyed a series of eight 400-metre line transects and seven five-minute point counts and recorded species detected by sight and sound. Perpendicular distance from the line to individual birds or centre of groups of individuals was recorded upon initial detection for line transects and radial distance from the observer to birds was recorded for point counts. More details on bird surveys and distance sampling methods can be found in Chapter 2.

4.3.3 Species movement categories

I classified species according to the Garnett et al. (2015) dataset used in Chapter 3 (see this chapter for more information on their dataset). Unlike Chapter 3, which critiques how well the Garnett et al. movement classifications predicted my own classifications based on species' occurrence and abundance patterns, here I use their movement classifications as a baseline to test my hypothesis that nomadic and resident species show differing responses to dynamic and static environmental conditions. Although this dataset may underestimate species movements as shown in Chapter 3 of my thesis, it is currently the most comprehensive and widely used thus its importance cannot be dismissed. Further, in this chapter I interpreted these classifications liberally, such that a species known to be capable of nomadism somewhere within its range is considered nomadic here (see below for further information). This dataset assigns binary scores to one or more of five movement categories: local dispersal, partial migrant, total migrant, nomadic or opportunistic, and irruptive. Garnett et al. (2015) defines nomadic or opportunistic movements as irregular in direction and timing depending on the erratic spatial and temporal distribution of resources at an annual scale, irruptive movements are defined as occurring for large numbers of birds to areas where they do not usually occur, often far from their normal ranges, and locally dispersing taxa are defined as largely sedentary with dispersal by juveniles over small distances. For the purposes of this study, I consider a nomad as any species capable of facultative (nomadic or irruptive) movements, a partial migrant as any species capable of partial migration, and a resident as a species with only local dispersal.

4.3.4 Model covariates

Climate extremes have been shown to dictate the extent of species distributions more so than climate means (Bateman et al., 2012; Lynch et al., 2014), especially in arid systems where extreme rain events rather than average rainfall are an important bottom-up influence on population dynamics (Letnic & Dickman, 2010). Further, short-term weather conditions better explain nomadic species distributions than long-term climate conditions (Reside et al., 2010). Thus, I included maximum rainfall and maximum enhanced vegetation index (EVI) as dynamic variables in the model from four different time aggregates ranging from one to 12 months prior to the survey month (Runge et al., 2015a). Temperature was not included as it not known to be an important driver of nomadic species movements and does not fluctuate markedly in magnitude between years for this region like rainfall (Australian Bureau of Meteorology; http://www.bom.gov.au/climate/data/). Further, mean maximum temperature did not vary markedly over the study period (Fig. 5.2b). Static variables included structural habitat characteristics, including extent of woodland and gibber habitats, and tree and shrub density at each site.

The spatial resolution of the EVI data I used was 250m x 250m for 16-day composites. Maximum and mean EVI values were taken across four different time period aggregates (see below). Rainfall data are from the Australian Bureau of Meteorology's Water Availability Project (http://www.bom.gov.au/jsp/awap/rain/index.jsp) and are interpolated from observed rainfall data using the method described in Jones et al. (2009). The spatial resolution of monthly gridded rainfall data is 0.05° x 0.05° (approximately 5km x 5km). Four different time aggregates were used, because lag effects of varying length have been shown to influence important dispersal and demographic processes (sensu Reside et al., 2010; Pavey & Nano, 2013a; Runge et al., 2015a). Generating time aggregate data involved two steps: 1.) Aggregating or "stacking" environmental data rasters from 1, 3, 6, and 12 months leading up to the survey month in each year and taking the temporal maximum across each time period for each grid cell; and 2.) Applying a 645-metre (145 metres out from 400-metre transect length as this served as an optimal truncation distance for most species in detection function models from Chapter 2 + extra 100 metre influence of surrounding vegetation on birds in area) buffer around the central GPS point of each census stop and taking the spatial maximum EVI and rainfall value of all cells whose centre falls within the buffered area. Grass cover at each site was calculated as the proportion cover of grassland within a 100-metre radius of each of seven point counts, averaged across all point counts at a site. Static variable data were collected in the field at each site. Extent of woodland and gibber were measured as the proportion of point counts at a site that that contained woodland and gibber habitat. Tree and shrub density were calculated from 2016 vegetation data using the corrected density point-centred quarter method from Dahdouh-Guebas & Koedam (2006) for sparsely vegetated assemblages and averaged across point counts at each site. To do this, I followed the formula:

$$D' = \frac{1}{(\sum_{j=1}^{n} d_j/n)^2} \times \frac{q_n}{q_t}$$

where D' is corrected density of trees or shrubs at a point, d_j is the distance to the nearest tree or shrub for tree or shrub j, n is the number of trees or shrubs sampled, q_n is the number of quadrants containing a tree, and q_t, is the total number of quadrants (i.e., four; Dahdouh-Guebas & Koedam, 2006). As there were seven point counts at each site, I averaged *D*' values to obtain one corrected density value for a site.

4.3.5 Scaling environmental variables

Because I hypothesized that nomads can actively seek out sites with greater relative suitability based on fluctuating conditions, I scaled each dynamic variable to have mean zero and unit variance within a year. As such, the raw data value for each site is transformed into its relative value for that year.

4.3.6 Model specification

My objective was to examine how environmental variables influence local abundance for a suite of species. I hypothesized that species would exhibit a wide range of responses to environmental variables, with resident species being less responsive to fluctuating (dynamic) resources than nomadic species. To do this, I used distance sampling survey data of observed species cluster counts, cluster sizes, and observation distances to: (1) estimate changes in local abundance for species through time; (2) explain changes in local species abundance by quantifying the amount of variance explained by dynamic and static environmental variables; and (3) rate species according to their response to dynamic environmental variables and apply movement categories to results to see which type of environmental variables were important for either movement group.

I used a Bayesian state-space formulation (Buckland et al., 2004) using the Winbugs language to divide the model into two general sections, (i) the ecological process describing the actual dynamics of the study system, and (ii) the observation (detection) process that maps the observed data to the “true” state of the system and accounts for observer error by describing the probability of detecting an individual at a site that is occupied (Kery & Chandler, 2012). I chose this modeling approach as it allowed me to model uncertain parts of the ecological and observation processes by framing variables in terms of probability distributions (i.e. uncertainty). Unlike a frequentist approach that infers the probability of observing the data given the hypothesis is true, my approach only assumes that the data are real, and infers probability of a hypothesis being true given the data.

Observation model (detection function)

Since the birds observed were often found in small groups, or clusters, I estimated distance to the centre of each cluster and cluster size in the field, which I was able to use in distance sampling formula referenced below. I began the observation model by modelling observed cluster abundance:

$yc_{jit} \sim \text{binomial}(Nc_{jit}, P_{jit})$

where Nc_{jit} is latent, or unobserved, cluster abundance for sites *j*, species *i*, and year *t*. The detection probability P_{jit} was determined using a hierarchical distance sampling formula from Amundson et al. (2014).

Because count data are often overdispersed with a high proportion of zeros, I employed a zero-inflated Poisson mixture model of latent cluster abundance (Kery & Schaub, 2012):

$Nc_{jit} \sim \text{Poisson}(z_{jit} / eSize_{jit})$

where z_{jit} is latent abundance of a species *i* at site *j* and time *t*, and

$Size_{jit} \sim \text{Poisson}(eSize_{jit})$

where *Size* is observed cluster size. I then modelled latent abundance according to the ecological process model.

Ecological process model

In the model, z_{jit} is the latent abundance of a species *i* at site *j* and time *t*. However, because counts are often overdispersed, I chose to use a zero-inflated Poisson mixture model (Kery & Schaub, 2012) to account for that overdispersion, such that:

$z_{jit} \sim \text{Poisson}(\lambda_{jit} * w_{jit})$

where λ is the mean of the Poisson distribution, and *w* is the latent inclusion variable, which I modelled as the outcome of a Bernoulli process:

$w_{jit} \sim \text{Bernoulli}(\psi_i)$

I modelled λ as a log-linear function of a suite of dynamic (β coefficients) and static (u coefficients) environmental variables (Equation 1):

$$\log(\lambda_{jit}) = \beta0_i + u1_i*\text{gib}_j + u2_i*\text{wood}_j + u3_i*\text{TD}_j + u4_i*\text{SHD}_j + \beta2_i*\text{grass}_{jt} + \beta3_i*\text{raint1}_{jt} + \beta4_i*\text{raint3}_{jt} + \beta5_i*\text{raint6}_{jt} + \beta6_i*\text{raint12}_{jt} + \beta7_i*\text{EVImax1}_{jt} + \beta8_i*\text{EVImax3}_{jt} + \beta9_i*\text{EVImax6}_{jt} + \beta10_i*\text{EVImax12}_{jt}$$

where “gib” is the proportion of sub-sites at a site j covered in gibber (desert pavement), “wood” is the proportion of sub-sites at a site j covered in woodland, “TD” is tree density, “SHD” is shrub density, “grass” is the dynamic measured grass cover, and dynamic weather variables—mean rainfall and maximum EVI—are named according to the different time aggregates, e.g. “rain1” is mean rainfall (mm) in the one month prior to the survey, “EVI3” is maximum EVI in the 3 months prior to the survey, and so on.

4.3.7 Variable selection and prior specification

Because environmental variables will have varying degrees of influence on species, therefore yielding un-parsimonious and potentially highly biased results when all variables are included for all species, I employed a model selection technique called stochastic search variable selection (SSVS; George & McCulloch, 1993; Mutshinda et al., 2011). This technique automates the selection of the best set of dynamic environmental variables to be included in any particular species’ sub-model. To accomplish this, I placed a spike-and-slab prior (see text below for an explanation of this terminology) on each β in Equation 1 such that, for every dynamic variable X:

$$\beta X_i \mid \gamma X_i \sim (1 - \gamma X_i)* \text{Normal}(0, c_1) + \gamma X_i* \text{Normal}(0, c_2)$$

In this formulation, γX_i is an auxiliary variable taking the form:

$$\gamma X_i \sim \text{Bernoulli}(pX_i)$$

indicating whether dynamic environmental variables are to be included in the estimate of λD for any species. The positive constants c_1 and c_2 were set to small and large values, respectively, so that when $\gamma X_i = 0$, βX_i is constrained to be around zero since the resulting prior is the “spike.” Conversely, when $\gamma X_i = 1$, the resulting prior βX_i is uninformative and flat (the “slab”), allowing the posterior to reflect the data. This then makes it possible to use

Bayes factors on γX_i to assess the relative importance of βX_i in the model for each species. The Bayes factor BX_i on γX_i is:

$$BX_i = [P(\gamma X_i = 1|\text{data}) / 1-P(\gamma X_{i\,i} = 1|\text{data})] * [1-P(\gamma X_i = 1) / P(\gamma X_i = 1)]$$

This measures the posterior support for including γX_i in the model. Bayes factors < 1 indicate negative support, $1<B_i<3$ indicates some support, $3<B_i<10$ indicates substantial support, and $B_i>10$ indicates strong support.

The prior structure in SSVS precludes the use of community modelling structures, whereby species-specific regression coefficients share a common hyper-distribution to ameliorate problems posed by rarely detected species (Zipkin et al., 2009; Ruiz-Gutierrez et al., 2010). I was thus unable to use this modelling approach to model the rarer species in my dataset.

4.3.8 Generating lists and ranking species using variance components

Our use of SSVS and Bayes factors not only allows a flexible model selection process, but also provides the means for a crucial test of the prediction that nomads respond to fluctuating environmental conditions when using sites. To generate the list of species whose abundance was influenced by fluctuating conditions, I filtered all the posterior β_i by their corresponding Bayes factors, selecting only those with a Bayes factor ≥ 1. Each species *i* from the filtered results was added to the list. To generate the list of species whose abundance was influenced by static conditions, I repeated the process for all posterior $u_{i,}$ and adding those species *i* to that list.

Finally, I ranked species based on their species-specific variance components of Equation 1. Since environmental covariates in Equation 1 were standardized to mean zero and unit variance (within a given year), the variance $dynV_i$ explaining site use for species *i* as a function of dynamic environmental variables takes the form (Equation 2):

$$dynV_i = \beta 2^2_i + \beta 3^2_i + \beta 4^2_i + \beta 5^2_i + \beta 6^2_i + \beta 6^2_i + \beta 8^2_i + \beta 9^2_i + \beta 10^2_i$$

According to my stated hypothesis, species with higher ranks of *dynV* would be more nomadic.

Similarly, the variance $statV_i$ explains site use for species i as a function of static environmental variables takes the form (Equation 3):

$$statV_i = u1^2_i + u2^2_i + u3^2_i + u4^2_i$$

4.3.9 Model fitting

I used Markov chain Monte Carlo (MCMC) in the *rjags* package (Plummer, 2016) to generate posterior samples for all β and u in Equation 1, as well as *dynV* (Equation 2) and *statV* (Equation 3) for each species. I ran two parallel chains, each of 55,000 iterations, discarding ("burning") the first 50,000 and retaining 5,000 posterior samples which I used to extract means and 95% highest density credible intervals (95% CI) for all unknown variables. I used the potential scale reduction factor ("r-hat" statistic) and visually inspected trace plots of the posteriors to assess model non-convergence (Gelman & Rubin, 1992). As noted above, each model covariate was scaled to mean zero and unit variance within year, which eases model coefficient interpretation and facilitates model convergence.

4.4 Results

In total, 147 species were detected over five years of bird surveys. However, only 64 species had enough observations for density estimation (Chapter 2) and were included in my model. Based on the Garnett et al. (2015) dataset, I classified 28 of the 64 species as nomadic (including irruptive species and species also described as having local dispersal), 19 as resident, 16 as partial migrants, and one as a total migrant (Table 4.1). Hierarchical models successfully predicted site usage using environmental variables for 16 of the 64 species; models did not converge for the remaining 48 species. For successful models, I extracted a list of species that each exhibited at least one β from Equation 1 with a Bayes factor ≥ 1, indicating some level of support for inclusion of the corresponding dynamic variable (Table 4.2a). Of the eight species in that list, four (~14% of all available nomads) were *a priori* classified as nomadic, compared to one (5% of all available residents) classified as resident and three partial migrants (~19% of all partial migrants; Fig. 4.1a), indicating that nomads and migrants were generally more responsive to dynamic conditions than resident species. However, this pattern was not statistically significant (Fisher's exact test $P = 0.57$). I also extracted a list of species that each exhibited at least one u from

Equation 1 with a Bayes factor ≥ 1, indicating some level of support for inclusion of the corresponding static variable (Table 4.2b). Of the 10 species in that list, four (21% of residents) were classified as residents, compared to four nomads (Fig. 4.1b) and two partial migrants (~13% of partial migrants), indicating that nomads and residents were equally responsive to static environmental variables and lending support for the relaxed hypothesis. I found no evidence of non-convergence in the model (Potential Scale Reduction Factor value; Table 4.1).

Table 4.1. List of all species included in the model, movement classifications used in this study, original movement classifications from Garnett et al. 2015*, the sum of dynamic and static variable variance components for each species, and accompanying potential scale reduction factor (psrf) values**.

* 'LD' = local dispersal; 'PM' = partial migrant; 'N' = nomadic; 'I' = irruptive; 'TM' = total migrant. **PSRF values close to 1 indicate model convergence.

Species	*Gibson et al classification*	*Garnett et al 2015 classification*	*Sum of dynamic vars*	*Dyn psrf*	*Sum of static vars*	*Stat psrf*
Australasian Pipit	Partial Migrant	LD-PM	0.011	1.01	0.004	1.00
Australian Magpie	Nomadic	LD-N	0.009	1.00	0.005	1.00
Australian Raven	Resident	LD	0.010	1.00	0.005	1.00
Banded Lapwing	Nomadic	N	0.011	1.06	0.004	1.01
Banded Whiteface	Resident	LD	0.009	1.02	0.004	1.00
Black Honeyeater	Nomadic	N-I	0.009	1.00	0.011	1.15
Black Kite	Nomadic	LD-PM-I	0.009	1.00	0.004	1.01
Black-faced Cuckoo-shrike	Partial Migrant	LD-PM	0.021	1.16	0.004	1.00
Black-faced Woodswallow	Partial Migrant	LD-PM	0.010	1.00	0.027	1.03
Black-shouldered Kite	Nomadic	LD-N-I	0.009	1.01	0.005	1.00
Brown Falcon	Partial Migrant	LD-PM	0.008	1.00	0.004	1.00
Brown Songlark	Total Migrant	TM	0.010	1.00	0.005	1.00
Budgerigar	Nomadic	N-I	0.073	1.62	0.233	1.20
Chirruping Wedgebill	Resident	LD	0.013	1.04	0.134	1.01
Cinnamon Quail-thrush	Resident	LD	0.009	1.00	0.003	1.00
Cockatiel	Nomadic	PM-N	0.164	2.21	0.004	1.00
Crested Bellbird	Resident	LD	0.010	1.02	0.004	1.00
Crested Pigeon	Resident	LD	0.012	1.05	0.016	1.09
Crimson Chat	Nomadic	N	0.021	1.08	0.007	1.06
Diamond Dove	Nomadic	LD-PM-N	0.101	2.36	0.005	1.01
Emu	Nomadic	LD-I	0.009	1.00	0.004	1.00
Fairy Martin	Partial Migrant	LD-PM	0.027	1.39	0.012	1.16
Flock Bronzewing	Nomadic	N-I	0.042	1.31	0.004	1.00

Galah	Resident	LD	0.016	1.01	0.006	1.01
Gibberbird	Nomadic	LD-N	0.009	1.02	0.005	1.01
Horsfield's Bronze-cuckoo	Partial Migrant	LD-PM	0.009	1.00	0.004	1.00
Inland Dotterel	Nomadic	N	0.020	1.19	1.348	2.27
Little Button-quail	Nomadic	LD-N-I	0.010	1.01	0.004	1.00
Little Corella	Partial Migrant	LD-PM	0.100	1.00	0.005	1.00
Little Crow	Nomadic	N	0.009	1.00	0.009	1.05
Little Eagle	Partial Migrant	LD-PM	0.012	1.00	0.004	1.00
Magpie-lark	Nomadic	LD-PM-N	0.011	1.06	0.004	1.00
Masked Woodswallow	Nomadic	N-I	2.710	1.59	0.005	1.00
Mistletoebird	Partial Migrant	LD-PM	0.016	1.06	0.004	1.00
Nankeen Kestrel	Partial Migrant	LD-PM	0.008	1.00	0.004	1.00
Orange Chat	Nomadic	LD-N	0.010	1.04	0.003	1.00
Pallid Cuckoo	Resident	LD	0.009	1.00	0.004	1.00
Pied Honeyeater	Nomadic	N	0.010	1.00	0.004	1.00
Red-backed Kingfisher	Nomadic	LD-PM-N	0.059	1.79	0.004	1.00
Red-browed Pardalote	Resident	LD	0.021	1.17	0.004	1.00
Red-capped Robin	Partial Migrant	LD-PM	0.009	1.01	0.004	1.00
Rufous Fieldwren	Resident	LD	0.011	1.06	0.011	1.13
Rufous Songlark	Partial Migrant	LD-PM	0.170	1.14	0.004	1.00
Rufous Whistler	Partial Migrant	LD-PM	0.011	1.01	0.022	1.34
Singing Honeyeater	Nomadic	LD-N	0.012	1.01	0.003	1.00
Southern Whiteface	Resident	LD	0.010	1.05	0.007	1.05
Spiny-cheeked Honeyeater	Partial Migrant	LD-PM	0.016	1.15	0.050	2.51
Spotted Harrier	Resident	LD	0.018	1.24	0.035	1.20
Striated Pardalote	Partial Migrant	LD-PM	0.014	1.00	0.004	1.01
Stubble Quail	Nomadic	LD-N-I	0.014	1.14	0.106	1.38
Thick-billed Grasswren	Resident	LD	0.009	1.00	0.004	1.00
Tree Martin	Partial Migrant	LD-PM	0.077	1.46	0.081	1.31
Variegated Fairy-wren	Resident	LD	0.123	1.08	0.004	1.00
Wedge-tailed Eagle	Resident	LD	0.008	1.00	0.004	1.00
Whistling Kite	Nomadic	LD-PM-N	0.009	1.00	0.004	1.00
White-backed Swallow	Resident	LD	0.009	1.00	0.005	1.00
White-browed Woodswallow	Nomadic	N-I	0.012	1.07	0.052	1.42
White-fronted Honeyeater	Nomadic	N	0.038	1.27	0.297	1.17
White-plumed	Resident	LD	0.013	1.14	0.076	1.09

Honeyeater						
White-winged Fairy-wren	Resident	LD	0.027	1.01	0.031	1.00
White-winged Triller	Nomadic	LD-PM-I	0.010	1.02	0.004	1.00
Willie Wagtail	Nomadic	LD-N	0.009	1.00	0.004	1.00
Yellow-throated Miner	Resident	LD	0.009	1.00	0.191	1.04
Zebra Finch	Nomadic	LD-N-I	0.114	1.27	0.041	1.00

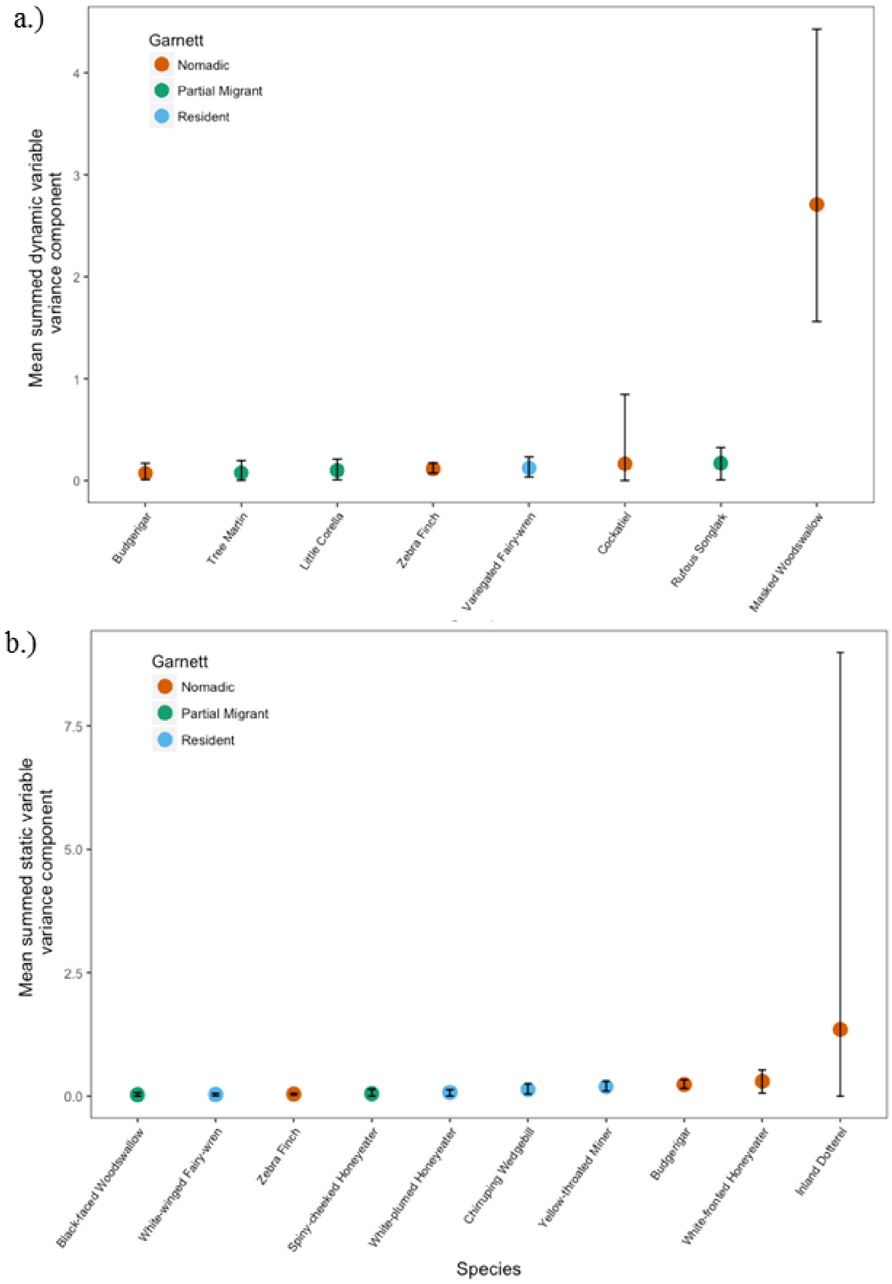


Figure 4.1. Means of the posterior distributions of the sums (*dynV* and *statV* in Equations 2 and 3, respectively) of variance components for species whose site usage was influenced by dynamic a) and static b) variables. Colours indicate different movement categories defined by Garnett et al. (2015).

Table 4.2. Means of the variance coefficients for dynamic (a) and static (b) environmental variables in the model, for variable * species combinations with Bayes Factor value ≥ 1. Movement classifications are adapted from Garnett et al., 2015- see Table 4.1. LCL = lower limit of 95% highest density credible interval, UCL = upper limit of 95% highest density credible interval.

a)

Dynamic Variable	*LCL*	*UCL*	*Mean*	*SD*	*Bayes Factor*	*Species*	*Movement classification*
Grass cover	-0.79	-0.26	-0.52	0.14	>100	Masked Woodswallow	Nomad
Grass cover	0.24	0.37	0.30	0.03	>100	Zebra Finch	Nomad
Rain t1	-1.79	-0.91	-1.27	0.25	>100	Masked Woodswallow	Nomad
Max rain t3	0.62	1.06	0.85	0.12	>100	Masked Woodswallow	Nomad
EVImaxt1	-0.05	0.43	0.15	0.16	1.84	Little Corella	Partial Migrant
EVImaxt1	0.01	0.34	0.20	0.10	6.44	Budgerigar	Nomad
EVImaxt3	-0.04	0.59	0.16	0.21	1.13	Cockatiel	Nomad
EVImaxt3	-0.06	0.42	0.12	0.16	1.10	Tree Martin	Partial Migrant
EVImaxt6	-0.07	0.46	0.14	0.18	1.51	Rufous Songlark	Partial Migrant
EVImaxt12	-0.05	0.55	0.23	0.21	2.71	Rufous Songlark	Partial Migrant
EVImaxt12	-0.03	0.46	0.28	0.14	12.6	Variegated Fairy-wren	Resident

b)

Static Variable	*LCL*	*UCL*	*Mean*	*SD*	*Bayes Factor*	*Species*	*Status*
Extent gibber	-0.53	-0.35	-0.44	0.05	>100	Budgerigar	Nomad
Extent gibber	-0.51	-0.21	-0.35	0.08	>100	Chirruping Wedgebill	Resident
Extent gibber	-0.23	-0.06	-0.16	0.05	6.63	White-winged Fairy-wren	Resident
Extent woodland	0.03	0.26	0.13	0.07	1.91	Black-faced Woodswallow	Partial Migrant
Extent woodland	0.07	0.26	0.18	0.05	14.9	Budgerigar	Nomad
Extent woodland	0.01	0.37	0.18	0.12	2.87	Spiny-cheeked Honeyeater	Partial Migrant
Extent woodland	0.30	0.76	0.53	0.12	>100	White-fronted Honeyeater	Nomad
Extent woodland	0.06	0.38	0.26	0.07	32.5	White-plumed Honeyeater	Resident
Extent woodland	0.32	0.55	0.43	0.06	>100	Yellow-throated Miner	Resident

Extent woodland	0.14	0.24	0.19	0.03	162.0	Zebra Finch	Nomad
Shrub density	-3.00	0.10	-0.58	1.01	1.05	Inland Dotterel	Nomad

Of the dynamic variables, grass cover and maximum EVI (from the previous 1-, 3- and 12-month periods) were important for all eight of the species whose changing abundance was explained by one or more dynamic variables (Table 4.2a). Grass cover and previous month's rainfall were negatively associated with Masked Woodswallow site usage, while maximum EVI from the previous one-month period was positively associated with site usage of Little Corella and Budgerigar, maximum EVI from the previous three-month period was positively associated with site usage of Cockatiel and Tree Martin, and maximum EVI from the previous 12-month period was positively associated with site usage of Rufous Songlark and Variegated Fairy-wren. Previous one month's rainfall and maximum rainfall from the previous 3-month period were negatively and positively associated with Masked Woodswallow site usage, respectively, and maximum EVI from the previous 6-month period was positively associated with Rufous Songlark site usage.

Of the static variables, extent of gibber and woodland were important for nine out of the 10 species with statistically supportive Bayes factor values (Table 4.2b). Extent of gibber was negatively associated with site usage of Budgerigar, Chirruping Wedgebill, and White-winged Fairy-wren, and extent of woodland was positively associated with site usage of Black-faced Woodswallow, Budgerigar, Spiny-cheeked Honeyeater, White-fronted Honeyeater, White-plumed Honeyeater, Yellow-throated Miner, and Zebra Finch. Shrub density was negatively associated with Inland Dotterel site usage (Table 4.2b).

4.5 Discussion

In this chapter, I make a first objective assessment of which environmental variables are important for arid bird species abundance and compare the relative importance of dynamic and static environmental variables under the prediction that nomadic species are more responsive to dynamic conditions. I found that dynamic and static environmental variables could only be fitted to a minority of species, indicating that the explanatory variables used were generally poor predictors of arid species abundances and underlines how difficult it is to capture the features that are driving nomadic bird distributions. This is a critical finding as it contradicts conventional wisdom that resource amount or habitat condition is a strong predictor of arid species distributions. This has important implications for our ability to predict species occurrence or change in distribution as the predictability of this relationship is a major underlying assumption of species distribution models. The lack of a clear result for most species could be due to a few reasons: 1) that individual habitat specificity, and by extension site usage, for arid zone birds in Australia is not influenced to any great degree by the general environmental variables we used in our model; 2) birds are not using directed cues to efficiently track optimal resources and therefore predicting their movement based on fluctuating resources is no better than random; and 3) birds do not perceive relative suitability at all, or are unable to commit search time to discover the best available site. The latter two explanations seem more plausible because dynamic desert organisms are undoubtedly driven by rainfall or lack thereof to some degree, whether directly or indirectly. Therefore either using rainfall as a variable was not specific enough, the resolution of the rainfall data was not high enough, or species movements are simply random with respect to relative resource availability. This does not mean that nomadic species do not actively seek suitability, but it might indicate that they do not necessarily select the best available habitat. Optimal foraging theory and marginal value theorem suggest that more searching can be disadvantageous if not absolutely necessary (Charnov, 1976). If this is true, then a future modelling approach could search for “threshold” resource values required for site usage, and then treat all sites meeting thresholds for use as equally suitable and randomly available.

Many of the species for which dynamic and static environmental variables could be fitted showed Bayes factor values less than 3, indicating some, albeit weak, support that select environmental variables were important for site use in those species (Table 4.2). For those sixteen species with sufficient statistical support in the model, I found that nomadic and resident species respond differently to fluctuating environmental conditions and found no pattern in how each group responded to static conditions, lending support for my research hypothesis and relaxed prediction. More specifically, dynamic variables influenced site usage of more nomadic species than resident species as classified by the literature, with grass cover, rainfall, and EVI important for nomadic species abundance. The static variables extent of gibber, extent of woodland, and shrub density were important for an equal number of nomadic and resident species. The fact that this pattern was shown not to be statistically significant indicates that either there is no signal of movement strategy and effect of dynamic environmental variables or could be due to an insufficient sample size.

Results showed that grass cover negatively influenced Masked Woodswallow site usage and positively influenced Zebra Finch site usage. Masked Woodswallow prefer habitats with sparse open canopies on which to perch and from which to hawk insects (Tischler et al., 2013) whereas grassy areas in the study were usually open and devoid of canopy. Zebra Finch are known to be commonly associated with grass as grass seeds form the primary part of their diet; however, the presence of grass does not necessarily indicate seed availability, the timing of which is complex and depends on factors such as temperature and amount and timing of previous rainfall (Zann et al., 1995).

Rainfall is thought of as being the primary driver, or at least highly influential, in arid and nomadic bird abundance and movements (Dean, 2004; Jonzén et al., 2011). In contrast, I found that rainfall was only important for one species—Masked Woodswallow—and negatively influenced site usage one month previous to the surveys but that maximum total rainfall three months previous to the survey period positively influenced site usage. This suggests that this species avoided sites immediately following rainfall but appeared a few months after, perhaps tracking insect and nectar abundance. These results are in line with studies showing that, although rainfall events clearly play a key role in arid ecosystems and movements of certain opportunistic species (Burbidge & Fuller, 2007; Letnic & Dickman, 2010; Pedler et al., 2014), it does not necessarily correlate directly with animal abundance or movement (Dean, 1997; Dean & Milton, 2001; Nano & Pavey, 2013). In contrast, EVI was found to positively influence site usage for four of the eight species at various time aggregates. This is expected because, unlike rainfall, vegetation productivity and resulting resource availability have been shown to strongly and directly predict mobile species dynamics (e.g. rodents and raptors—Pavey & Nano, 2013b; nectar and Swift Parrot—Webb et al., 2014). Many of the species influenced by EVI are known granivores—Budgerigar, Cockatiel, and Little Corella—indicating that EVI captured ephemeral vegetation growth and may be a good indicator of seed availability. Only one resident species appeared to be influenced by dynamic environmental variables– Variegated Fairy-wren– indicating that this species may display locally nomadic rather than resident behaviour. In terms of time lags, nomads appear to be more responsive to dynamic variables measured close to or at the time of surveys—grass cover, rainfall one month prior (t1), maximum rainfall three months prior (t3), maximum EVI one month prior, and maximum EVI three months prior (Table 4.2a)— rather than six or more months prior. These results support the idea that nomadic species respond quickly to stochastic weather and resulting environmental conditions (Burbidge & Fuller, 2007; Tischler et al., 2013; Jordan et al., 2017). The importance of structural habitat components such as presence of woodland has been shown for many arid species (Pavey & Nano, 2009; Tischler et al., 2013) and is reiterated here, where it influenced site usage for seven out of ten species. All of these species are most commonly found in woodland compared with other arid habitats, where structure plays a role in foraging, in the case of Black-faced Woodswallows that hawk insects from exposed branches and honeyeaters that feed on the nectar of eucalypt blossoms, and nesting substrate for Zebra Finch.

As with any model, the results and conclusions are limited by the quality and appropriateness of the covariates as surrogates for actual ecological drivers of site usage. In that regard, I felt that the method of using SSVS helped to ensure that I did not reach any spurious conclusions about the influence of the covariates on the system. A major drawback to using SSVS is that it necessarily decreases the number of species for which I can draw inference about their status as a nomad or resident. This is because the “spike” part of the prior is selected when there is insufficient evidence to include a particular covariate in a particular species’ part of the overall model, resulting in a coefficient value very close to zero and Bayes factors < 1. This again reflects the uncertainty about how well the chosen model covariates adequately reflect the true underlying system. This means that exhaustive ranked lists of species based on their nomadism are not feasible. However, as I have demonstrated, the technique can be used to generate reduced lists of species that are strong candidates for classification either as nomads or residents, which can in turn confirm or question previous classification schemes, particular in under-studied systems such as Australia’s arid interior. This shortfall highlights the challenge of understanding large-scale species dynamics that may be influenced by dynamic local-scale variables (e.g. seed and nectar availability, insect biomass, etc.) and that may not be detected by large-scale variables like rainfall and EVI.

Both predictions assume that residents are restricted in their site use patterns and are less able to make full use of fluctuating resources in the absence of static habitat requirements. This becomes problematic in the case of irruptive species, which can exhibit residency punctuated by sudden large-scale erratic movements based on fluctuating resources (Newton, 2006b; Jonzén et al., 2011), essentially mirroring nomadic immigration. It would be ideal to be able to statistically separate changes in abundance into demographic and movements-based components, and therefore allow identification of nomads versus resident and irruptive species. However, that would require data on the demography of individual species (e.g. generation time) and their movements, which are not currently available and difficult to obtain given the potential for large movements, limited property accessibility, and technological/financial limitations (GPS transponder size limitations, bird movement beyond VHF tracker range, etc.). Given these limitations, and that this study essentially assumes open populations between observations and the potential for nomadism, I feel that the simple approach of modelling site usage, rather than changes in abundance between years (as in a fully dynamic model) or movements between sites, is entirely appropriate for distinguishing between species that may respond to static and fluctuating environmental conditions differently. This is, however, only tractable when dynamic variables are scaled to mean zero within year, rather than among years, which I have done. While multiple site-visits within a single season or year would also have been ideal, given that I would have had to assumed an open population between visits (due to nomadism), the only benefit to multiple visits within a season would have been the addition of data points. With 150 sites visited each of five years, I had a sufficient amount of data points.

This study focused on exogenous drivers of species movements. An alternative would be to investigate drivers of nomadic species movements or abundance from year to year by incorporating species reproductive traits, for instance, such as clutch size and ability to have multiple broods. Similar models would benefit from more detailed site-level habitat characteristics, such as presence of important plant species (e.g. cane grass *Zygochloa paradoxa*, spinifex *Triodia sp*, nectar-producing *Eremophila sp*) and seed and nectar availability. The rainfall data used here was extrapolated across large areas from select weather stations in the region. Availability of better spatial resolution rainfall data would be beneficial, as would testing the effect of rainfall connectivity rather than quantity on arid species dynamics (Nano & Pavey, 2013).

The results of this study show that for a minority of nomadic species site usage and movements by extension are more influenced by dynamic general environmental variables than resident species, but that dynamic conditions and static habitat variables both influence site usage of nomadic species, the latter to the same degree as resident species. This finding suggests that habitat specificity might play an important role in how arid and nomadic species move through the landscape and that ephemeral resources may play less of a role than previously thought (Pavey & Nano, 2009). A potential consequence of this is that nomads, which are sometimes thought to be pre-adapted to disturbances due to their ability to track favourable conditions (Jonzén et al., 2011; Stojanovic et al., 2015), could still be quite vulnerable to processes that impact habitat structure in Australia’s arid interior, such as grazing, geological exploration, despite an increase in resource abundance following extreme rains. Further work is needed to assess vulnerability of arid and nomadic species to climate and land-use change by identifying robust environmental predictors of species movements, quantifying breeding success and reproductive rates, and tracking species movements.

5

Quantifying the influence of rainfall on bird community flux in Australia's arid zone

5.1 Abstract

Resource pulses are important bottom-up drivers of arid biological communities. The Lake Eyre Basin in Australia’s interior has one of the most variable climates of any arid region globally and little is known of large-scale impacts of fluctuating resources on the avian community. I explore how the avian community responds to fluctuating weather conditions, testing the extent to which species reshuffle or leave the system, and model community response to time-dependent environmental variables. I surveyed 150 sites once annually across arid Australia over a five-year period to assess temporal variation in overall avian density, biomass, species richness and turnover following an unprecedented rainfall event. I found significant fluctuations at the site level for avian density, biomass, and species richness from year-to-year. Species turnover was consistently high at sites and low for all sites pooled, and relative abundances of common species were similar between years. Rainfall alone did not significantly influence any avian community response variable but interacted with NDVI from a prior period to positively influence total species density, biomass, and species richness. Results indicate that many individuals and species disappear and reappear at the site level from year-to-year in the arid zone, especially during wet-to-dry and dry-to-wet transitions, and that a core of common species reshuffles at the landscape level. Findings highlight the importance of considering multiple spatial scales over multiple years when assessing the impact of time-dependent environmental conditions on this widespread assemblage.

5.2 Introduction

The importance of rain events in structuring key processes in biological communities is often emphasized for arid ecosystems (Noy-Meir, 1973; Morton et al., 2011). Arid ecosystems are characterised by short, stochastic pulses of heavy rainfall that disrupt long dry periods and result in peaks of biological activity (Noy-Meir, 1973). Understanding the relationship between rainfall, resource pulses, and biotic fluctuation is important for managing arid populations and predicting their response to unpredictable and extreme future climate scenarios, but is not straightforward. Studies from deserts around the world found varying community responses depending on taxa, time since the rain event, and the nature of the rain event itself. In the deserts of Chile and Australia, heavy rain triggered by

El Niño southern-oscillation (ENSO) events resulted in prolific vegetative growth and seed production, followed by a marked increase in granivorous rodent abundance and richness, and then an increase in vertebrate predator and raptor abundance and richness (Jaksic et al., 1997; Pavey & Nano, 2013). In South Africa, arid bird abundance increased in response to new plant growth following rain (Dean & Milton, 2001), and in arid Western Australia, bird species richness, community composition and abundance increased significantly following drought-breaking high rainfall (Burbidge & Fuller, 2007). Also in arid Australia, short (130mm) and long (540mm) rainfall phases elicited distinct responses among plant functional types (Nano & Pavey, 2013). Community responses can also be mediated by exogenous factors such as increased predation. For example, an increase in raptors and dingos following a major rain event in arid Australia resulted in hyper-predation and subsequent declines of irrupted populations of primary consumer species (Letnic & Dickman, 2006).

Here, I explore the strength of the relationship between rainfall, vegetation productivity, and community variables of Australia's arid birds over an extensive area and over a five-year period. Given what is known from other systems and taxa, I expect this community to respond positively to large rain events, showing an increase in overall species abundance, biomass, and richness, and causing an increase in species turnover. As previous studies have shown that rainfall impacts on biotic communities are mediated by plant growth, I expect community response to be correlated more strongly with vegetation productivity than rainfall.

Globally, the arid region with the greatest rainfall variability is inland Australia's Lake Eyre Basin (McMahon et al., 2008; Morton et al., 2011). The Lake Eyre Basin is ideal for a study of dynamics in desert environments more generally, as the extreme changes should allow us more easily to detect different responses among species. Here, arid species capitalize on the ephemeral resource surpluses that arise in association with periodic water availability by breeding and/or moving into areas of newly available resources and habitat (Roshier et al., 2001; Burbidge & Fuller, 2007; Greenville et al., 2013) and shape future trajectories of species populations (Letnic & Dickman, 2006). This can lead to population booms and also busts, as wet years leave some species vulnerable to predation by mesopredators and impacts from grazing (Letnic & Dickman, 2006; Frank et al., 2013). To cope with heterogeneous environments, some species have evolved nomadic and irruptive movements to track resource peaks (Newton, 2006b; Singh et al., 2012) and breed opportunistically (Zann et al., 1995; Burbidge & Fuller, 2007). Australia's arid bird assemblage contains one of the highest proportions of nomadic and irruptive species worldwide (30-46%; Dean, 2004) but remains an enigmatic group as they are difficult to monitor and the events shaping their distributions are sporadic.

In 2010 and 2011, La Niña-driven rain events caused unprecedented flooding (National Climate Centre, 2012) across inland Australia, including the Lake Eyre Basin. Studies investigating the impact of these rain events found widespread increases in abundance and range expansions for native mammals, raptors, and amphibians (Greenville et al., 2013; Pavey & Nano, 2013; Mac Nally et al., 2014). Small mammal distributions were found to be strongly associated with both vegetation structure and rainfall patterns, but the relative importance was species-specific (Kelly et al., 2013). Studies on terrestrial birds found that species abundance, biomass, and richness generally increased following this large rain event, especially for nomadic species (Tischler et al., 2013; Jordan et al., 2017); however, these studies were conducted at the reserve-scale and hence consider only a fraction of the spatial extent at which this ecosystem functions. Understanding how arid bird assemblage responds to pulsed rain events therefore requires large-scale, multi-year studies. There is an especially urgent need for this work given projected changes in the spatial patterns of ENSO-driven variability in precipitation and an increase in frequency of extreme El Niño events in the future (Power et al., 2013; Cai et al., 2014).

Here, I explore arid bird assemblage composition and dynamics, through a series of wet and dry years, and investigate the influence of environmental variables on these assemblages. I use a five-year bird abundance dataset collected from 150 sites over a vast area of the Lake Eyre Basin. First, I assess temporal changes in avian community density, biomass, species richness and turnover at the site level. Second, I model community metrics in relation to vegetation productivity (NDVI) and rainfall. I propose two hypotheses of how the avian community responds to fluctuating resources: 1.) species experience decreases and increases uniformly across the landscape during dry and wet years, respectively, either due to emigration/immigration or deaths/births; or 2.) species reshuffle within the arid zone, e.g. by taking refuge during dry years and irrupting in wet years when resources are abundant. Under the first scenario, avian community metrics should vary significantly across sites between dry and wet periods. I expect that because dry periods are resource-limited and this assemblage contains a high proportion of opportunistic species, many species will leave the system (either by movement or deaths) rather than reshuffle. Under the second scenario, I would expect there to be negligible changes in community metrics on average at the site level (but higher among-site variation in the case of species contraction during dry years).

5.3 Methods

I explore temporal dynamics in the arid bird assemblage of the Lake Eyre Basin region of inland Australia. I quantify avian community dynamics—total species density, biomass, and richness— across a 5-year period (2012–2016 inclusive) at 150 sites. I then statistically test the effect of two time-dependent environmental variables (mean monthly NDVI and total monthly rainfall) on species density, biomass, and richness.

5.3.1 Study Region

The study region covers an area of approximately 160,000 km^2 in size within inland Australia's Lake Eyre Basin (Fig. 5.1). Baseline weather data from a 30-year standard reference period (1961–1990) as defined by the World Meteorological Organisation (https://www.wmo.int) were available from the Australian Bureau of Meteorology (www.bom.gov.au/climate/data) for three representative weather stations (Birdsville Police Station, Marree, and Oodnadatta Airport) within the study region (Fig. 5.1). During this period mean annual temperatures range from 14.5 °C (mean minimum) to 29.5 °C (mean maximum) and mean annual rainfall is 186mm (CV of annual rainfall 0.5-0.8; McMahon et al., 2008). Vegetation type at the survey sites was dominated by chenopod shrublands, samphire shrublands and forblands (47% of sites; National Vegetation Information System (NVIS)—Major Vegetation Groups version 4.2. Table 2.2) and local-scale groundcover was predominantly a mixture of gibberplain and annual grasses. The remainder of the sites contained tussock grassland (29% of sites), and eucalypt and acacia woodland (10% of sites combined), hummock grassland (6% of sites), acacia shrubland (5% of sites), aquatic, naturally bare, and other shrublands and grasslands (3% of sites combined).

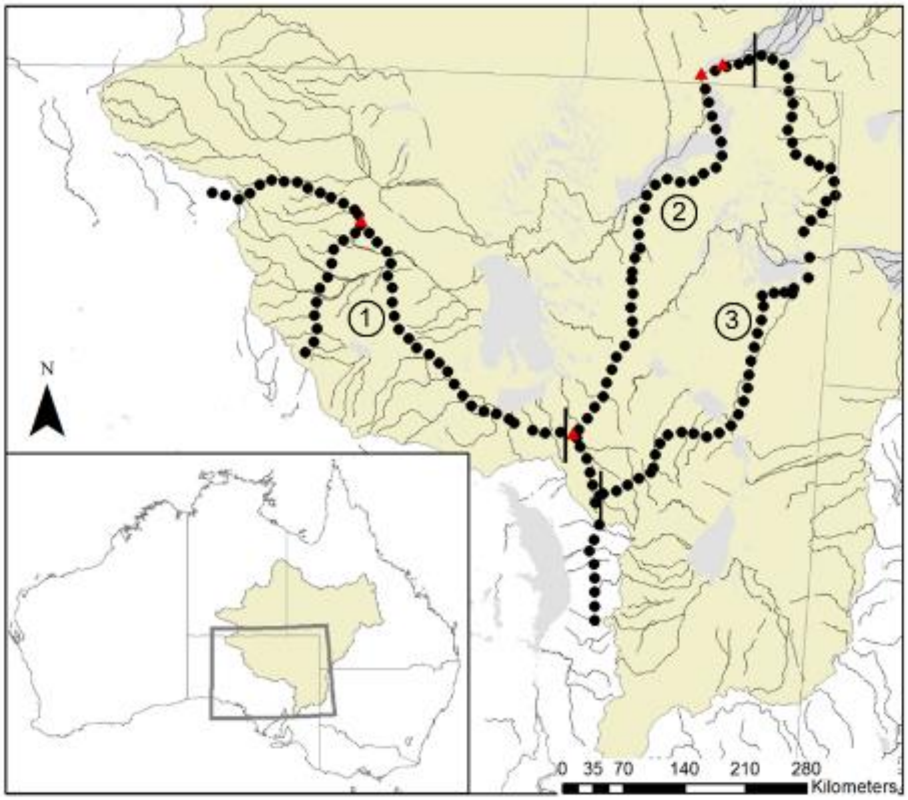


Figure 5.1. Study region within Lake Eyre Basin (beige region) in inland Australia, showing drainage (black lines) and ephemeral waterbodies (grey shapes). Survey sites (black dots) are located along three driveable tracks ([1] Oodnadatta track, [2] Birdsville track, [3] Strzelecki track). Red triangles indicate weather stations*, and vertical lines indicate where tracks begin or end. * Left to right: Oodnadatta Airport, Marree, Birdsville Police Station, and Roseberth.

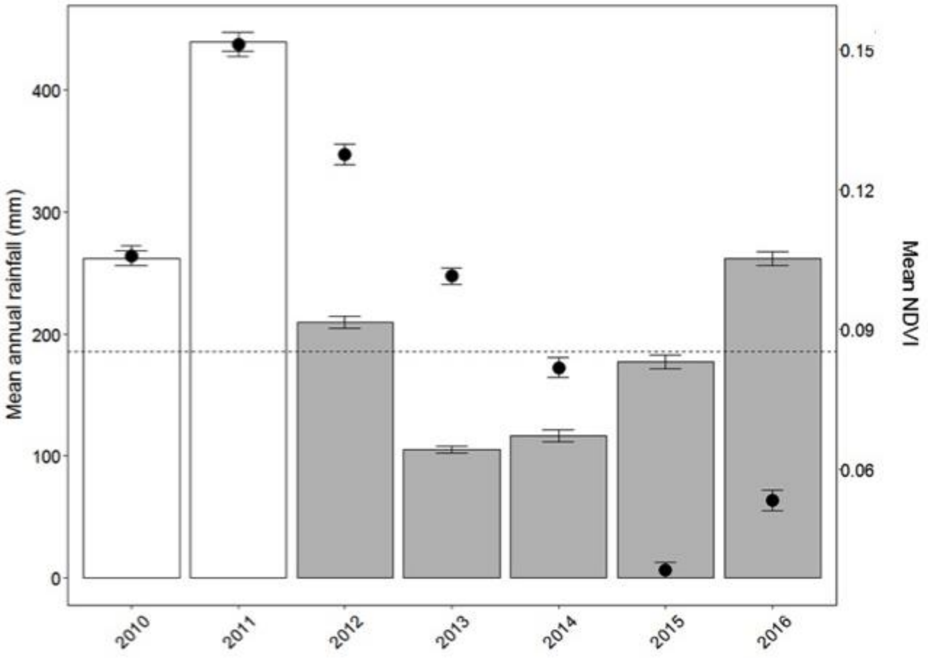
5.3.2 Bird surveys

From 2012 to 2016, survey teams visited 150 survey points each year located at 16km intervals along three major navigable tracks that dissect the region (Oodnadatta, Birdsville and Strzelecki tracks; Fig. 5.1). At each survey site, teams conducted eight 400-metre line transects between sunrise and sunset, avoiding periods of high temperature in the middle of the day (Fig. 2.1c). Observers used standardised distance sampling survey techniques, which are designed to estimate animal abundance within a surveyed area while accounting for missed individuals and species-specific detection probabilities (Buckland et al., 2001). Observers walked the transect line at a moderate pace and recorded all bird species detected by sight or sound, group size, and perpendicular distance from the transect line between the start and end points of the transect. A laser range finder (Bushnell Yardage Pro Sport 450) was used whenever possible to record distances from observers to Birds. Survey teams comprised highly experienced ornithologists trained in the identification by sight and sound of all local species, and followed a strict survey protocol.

5.3.3 The ‘Big wet’

Just prior to this study, the wettest two-year period on record occurred in central and eastern Australia, referred to as the “Big wet” (National Climate Centre, 2012). Mean annual rainfall in the study region during the wet period (January 2010 to December 2011), calculated from monthly totals across study sites from the Australia Water Availability project (http://www.bom.gov.au/jsp/awap/), was 340 mm compared to the 1961–90 baseline of 186 mm (Fig. 5.2a). Vegetation greenness during the wet period, measured as the proportion of photosynthetically active vegetation reflected by a plant (normalized difference vegetation index — NDVI), was double the long term average for much of inland Australia (1992-2008; Wardle, Pavey, & Dickman, 2013; http://www.bom.gov.au/jsp/awap/ndvi/archive.jsp). The greening of semi-arid Australia in this period was extreme and was shown to be a primary driver of the global carbon sink anomaly of 2011 (Poulter et al., 2014).

(a)


Mean annual rainfall (mm)
0
100
200
300
400
Mean NDVI
0.06
0.09
0.12
0.15
2010
2011
2012
2013
2014
2015
2016

(b)

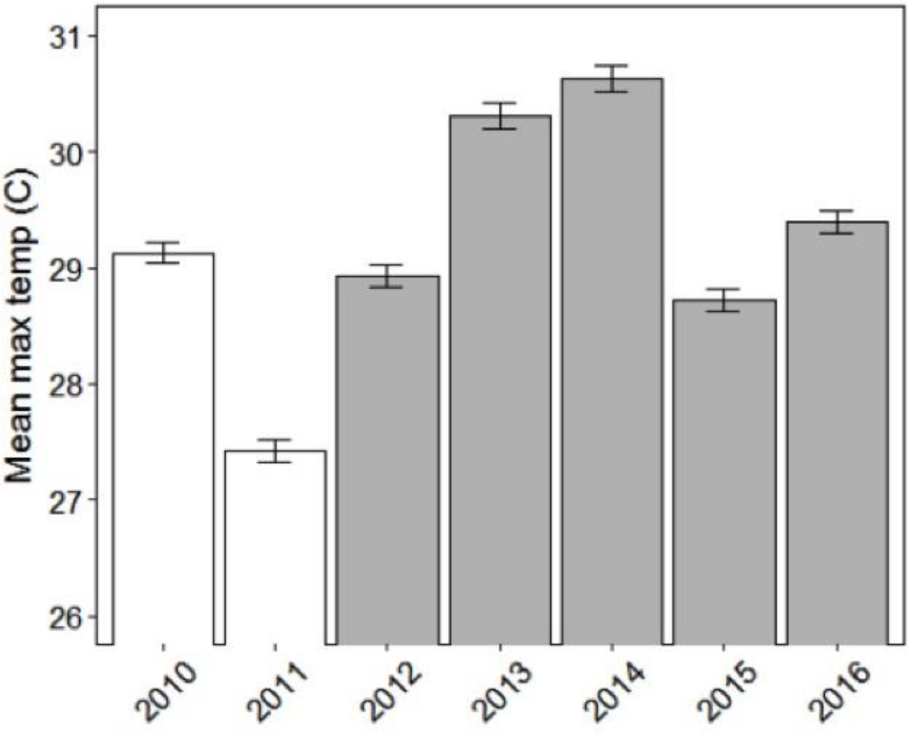

Mean max temp (C)
26
27
28
29
30
31
2010
2011
2012
2013
2014
2015
2016

Figure 5.2. (a) Temporal variation of mean total annual rainfall (bars) and mean NDVI (points) ± standard error averaged across all survey sites from 2010 to 2016. The dashed horizontal line is the interpolated 30-year annual rainfall mean from 1961 to 1990 (186mm). Shaded boxes indicate survey years. Data are from the Australian Bureau of Meteorology (http://www.bom.gov.au/jsp/awap/). (b) Temporal variation of monthly mean maximum temperature ± standard error averaged across all survey sites from 2010 to 2016. Shaded boxes indicate survey years.

5.3.4 Local environmental conditions

The wettest survey years averaged across study sites with mean annual rainfall above the long-term average were 2012 and 2016 (210mm and 262mm, respectively). The driest years with mean annual rainfall well below the long-term average were 2013 and 2014 (105mm and 117mm; Fig. 5.2a). In contrast, vegetation greenness peaked in 2011, with 2012 and 2013 being the greenest survey years (NDVI values 0.13 and 0.10, respectively), and gradually decreased in subsequent years (Fig. 5.2a & Fig. 5.3). Monthly mean maximum annual temperature, averaged across sites, during survey years ranged from 28.9° C in 2012 to 30.6° C in 2015 (Fig. 5.2b).

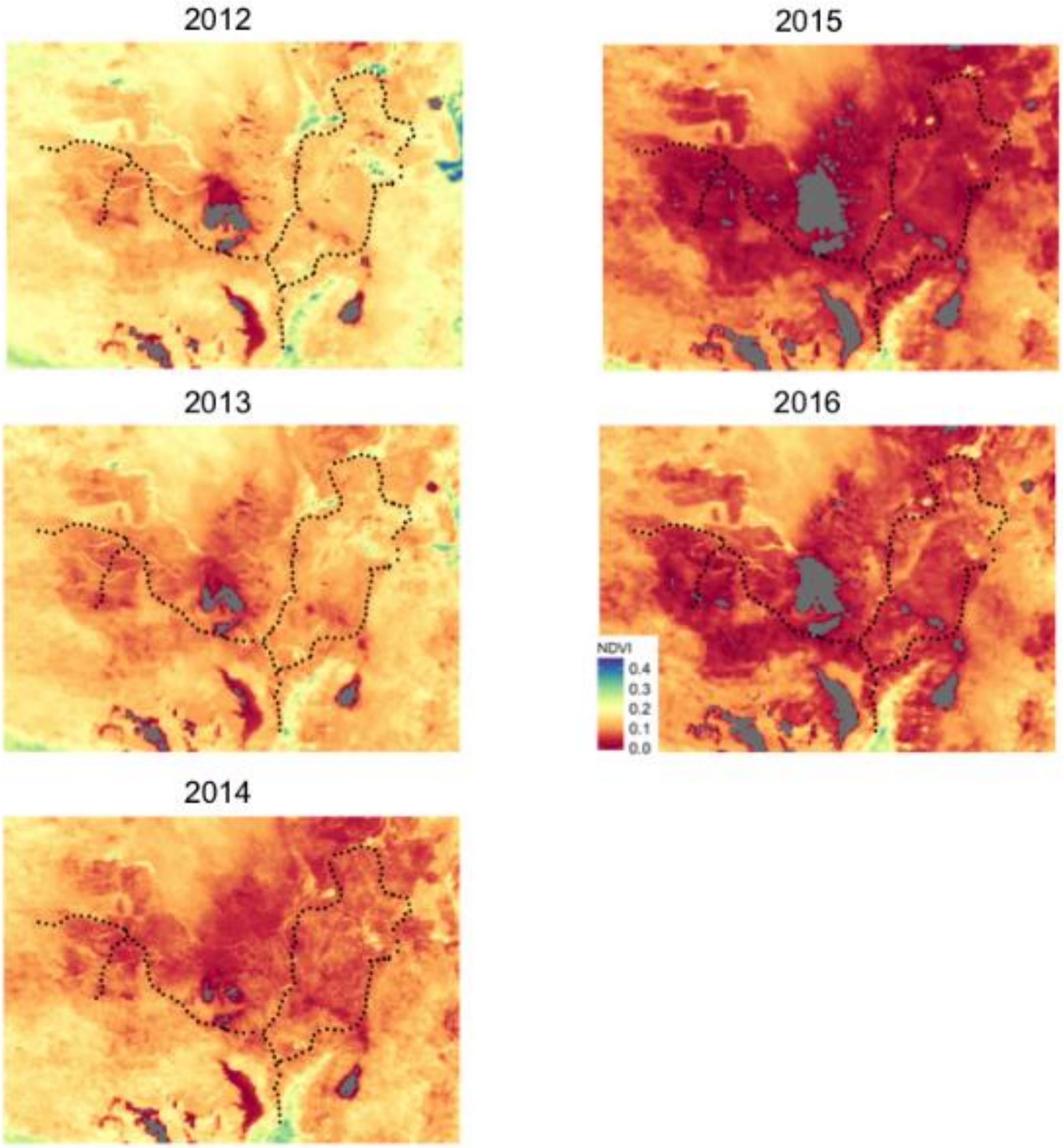


Figure 5.3. Spatial variability of average NDVI from the 12-month period prior to surveys in each year across the study region. Black dots are survey sites, and grey areas indicate standing water.

Monthly data for the period just prior to the La Niña rainfall event through to the last survey period were obtained from the Australia Water Availability project for mean NDVI, mean maximum temperature, and total rainfall (http://www.bom.gov.au/jsp/awap/). These data have a spatial resolution of 0.05° × 0.05° (approximately 5 km × 5 km; Jones et al., 2009), NDVI data were satellite-derived, and rainfall and temperature data were interpolated from observed rainfall data. The interpolation method uses an optimized

Barnes successive correction technique that applies a weighted averaging process to weather station data and incorporates topographical information by using the ratio of actual rainfall to the monthly average (Jones et al., 2009). Using these data, I compiled four different NDVI and rainfall time aggregates to test the effect of more recent conditions as well as potential lag effects of environmental variables on each community response variable; mean monthly NDVI and total monthly rainfall were averaged at 1, 3, 6, and 12-months prior to the survey month (t1, t3, t6, t12; Reside et al., 2010; Runge et al., 2015a). Monthly climatic conditions at each survey site were obtained for the grid cells that contained a site's central coordinate (Hijmans, 2016).

5.3.5 Density, biomass, and species richness estimates

I estimated densities for 64 species in total, which comprised 96% of all observations and 98% of all individual birds detected from 2012 to 2016. Individual species densities (birds/ha) were estimated using distance sampling methods, which model detection probability as a function of distance (Buckland et al., 2001). Details on distance sampling theory and the methodology for estimating species' densities can be found in the Chapter 2 Methods (sections 2.3.5 and 2.3.6).

I obtained total avian density values at each site in each year by taking the sum of individual species' densities (hereafter referred to as "avian density"). I estimated biomass (g/ha) for the 64 species with density estimates by multiplying density at a site by that species' mean body mass (latter from Garnett et al., 2015; Table 2.3) and obtained total avian biomass values at each site in each year by summing individual species' biomass (hereafter referred to as "avian biomass"). I then averaged avian density and biomass across all sites within a year to calculate mean total values. To investigate the relative contribution of large- (body mass > 500g), medium- (150 < x < 500g), and small-bodied (< 150g) species (Table 2.3) to patterns in mean avian biomass, I broke down body mass into three size groups. Species richness was estimated as the number of unique species observed at each site in each year. Temporal turnover of all species between pairs of consecutive years was calculated at the individual site level and for all sites pooled (Hallett et al., 2016), where

$$Total\ turnover = \frac{Species\ gained + species\ lost}{Total\ species\ observed\ in\ both\ time\ points}$$

Turnover values range from 1 (no species similarity at a given site across time) to 0 (complete species similarity at a given site across time). I measured the degree of species reordering (mean rank shift, 'MRS') between consecutive years using changes in species rank abundances (Hallett et al., 2016), where "abundance" is the total count of an individual species at a site.

$$MRS = \sum_{n=i}^{N} \left| R_{i,t+1} - R_{i,t} \right| / N$$

where N = the number of species in common in both time points, t is the time point, and $R_{i,t}$ is the relative rank of species i in time t. All community measures excluded nocturnal and aquatic species. I tested for significant differences between pairs of consecutive years for mean avian density, biomass, species richness, species turnover, and mean rank abundance using one-way ANOVAs and post-hoc Tukey tests in R (R Core Team, 2016).

5.3.6 Modelling community response to NDVI and rainfall

I used linear mixed-effects models to relate time-dependent variables (rainfall and NDVI) to the three separate avian community response variables: avian density, biomass, and species richness (Pinheiro et al., 2016). Year was specified as a random effect to account for non-independence of observations occurring in the same year at different sites, and site GPS coordinates were included in the model correlation structure to account for spatial-autocorrelative effects. Density and biomass were $\log_{10} + 1$ transformed to reduce highly skewed values of flocking species, and weather variables were standardized prior to fitting models by subtracting the mean of each variable from individual values and dividing by the standard deviation (Schielzeth, 2010). I fit multiple candidate models using different combinations of NDVI and rainfall time aggregates (e.g. NDVI_t1 * Rain_t1, NDVI_t1 * Rain_t3, etc.) to find the optimal combination using Akaike's Information Criteria (AIC) and a delta AIC threshold of 2, indicating substantial support for the model (Burnham & Anderson, 2002). Pearson correlation coefficients of all NDVI and rainfall time aggregates were less than 0.7. Coefficient of determination (R^2) was used to measure goodness of fit

(Nakagawa & Schielzeth, 2013). Model validation was performed using diagnostic tests to examine patterns in the model residuals (Zuur et al., 2009).

5.4 Results

5.4.1 Inter-annual community changes

Mean avian density, biomass, and species richness (averaged across sites) fluctuated significantly over the study period on average at the site-level (density: $F_{(4,710)} = 10.2$, $P < 0.0001$; biomass: $F_{(4,710)} = 2.6$, $P < 0.05$; species richness: $F_{(4,705)} = 28.8$, $P < 0.0001$) and indicated that more individual birds and species were detected at a given site in wetter years (2012 and 2016) compared to drier years (Table 5.1; Figs. 5.4 & 5.5a). Mean avian density was three times higher on average at the site level in the wettest year than in the driest year, and biomass and species richness were approximately twice as high on average at the site level in 2016 compared to 2015 and 2013, respectively (Figs. 5.4 & 5.5a). Large-bodied species drove mean biomass in 2016 (estimate = 225; *t*-value = 5.3; $P < 0.0001$), which more than doubled from 2015 to 2016 due to a high density of Emu (Fig. 5.6). When Emu were excluded, temporal variation of biomass more closely resembled that of density, with 2013 having approximately half of the bird biomass per site as in 2012 (Fig. 5.7). Species richness was significantly higher in the wettest years—2012 and 2016—with 14 and 16 species per site on average, respectively, and lowest in the driest years—2013 and 2014—with 9 species per site on average (Table 5.1; Fig. 5.4a). Total species richness in each year for all sites pooled resembled that of site-level species richness and was greatest in the wettest years (2012 = 102; 2013 = 93; 2014 = 98; 2015 = 97; 2016 = 106). Species turnover at the site-level was consistently high, ranging from 0.66 to 0.73, and was greatest between the wettest and driest survey years— 2012 and 2013 (Fig. 5.4a). Species turnover at the site level was significantly affected by year ($F_{(3,550)} = 6.9$, $P = 0.0001$) between 2012/13 and 2015/16 and 2013/14 and 2015/16 (Table 5.1). Species turnover across all sites (pooling data across sites) was consistently lower (2012-2013 = 0.16; 2013-2014 = 0.26; 2014-2015 = 0.24; 2015-2016 = 0.17), suggesting a relatively fixed regional-scale assemblage with reshuffling at the local scale. Mean rank abundance was significantly affected by year ($F_{(6, 521)} = 4.8$, $P < 0.0001$) and was higher between 2015 and 2016 than all other year-pairs (Table 5.1; Fig. 5.4b) but was low at the site-level — ranging from 1.1 to 1.7 between pairs of years — indicating that when species are consistently present between two years, their abundance shifts little relative to other consistently present species (i.e. species only shift their rank between an order of one and two; Fig. 5.4b).

Table 5.1. Results of significant Tukey HSD post-hoc tests from one-way ANOVAs of the effect of year on avian community variables. Difference in the observed year means, significance level, and lower and upper bounds of 95% confidence intervals are shown.

Avian community variable (site-level)	Year	Mean difference	*P*-value	95% CI	
				lower	upper
Density	2012-2013	2.2	2.00E-05	-3.45	-0.94
	2012-2014	1.6	3.40E-03	-2.88	-0.38
	2013-2015	-1.7	1.80E-03	0.45	2.87
	2013-2016	-2.3	4.00E-06	1.08	3.58
	2014-2016	-1.8	1.10E-03	0.52	3.01
Biomass	2015-2016	-200.2	3.84E-02	6.70	393.67
Species richness	2012-2013	4.8	1.00E-07	-6.86	-2.72
	2012-2014	4.4	1.00E-07	-6.47	-2.34
	2013-2015	-3.1	3.36E-04	1.05	5.06
	2013-2016	-6.7	1.00E-07	4.63	8.74
	2014-2015	-2.7	2.58E-03	0.67	4.67
	2014-2016	-6.3	1.00E-07	4.25	8.35
	2015-2016	-3.6	1.48E-05	1.58	5.68
Turnover metrics	Year-pair				
Species turnover	2012/13-2015/16	0.1	2.27E-04	-0.11	-0.03
	2013/14-2015/16	0.1	1.40E-03	-0.10	-0.02
Mean rank shift	2012/13-2015/16	-0.4	9.92E-03	0.07	0.83
	2013/14-2015/16	-0.6	9.66E-05	0.21	0.96
	2014/15-2015/16	-0.5	3.76E-04	0.17	0.89

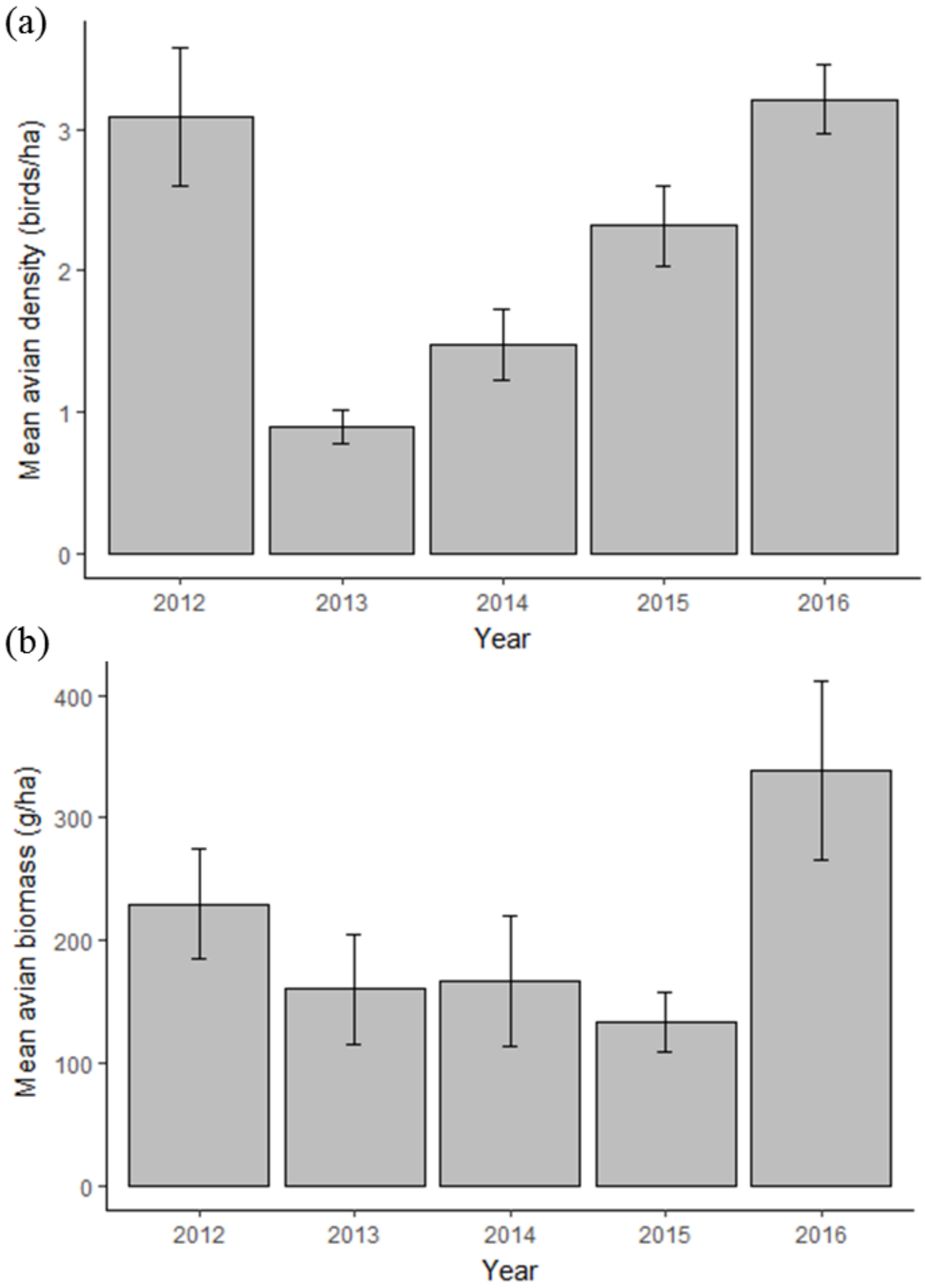


Figure 5.4. Inter-annual mean avian density for all species (a) and biomass of all species b) averaged across sites. Error bars show standard error of mean values among sites.

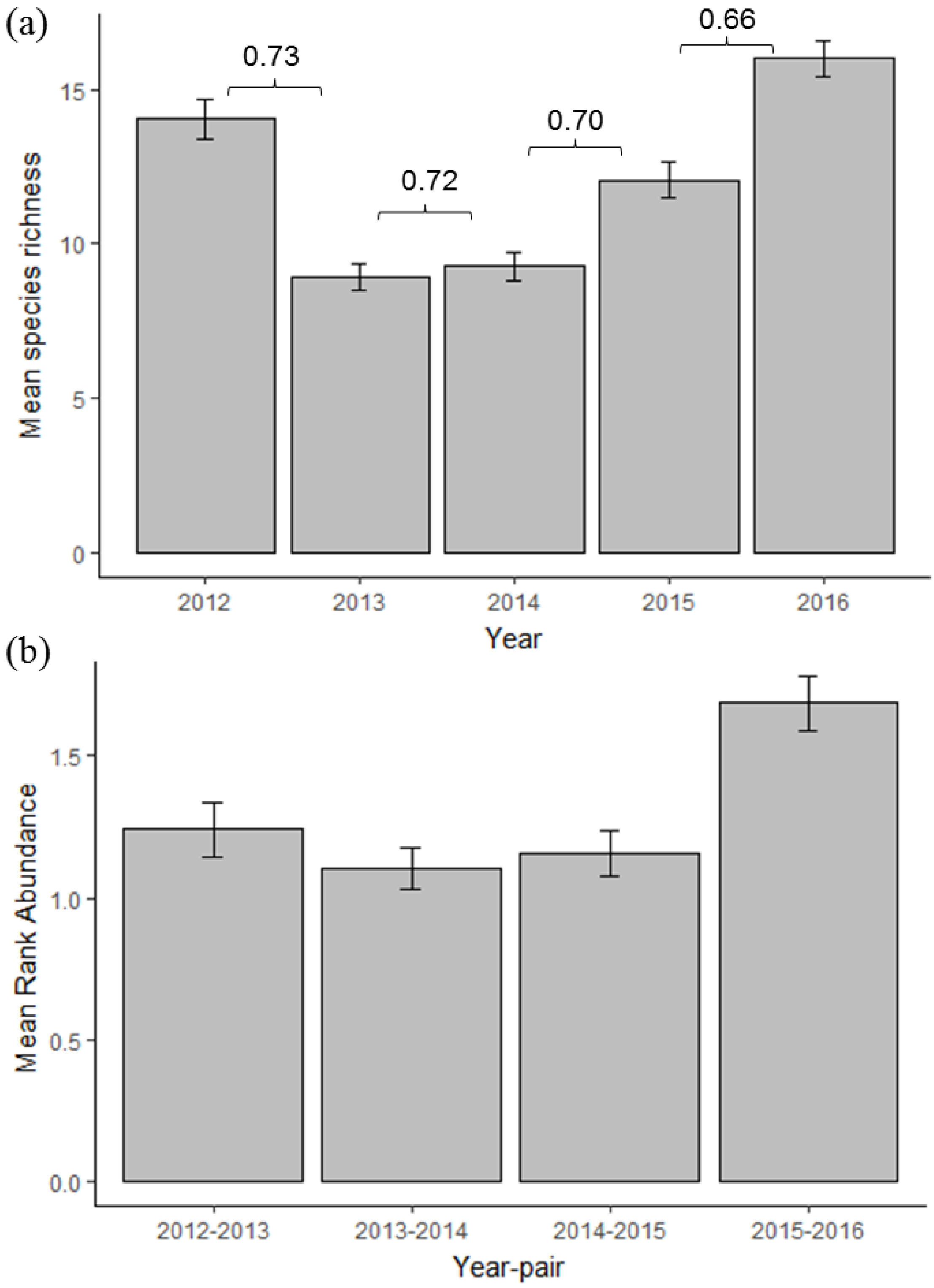


Figure 5.5. Changes in inter-annual species composition averaged across sites. Mean species richness with species turnover between pairs of years shown in brackets (a) and the extent of reordering in species' relative abundances between pairs of years (mean rank abundance) (b) ± standard error averaged across sites.

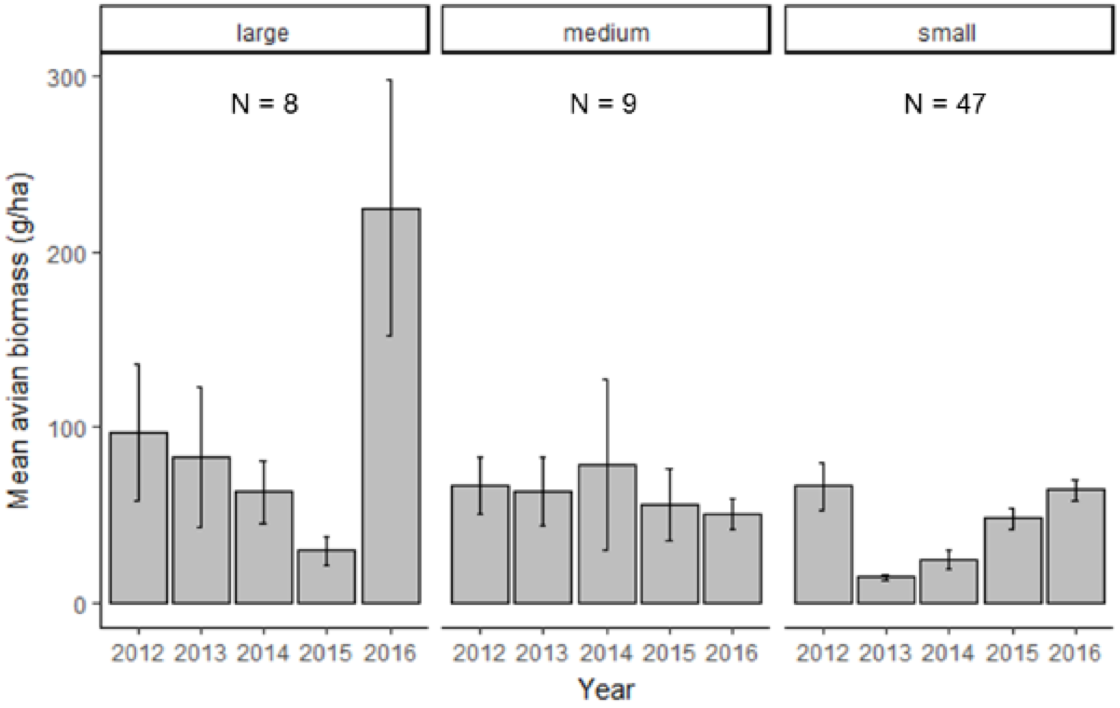


Figure 5.6. Mean avian biomass per site (Fig. 5.3b) grouped by species body mass: large (500g <); medium (150 < X < 500g); small (< 150g). Error bars show standard error of mean values among sites.

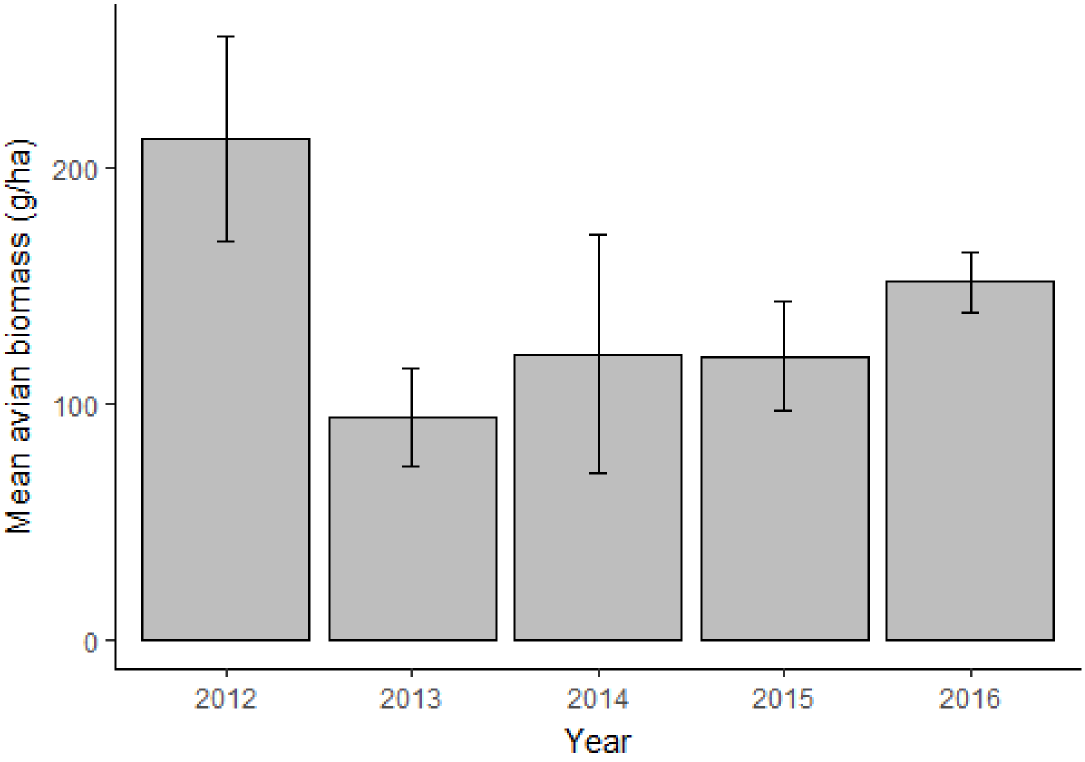


Figure 5.7. Inter-annual mean avian biomass for all species, excluding Emu, averaged across sites. Error bars show standard error of mean values among sites.

5.4.2 Community response to NDVI and rainfall

NDVI and NDVI x rainfall interaction emerged as important predictors in the best performing mixed effects models of avian density, biomass, and species richness (Tables 5.2 & 5.3; Fig. 5.8). Rainfall alone was a weak predictor of avian community response in all of the final models with the exception of species richness. The best performing density model showed that total rainfall from the previous 6-month period interacted positively with average NDVI from the previous 12-month period, and that NDVI from the previous 12-month period was important on its own. The best performing biomass models included a positive interaction between mean NDVI from the previous 12-month period and total rainfall from the previous 1-month, 3-month or 6-month period, indicating an important carry-over effect of NDVI on rainfall and that NDVI from the previous 12-month period was important on its own. The species richness model showed that rainfall from the previous 1-month period interacted positively with average NDVI from the previous 3-month period and that NDVI was important on its own, indicating that more immediate environmental conditions best predicted species richness. The strength of the relationship between NDVI and community response variables increased with increasing rainfall (Fig. 5.8). Predictive power of my models was fairly low as shown by R^2 values and plots of predicted versus observed values (Table 5.2; Fig. 5.9).

Table 5.2. Results from mixed-effects models using maximum likelihood with rain time aggregate * NDVI time aggregate as fixed effects, year as a random effect, and Gaussian spatial correlation structure. Only results are show for models with delta AIC less than 2; AIC scores of top candidate models can be found in Table 5.3. All models were run with the lme function from the 'nlme' package in R. R^2 values indicate model fit based on fixed effects only (marginal) and that incorporates random effects (conditional). t3, t6, and t12 indicate aggregated weather variables averaged across three, six, and twelve months prior to the survey month in a given year.

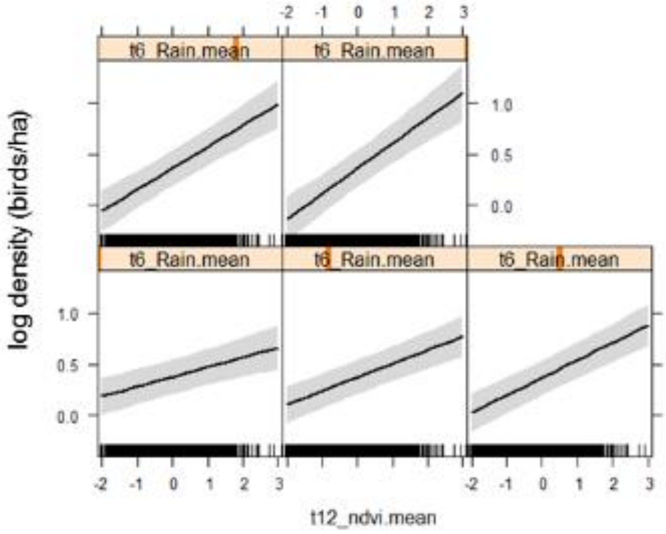
Model	Predictor variable (fixed effects)	Coef	SE	DF	*t*	R^2 (marginal/conditional)
Density	(Intercept)	0.37	0.09	706	4.36	0.17 / 0.45
	t6_Rain	0.00	0.01	706	-0.38	
	t12_ndvi	0.13	0.02	706	7.43	
	t6_Rain:t12_ndvi	0.04	0.01	706	3.61	
Biomass	(Intercept)	1.71	0.15	706	11.51	0.11 / 0.28
model 1	t6_Rain	0.04	0.03	706	1.29	
	t12_ndvi	0.23	0.05	706	5.06	

	t6_Rain:t12_ndvi	0.09	0.03	706	3.23	
model 2	(Intercept)	1.74	0.15	706	11.36	0.08 / 0.27
	t3_Rain	0.04	0.03	706	1.42	
	t12_ndvi	0.23	0.04	706	5.21	
	t3_Rain:t12_ndvi	0.07	0.03	706	2.43	
model 3	(Intercept)	1.71	0.16	706	10.84	0.11 / 0.30
	t1_Rain	0.07	0.03	706	2.62	
	t12_ndvi	0.24	0.04	706	5.50	
	t1_Rain:t12_ndvi	0.03	0.03	706	1.28	
Species richness	(Intercept)	11.89	1.32	706	9.03	0.18 / 0.33
	t1_Rain	0.43	0.28	706	1.54	
	t3_ndvi	2.92	0.33	706	8.95	
	t1_Rain:t3_ndvi	0.77	0.27	706	2.85	

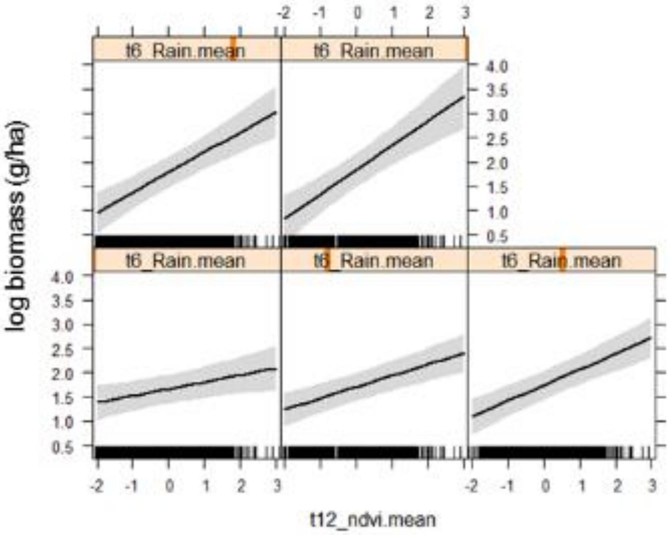
Table 5.3 Model selection table showing AIC scores of the top linear mixed-effects models tested out of a total 65 possible models for each response variable. t3, t6, and t12 indicate aggregated weather variables averaged across three, six, and twelve months prior to the survey month in a given year. t1 indicates aggregated weather variables from the month previous to the survey month.

Response variable	Predictor variables	AIC	ΔAIC
Density	t6_Rain.mean * t12_ndvi.mean	149.68	0.00
	t3_Rain.mean * t12_ndvi.mean	156.87	7.19
	t6_Rain.mean * t6_ndvi.mean	157.09	7.41
	t1_Rain.mean * t12_ndvi.mean	157.25	7.57
Biomass	t3_Rain.mean * t12_ndvi.mean	1483.54	0.00
	t6_Rain.mean * t12_ndvi.mean	1483.75	0.21
	t1_Rain.mean + t12_ndvi.mean	1484.91	1.37
	t1_Rain.mean * t12_ndvi.mean	1485.29	1.75
	t3_Rain.mean + t12_ndvi.mean	1487.37	3.83
Species richness	t1_Rain.mean * t3_ndvi.mean	4598.08	0.00
	t6_Rain.mean * t3_ndvi.mean	4600.94	2.87
	t3_Rain.mean + t3_ndvi.mean	4601.79	3.71
	t3_Rain.mean * t3_ndvi.mean	4601.95	3.87

a.)


t6_Rain.mean
log density (birds/ha)
0.0
0.5
1.0
-2
-1
0
1
2
3
t12_ndvi.mean

b.)


t6_Rain.mean
log biomass (g/ha)
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
-2
-1
0
1
2
3
t12_ndvi.mean

c.)

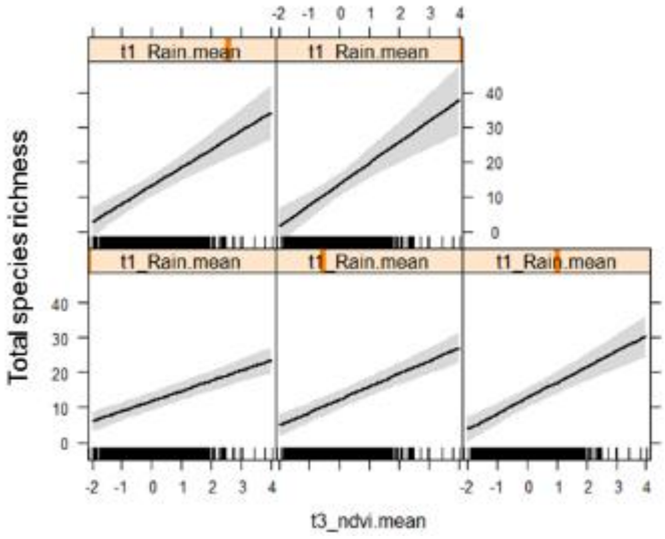
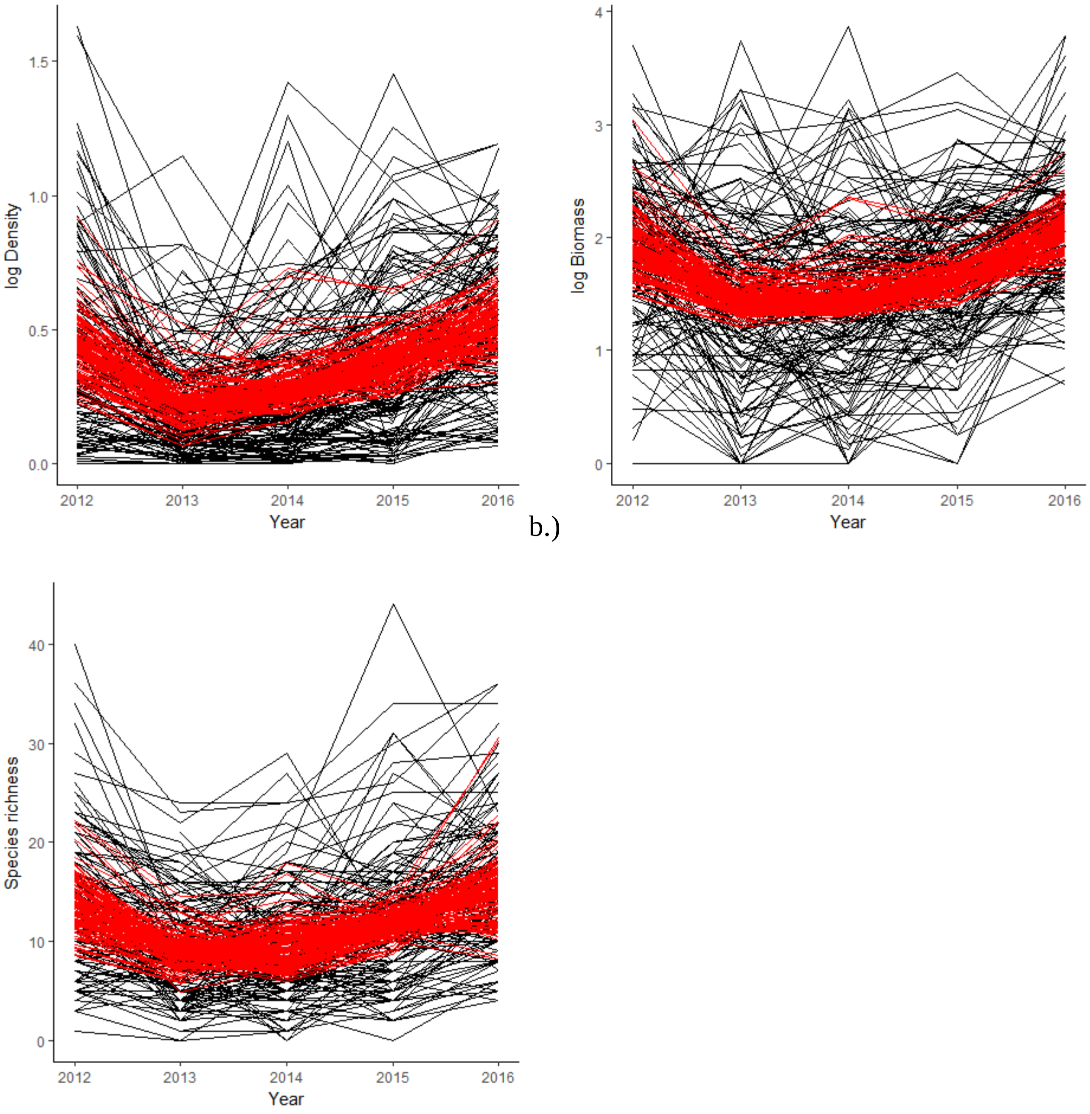

t1_Rain.mean
Total species richness
0
10
20
30
40
-2
-1
0
1
2
3
4
t3_ndvi.mean

Figure 5.8. Results of mixed-effects models showing significant relationships between avian density (a), biomass (b), and species richness (c) with NDVI and mean total rainfall time aggregates at the site level. t3, t6, and t12 indicate aggregated weather variables averaged across three, six, and twelve months prior to the survey month in a given year. Panels (starting from bottom left, moving left to right) show how the slope of the relationship between NDVI and the given community metric increases as the rainfall variable increases (relative rain value indicated by orange bar).



a.) b.) c.)

Figure 5.9. Predicted (red) vs observed (black) values showing model fit of a.) density, b.) biomass, and c.) species richness mixed-effects models. Models were conducted using the lme function in the ‘nlme’ package and predicted values were calculated using the predict function in R.

5.5 Discussion

I found significant temporal changes in mean avian density, biomass, and species richness, consistently high species turnover and mean rank abundance at the site level, and consistently low species turnover for all sites pooled. Findings lend support to my first hypothesis that many individuals and some species disappear and reappear across sites in the arid zone (due to either demographic or movement processes) from year-to-year, especially during wet-dry transitions, and also lend support to my second hypothesis that a common core of species reshuffles at the landscape level with similar relative abundances at the site level. The idea that this system collapses and reassembles as a consequence of variable weather and environmental conditions ("boom and bust") may hold true at a local scale but not necessarily on a landscape scale.

Results show that community metrics respond positively to environmental conditions but at different time lags, specifically to the interaction of shorter-term rainfall (mean total rainfall 1 and 6 months prior to surveys; Fig. 5.8) with longer-term vegetation greenness (NDVI 12 months prior to surveys; Fig. 5.8) and vegetation greenness alone. Runge et al (2015a) found that weather variables (including vegetation productivity and rain related measures) three months prior to occurrence records were important predictors of arid bird distributions. Further, Kutt et al (2012) found that bird abundance and species richness in tropical savannas were highest with preceding 3-month rainfall. I found that rainfall one month prior in combination with NDVI three months prior to surveys was an important predictor of species richness and that rainfall six months prior in combination with NDVI 12 months prior to surveys was an important predictor of bird abundance and biomass. Unlike these studies that encompassed the extreme rainfall event of 2010 and 2011, rainfall during and directly preceding (<12 months) the surveys was not markedly above the 30-year average and may not have surpassed the threshold necessary to stimulate short-term ecological responses (Roshier et al., 2008; Greenville et al., 2013; Nano & Pavey, 2013). Further, a significant positive interaction of NDVI over the period prior to rainfall with rainfall suggests that connectivity of greening periods followed by wet periods is important for the bird community. Nano and Pavey (2013) similarly showed that amount and connectivity of rainfall pulses were more important for arid plant communities than total rainfall amount, likely due to how rainfall translates into soil moisture.

Previous studies report an influx of birds following rain events in Australia's arid zone (Burbidge & Fuller, 2007; Tischler et al., 2013; Jordan et al., 2017) and one study showed that vegetation patterns were more important than resource availability in explaining arid bird assemblage patterns (Pavey & Nano, 2009). The magnitude of change in the arid bird community in wet versus dry years that I found was similar to Jordan et al. (2017) who found a four- and two-fold increase in bird abundance and species richness, respectively, in wet compared to dry years at a reserve in central Australia over a six-year period.

I show that, when considering only temporal variation at the landscape scale (averaged across all sites), density, biomass (excluding Emu), and species richness appear to mirror rainfall (Figs. 5.4, 5.5, & 5.7); however, results from the mixed effects models show that rainfall alone was not an important predictor of bird abundance, biomass or species richness. Rather, it appeared to impact the bird community through a combined effect with vegetation. This is in line with other studies demonstrating that the relationship of rainfall on biological communities is mediated by environmental characteristics. Absolute rainfall amount in itself may not be as important as the connectivity of rainfall events that influence the amount of moisture available in the soil (Nano & Pavey, 2013). Ultimately, rainfall events result in resource availability, such as food and nesting substrate, which is readily used by animals, e.g. grass seeds, nectar, and small mammals. For example, Dean and Milton (2001) found an effect of new plant growth on nomadic bird abundance but no measurable effect of rainfall in arid South Africa following a rain event. Similarly, Pavey and Nano (2013) found that rodent-specialist raptors only appeared 6–9 months following a rodent irruption, which followed seed production, rather than directly following a major rain event.

Though I found significant relationships between avian community response and environmental variables, the overall model showed spatial deviation of observed values from the predicted trends (Fig. 5.9). This deviation could be due to a number of reasons. A study by Webb et al. (Webb et al., 2014) on nomadic Swift Parrots (*Lathamus discolor*) found that only a fraction of the predicted suitable breeding range was occupied in any given year because suitable habitat required the co-occurrence of two important environmental variables (tree hollow and nectar availability), which varied year to year. The surveys took a once a year ‘snapshot’ approach at assessing inter-annual variation in species assemblage and disturbance events could have happened between survey periods that impacted the bird community. For example, heat waves of up to 49° C have been recorded in central Australian summers and can kill thousands of arid-adapted birds (McKechnie et al., 2012). Wetter winters also result in increased cattle stocking rates that can impact on desert biota; however, this is also impacted by grazing history and access to stocking records is currently unavailable (Frank et al., 2013). While capturing these seasonal events through multi-season sampling is ideal, it is extremely logistically difficult, whereas winter surveys capture peak rainfall for this region and peak breeding season for many species of bird.

While most previous studies are done on the reserve scale, these results indicate the importance of considering a landscape scale when assessing inter-annual changes in a regional species assemblage. Large-scale stability of this assemblage relies on connectivity at smaller scales to enable species movements amongst sites; small, static reserves are not likely to provide protection at the scale necessary for such a dynamic community that does not remain stable at a local level. This need for connectivity is especially important considering the extreme magnitude of habitat and soil patchiness that characterises this landscape (Morton et al., 2011). Additionally, the Lake Eyre Basin is a pastoral-dominated landscape (83%), with only 15% managed for nature conservation (Land Use of Australia, Version 4, 2005-2006; http://data.daff.gov.au/anrdl/metadata_files/pa_luav4g9abl07811a00.xml), thus much of the arid bird assemblage is likely to fall on grazing lands at any given time. Future conservation efforts in this region should seek to identify approaches to maintaining healthy ecosystems that consider the needs of both graziers and arid birds communities, especially during times following rains that connect greener periods.

The results I present here show that the arid bird assemblage fluctuated markedly year to year in measures of abundance but appeared to maintain a stable structure at a landscape scale. These findings support the idea that this avian community is defined not just by its dramatic fluctuations and ability to flourish in wet times, but also by its stability and ability to persist in dry times (Jordan et al., 2017). Continued monitoring and conservation of this group is nonetheless important as the sporadic and extreme weather events with which this assemblage has evolved are predicted to intensify and become more infrequent with climate change (IPCC, 2013; Power et al., 2013). Furthermore, changes in large-scale weather patterns have the potential to magnify small changes in the community structure attributable to opportunists that migrate into and out of this system; this, combined with potential synergies with habitat-degrading land use practices, such as grazing (Mac Nally et al., 2009) and lack of protected habitat in this region, demands improved conservation of this group and this arid landscape.

6

General Discussion

6.1 Synthesis

Species with dynamic distributions and aseasonal movements are poorly understood, and studies investigating the patterns and drivers of their movements are lacking (Cottee-Jones et al., 2015). The vast majority of current conservation approaches use protected areas and assume species distributions to be static, which is inappropriate for the protection of highly mobile species that track temporally and seasonally variable resources (Runge et al., 2014). Further, mobile species are among the most vulnerable groups to climate change (Foden et al., 2008; Robinson et al., 2009). Nomadic and irruptive species movements are thought to be driven by major rainfall events, which have increased in frequency and predicted to continue through the current century (Meehl & Tebaldi, 2004; IPCC, 2013), thus there is a critical need to improve conservation of this group. To meet the conservation needs of nomadic and irruptive species, it is necessary to collect occurrence and abundance data over relevant timescales and to assess important environmental correlates associated with changing distributions. Existing studies have documented changes in mobile species abundance or occurrence over shorter periods or smaller areas than the dynamics of this group are expected to operate (Burbidge & Fuller, 2007; Tischler et al., 2013), and species movements are sometimes inferred from opportunistic observations or expert opinion. There remains a need for a large-scale, multi-year, standardized dataset to better understand the movement ecology and to improve conservation management of mobile, nomadic, and irruptive species. In my thesis, I have made important contributions toward understanding species- and community-level changes over space and time in response to environmental variables for arid Australian birds.

In this thesis, I investigated changes in abundance and distribution of Australian arid zone birds over time and space with the aim of addressing major gaps in the knowledge of this poorly understood, largely nomadic group. I outlined a novel standardized monitoring protocol to detect changes in the terrestrial species assemblage and evaluated the efficacy of two different distance sampling survey methods (Chapter 2), made a first objective assessment of their movement dynamics compared to existing movement classifications (Chapter 3), explored temporal changes in avian community structure and the role of rainfall (Chapter 4), and disentangled relative influence of static and dynamic environmental variables on species' site abundance (Chapter 5).

6.2 Summary of findings

Objective assessments of species population trends and conservation status depend on standardized datasets of abundance or occurrence. Compared with migratory species, little is known of the annual biogeographical patterns of species with aseasonal, facultative movements (Cottee-Jones et al., 2015). Current knowledge of nomadic and irruptive species movements is founded on expert opinion or opportunistic evidence (Griffioen & Clarke, 2002; Newton, 2010) and to date, no standardized time series of large-scale patterns of abundance and occupancy for these species exists. In Chapter 2 of my thesis, I proposed a methodology for monitoring nomadic species abundance and occurrence that used two common survey approaches for measuring animal abundance under a distance sampling framework. Distance sampling allows for reliable estimates of animal density by generating a detection function based on the assumption that animals further from the observer are less likely to be detected. Line transect surveys detected more species and more individuals than point counts so count data were used for density estimation. Point count surveys detected a cryptic species not detected on line transects and contributed to a more complete species list so were deemed worth retaining in the survey design. Species detection probabilities indicated that many individuals were missed during the surveys, which lends support for using distance sampling over simple count data to measure arid bird abundance. I generated robust density estimates for 64 species and found that the majority fluctuated markedly over the five-year survey period. These data are useful for assessing temporal patterns in species occurrence and abundance, which I do in Chapter 3, and for relating species occurrence and abundance data to environmental variables, which I do in Chapter 4 and Chapter 5. This chapter confirms the validity of a repeatable protocol that can be continued and adopted for other taxa to rapidly assess changes in arid biological communities over a large scale and in a relatively short period of time.

Measuring the extent of movement in nomadic species is inherently difficult as species characteristically do not display seasonal movement. Bird ring recoveries have provided some limited evidence for irruptive species who show some seasonality in breeding sites (Newton, 2006b) and tracking devices have revealed pathways of ranging and directed movements in nomadic waterfowl (Roshier et al., 2008). However, movements of terrestrial nomadic birds are still poorly understood and recent studies show that the need to better understand them is urgent for improving their conservation as current schemes are unlikely to provide adequate protection (Cottee-Jones et al., 2015; Runge et al., 2015a). In Chapter 3, I developed a first quantitative assessment of nomadism in Australian arid zone birds. Using occurrence data and density estimates from Chapter 2, I analysed changes in species site persistence and measured variability in species' densities over a five-year period as an approximation of movement, and compared results with existing movement classifications from the literature. This chapter showed two important findings: 1.) extent of species movement varied along a gradual continuum rather than falling into resident and nomadic groups; and 2.) many species currently classified as resident showed site persistence and density variability comparable to species currently classified as nomadic. These findings indicated that the current movement classification paradigm likely underestimates species movements within arid regions of their distribution, and highlights that movement patterns in Australian birds are heavily environment-dependent.

In Chapter 4 of my thesis, I extend my analysis of arid bird movements to include environmental drivers of species abundance. It is generally assumed that fluctuating environmental conditions drive nomadic species movements, either directly or indirectly, in response to major rainfall events (Simmons et al., 2004; Burbidge & Fuller, 2007; Jonzén et al., 2011; Tischler et al., 2013; Jordan et al., 2017). This has, however, only been explicitly tested in a handful of studies, most of which found weak relationships between rainfall and environmental cues with nomadic species movements (South African desert birds, Dean & Milton, 2001; Grey Teal, Roshier et al., 2008; Swift Parrot, Webb et al., 2014). The role of static habitat features is often underplayed in how we think about nomadic species movements, but vegetation characteristics are undoubtedly important in foraging and nesting requirements for species (Pavey & Nano, 2009). In Chapter 4, I assessed the relative influence of four static and three dynamic environmental variables on arid bird abundance patterns, hypothesizing that nomadic and resident species respond differently to fluctuating versus static environmental conditions. I found that variables could not be fitted for most species used in my model, highlighting the difficulty in choosing predictors of abundance for this highly dynamic assemblage. Out of the dynamic variables tested, vegetation productivity from three different time periods (one, three, six, and twelve months prior to the survey month) was important for most species, half (4/8 species) of which were nomadic as classified by the literature as opposed to only one classified as resident. Out of the static variables tested, extent of woodland was important for most species, and static variables were important for an equal number of nomadic and resident species. I showed that dynamic variables appeared to be more important for nomadic species relative to resident species and that static variables were equally important for nomadic and resident species. These findings supported the idea that measures of habitat structure are important in combination with fluctuating conditions to explain nomadic species movements.

In Chapter 5, I take a more holistic approach at understanding species dynamics by investigating the role of rainfall on the arid bird assemblage. In arid systems, rainfall events and consequent resource pulses are assumed to be a major driving force of ecological booms and are often associated with increases in species abundances soon after rains (Noy-Meir, 1973; Burbidge & Fuller, 2007). Studies from various arid regions around the world have found differential responses in biotic communities based on the taxa examined, species life history traits, and time since rainfall (Meserve et al., 1995; Jaksic et al., 1997; Dean & Milton, 2001; Pavey & Nano, 2013). Letnic and Dickman (2006) showed that Australian desert mammals were actually more vulnerable following a rainfall event due to hyper-predation, increased grazing, and increased risk of wildlfire. Understanding the relationship between rainfall, resource pulses, and biotic fluctuation is critical for managing arid populations and being able to predict their response to future climatic disturbances. In Chapter 5, I investigated the relationship between these three variables for Australia's arid bird assemblage. Specifically, I used total monthly rainfall and mean monthly vegetation productivity, and focused on four key structural community metrics: overall species density, overall species biomass, species richness. I also measured species turnover at the site level and for all sites pooled. Similar to other studies, I showed that rainfall alone did not influence community response but interacted with vegetation productivity to positively influence all community metrics (Meserve et al., 1995; Dean & Milton, 2001). As expected from previous studies from this region, I found that the arid bird community underwent large shifts in overall density, overall biomass, and species richness at the site-level from year to year; unexpectedly, I found evidence of stability for this community at the landscape-level as indicated by low species turnover for all sites pooled and similar relative abundances of common species between years. These findings underscore the importance of connectivity between suitable habitats within this landscape to enable species to reshuffle among sites. Importantly, current conservation approaches using small-scale static reserves are not likely provide adequate protection at the scale necessary for such a dynamic community that does not remain stable at a local level.

6.3 Assumptions and limitations

My thesis chapters contributed novel information about drivers and patterns of arid bird occurrence and abundance. However, given that little was known about this group previously, I made certain assumptions and focused only on key questions that I felt I was able to address with the data collected. Here, I address those assumptions and caveats that should be considered when interpreting key findings.

Given the time and budget limitations of the field survey, certain improvements could be made in future years or if the protocol is used with different taxa. For ease of work conditions, the bird surveys outlined in Chapter 2 are conducted in winter each year. However, to fully understand arid bird movements and map their complete distribution, we need to know where they occur year-round over multiple years that span extreme wet and dry conditions. During summers where temperatures are increasingly exceeding species' physiological limits (40° C; McKechnie et al., 2012), birds likely die, disperse, or seek shelter in habitat refugia (Mackey et al., 2012; Selwood et al., 2015). Following rains, species could conceivably breed and increase numbers once again by winter. Burbidge and Fuller (2007) found significant seasonal differences in arid bird assemblage of Australia's Gibson desert; thus, surveying in just one season could give unrepresentative picture of overall species population trends. One possible solution to this gap in knowledge is to survey in other seasons. Summer surveys would likely only be feasible if observations took place at dawn and dusk as mid-day bird activity during scorching peak temperatures would be significantly lower and could lead to biased detection; however, autumn and spring surveys would be more feasible. Another alternative is using acoustic monitoring devices to record birds year-round paired with automated species identification to assess seasonal changes in the bird community (Ross et al., 2018).

An underlying assumption of Chapter 3 and Chapter 4 of my thesis is that changes in species occupancy and abundance are indicators of species movements. Such changes could also be attributable to demographic processes, mainly breeding and death. One way to disentangle the two processes would be to incorporate species breeding rates and generate population growth models. The most straightforward, but expensive, way to separate movement processes from births and deaths, would be to attach remote tracking devices (Cottee-Jones et al., 2015). However, a substantial number of individuals would need to be tracked to account for variation in individual movements (see Roshier et al., 2008).

The analysis for Chapter 4 uses existing movement classifications (Garnett et al., 2015) as a baseline against which to compare my results. As previously demonstrated in Chapter 3, these classifications may not accurately represent the extent of species movement in arid regions; however, they are the most comprehensive data currently available for Australian birds. Further, even if these classifications underestimate the extent of species movements, it would not change my results of which environmental variables are important for certain species. In this chapter, I found that dynamic and static environmental variables could only be fitted to 16 out of the 64 species used in the model, indicating weak explanatory power of these environmental variables on species' abundance. This limitation serves as an important consideration for future studies that use such variables in species' distribution models for arid zone birds as they assume habitat or climate variables to be reliable predictors of species' occurrence or abundance.

Chapter 4 and Chapter 5 of my thesis focus on the effect of rainfall, vegetation productivity, and vegetation characteristics on the inter-annual bird community. I do not consider the effect of other important factors, such as fire, predation, or availability of specific food resources (e.g. nectar, seeds), on arid birds over the survey period. Fire and predation have been documented as important in structuring Australia's arid communities, especially following extreme rain events (Letnic & Dickman, 2006; Pavey & Nano, 2013). Fire is a known driver of arid and sub-tropical savannah ecosystems in north-central Australia where return times are relatively short and less prevalent further south in the Lake Eyre Basin where return time of fire for chenopod shrubland is more than 50 years (Morton et al., 2011); nonetheless, fires can substantially restructure biotic communities and fire events should ideally be included as a factor influencing inter-annual abundance and richness of communities, if possible. Predation of arid birds by raptors and of ground-nesting species by cats, foxes, and dingos can negatively influence bird abundance (Pavey & Nano, 2013; Gordon et al., 2017). Analyses that account for species co-occurrence could give important insight into the extent to which these factors influence inter-annual bird abundance. Incorporating data on fine-scale habitat features like food availability or specific plant species could improve models of local abundance of certain species. For example, presence of nectar-producing flowers could explain honeyeater abundance, presence of seed-bearing plants could explain abundances of Zebra Finch, Budgerigar, Little Corella, and presence of cane grass and dunes could explain Eyrean grasswren occurrence. Studies incorporating detailed site-level features have greatly increased our understanding of nomadic species such as Swift Parrots (Webb et al., 2014; Stojanovic et al., 2015), and arid bird feeding guilds (Tischler et al., 2013).

6.4 Synopsis and future directions

In my thesis, I provided a novel standardised protocol for monitoring nomadic and arid-zone birds and reliable detection probabilities, with which I showed varying inter-annual densities for a majority of species (Chapter 2). I provide a first measure for quantifying the extent of nomadism among this assemblage using patterns of species' site persistence and variation in abundance, and showed that resident and nomadic species' movements varied along a continuum rather than falling into two distinct groups, and that the extent of nomadism is likely underestimated by existing classification standards (Chapter 3). I added to a handful of studies explicitly testing key environmental variables influencing species' site usage and found that dynamic variables were more important for nomadic versus resident species but that static variables were equally important for nomadic and resident species (Chapter 4). Finally, I unpacked the relationship between a major rainfall event, resource availability, and fluctuations for Australia's arid bird community, and found that the importance of rainfall was mediated through vegetation growth and that this community is dynamic at a local level but exhibits stability at a landscape level (Chapter 5).

My thesis chapters contribute to a growing body of knowledge about this difficult-to-study group of birds and highlight several areas where future work is necessary. We should continue monitoring arid-zone birds to contribute to a growing dataset that enables an objective assessment of movement patterns and drivers of movement. We still do not understand the extent to which these species move, breed and die within a year. Monitoring should be expanded to different seasons, either by conducting field surveys, deploying remote acoustic recorders, or using weather radar, to collect a comparable dataset to that presented here. No two clear movement groups exist in this assemblage and my results challenge the idea that we can glibly label species as nomadic or resident. Data measuring and comparing movements in disparate parts of species' ranges will be necessary to move away from a simple resident / nomad dichotomy. Disentangling movement from demographic processes has yet to be done, and to do so requires data on the rate at which species are capable of reproducing following rain. Collating existing breeding data and supplementing gaps with multi-year field studies of species breeding is needed to enable such analyses. Alternatively, or additionally, attaching remote tracking devices would provide definitive evidence for the extent, direction, and rate of species movements. Such technology is needed to unravel species-level variation in movement and should target large numbers of small species. The feasibility of this may increase in coming years as the mass of the devices becomes sufficiently low. There remains a need to identify key local and regional environmental drivers of abundance for a majority of arid-zone species. Including data on fine-scale habitat features and top-down drivers of species dynamics could improve such models. Only when we can identify strong predictors of arid bird species abundance can we generate reliable species distribution models and begin to predict the impact of future climate scenarios on this assemblage.

The findings presented in my thesis advance our understanding of nomadic species dynamics and lay groundwork for improving protection of this group by identifying priorities for future research. The way nomadic species are currently managed for conservation is likely inadequate and a lack of dynamic conservation approaches could be leaving many unprotected in large parts of their annual ranges, thereby leading to population declines over time. Generating reliable assessments of population trends and threat status for these species has yet to bear fruit, and the results from this thesis contribute toward and highlight the kind of data and studies needed to do so. My thesis helps shift the way we think about arid bird movement ecology away from conventional wisdom and inference and toward a growing knowledge base founded in empirical evidence. Only with an improved understanding of nomadic species distributions and ecology within and between years in relation to known environmental drivers can we begin to conserve this unique group of animals.

7

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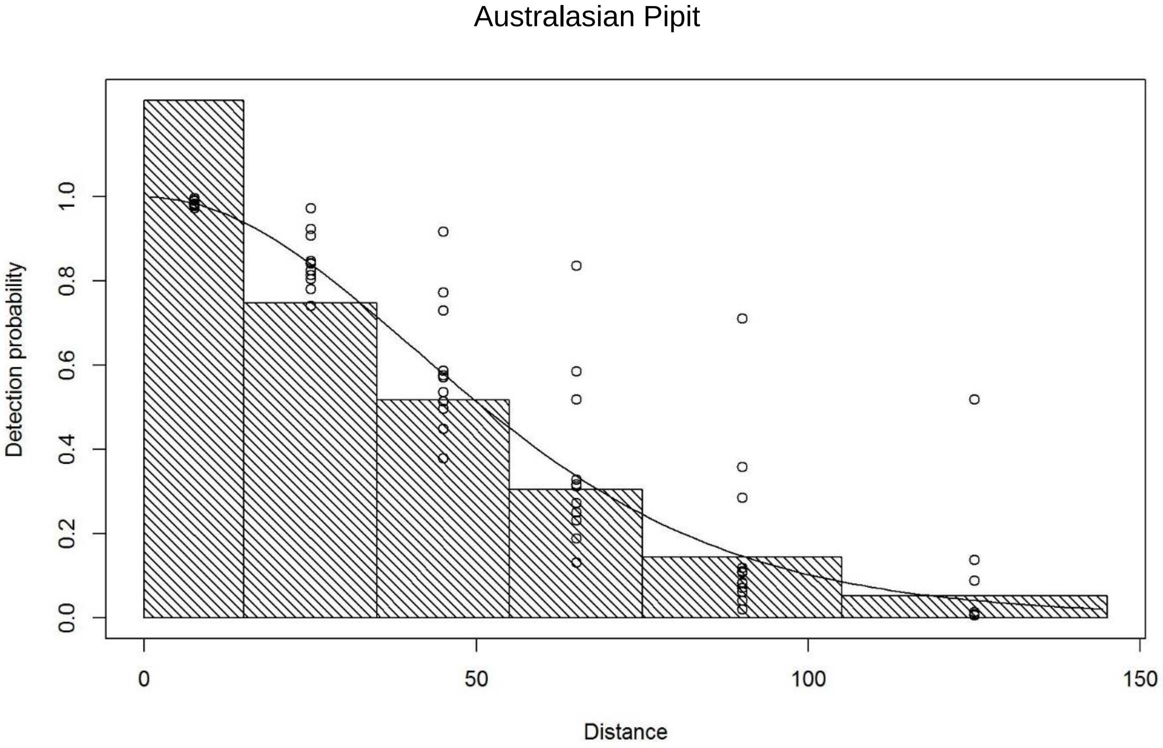
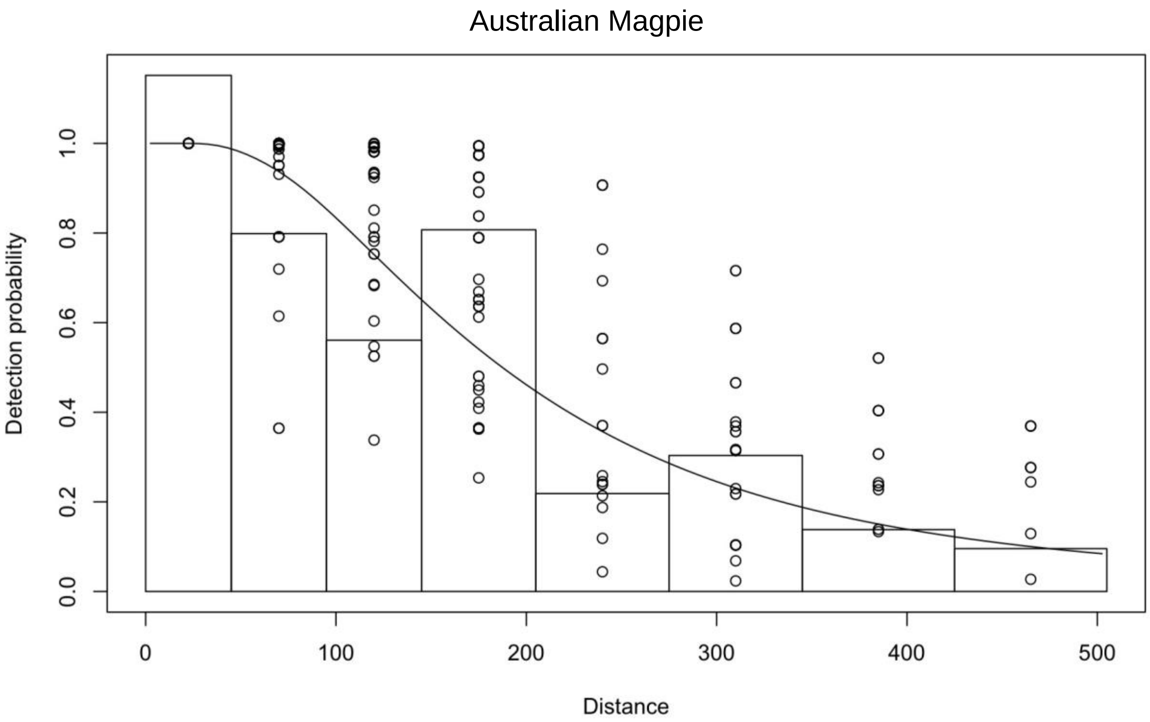
8

Appendices





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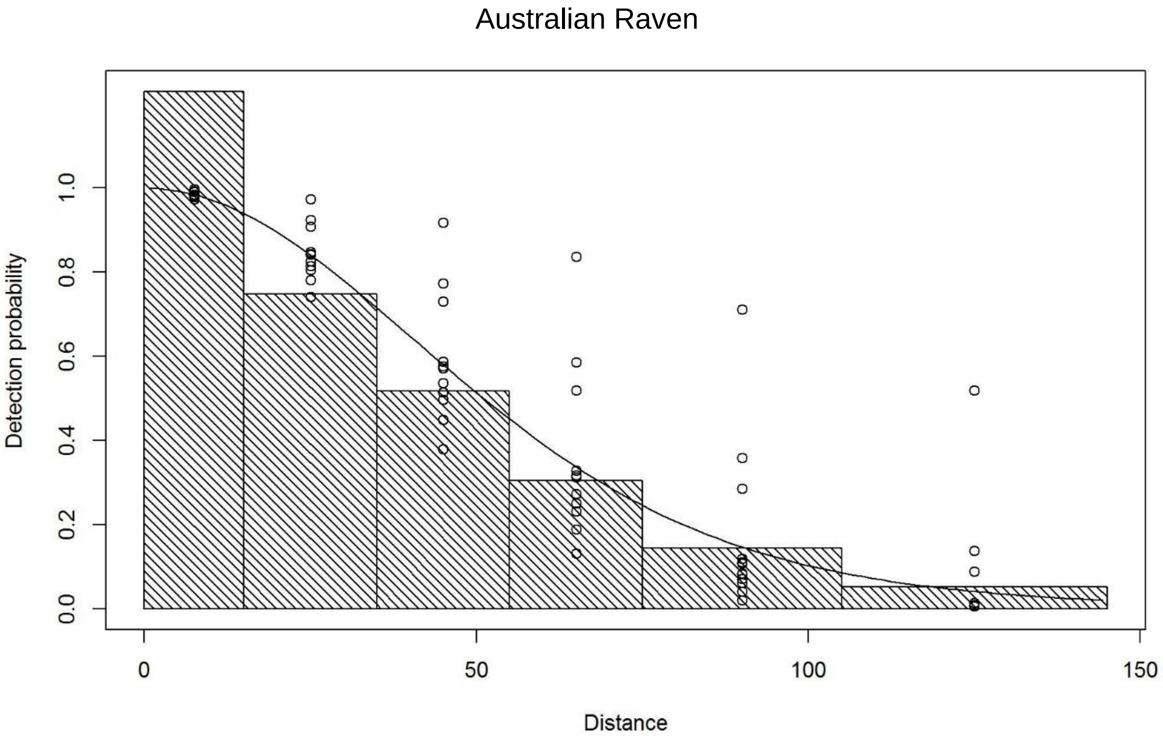

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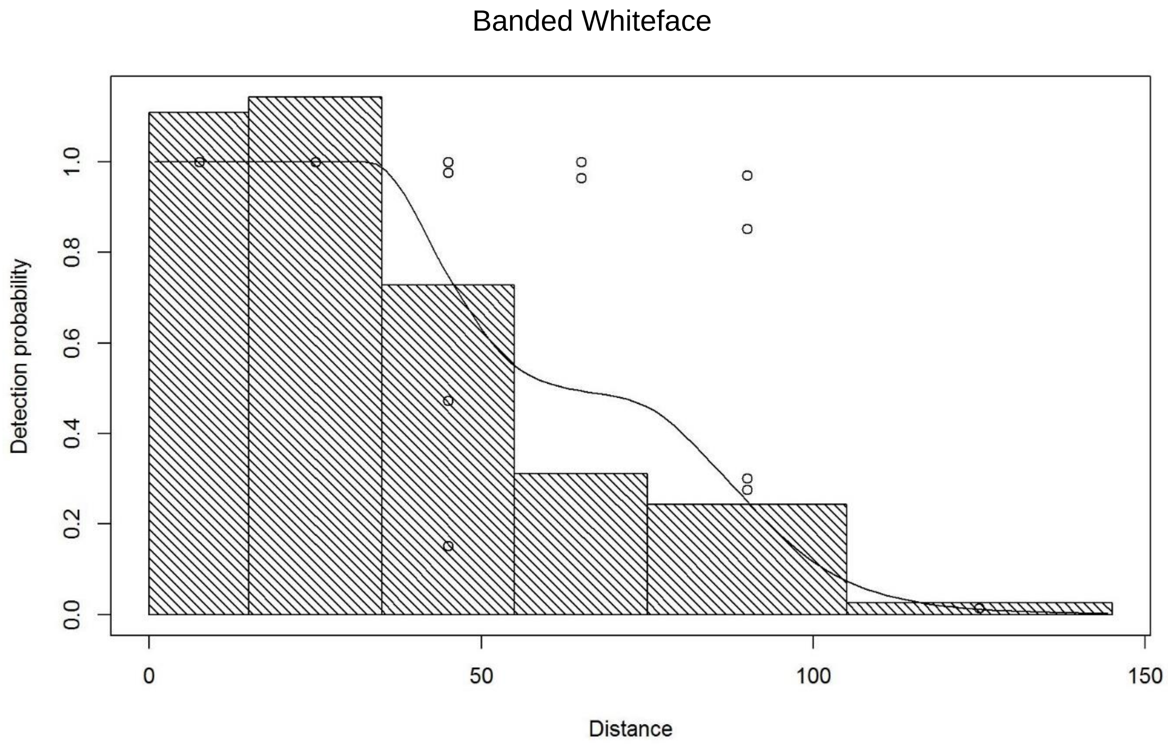
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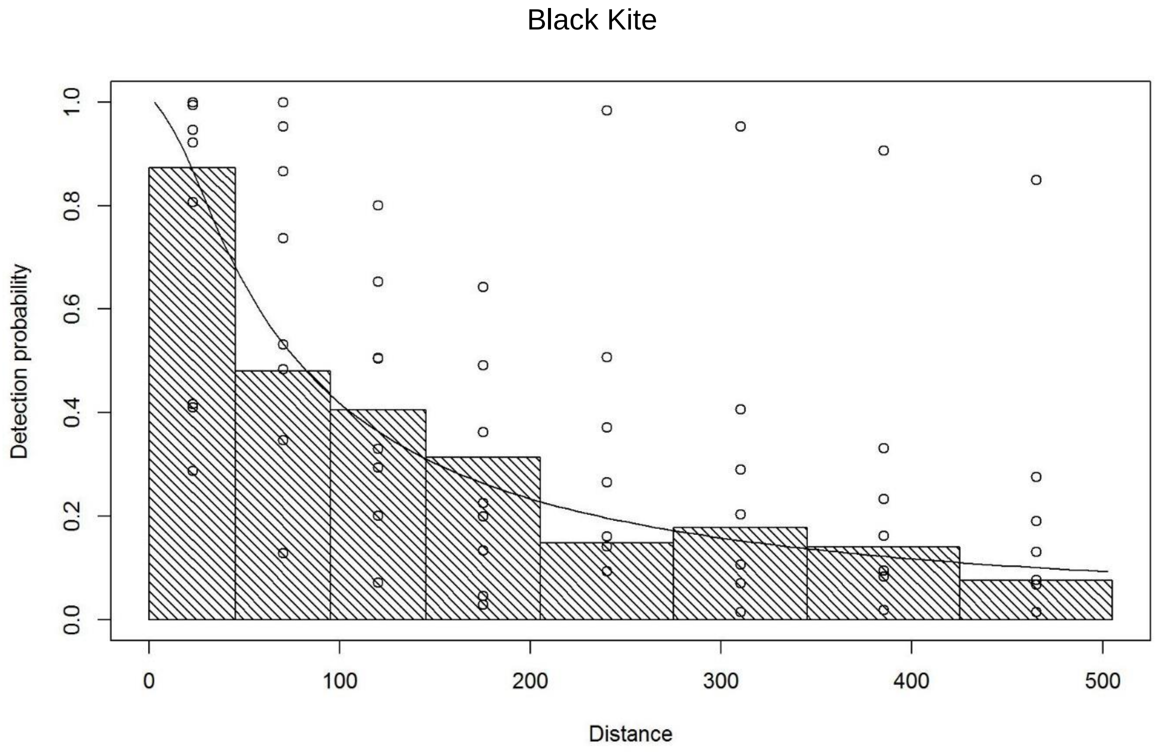
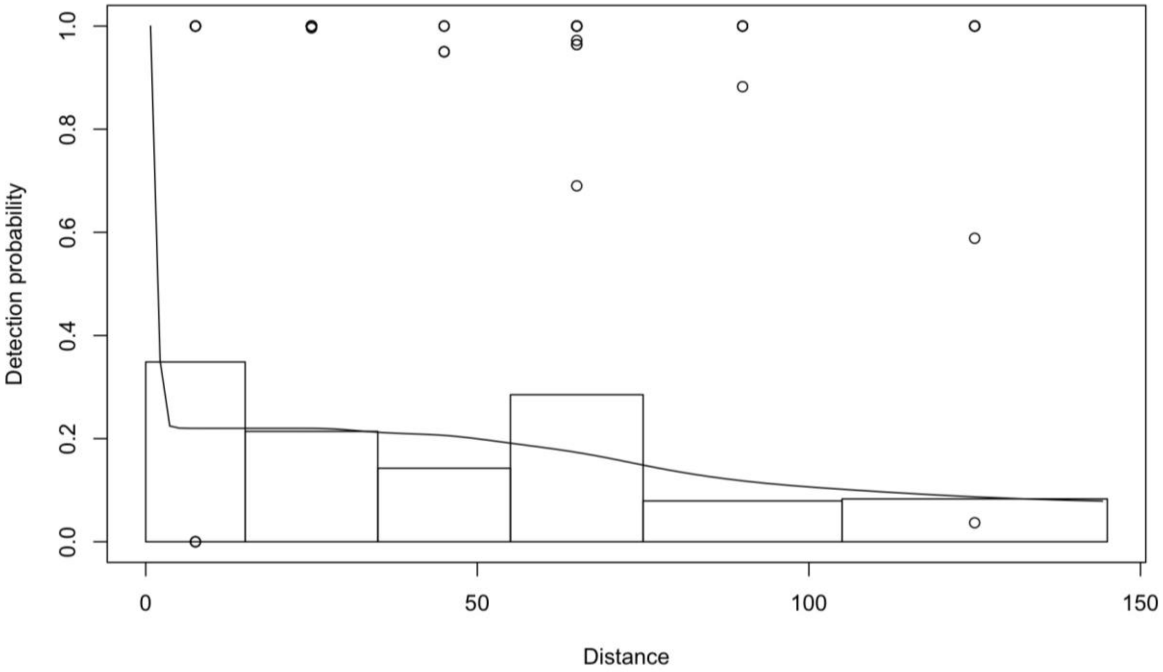

Black Kite

Black-faced Cuckoo-shrike



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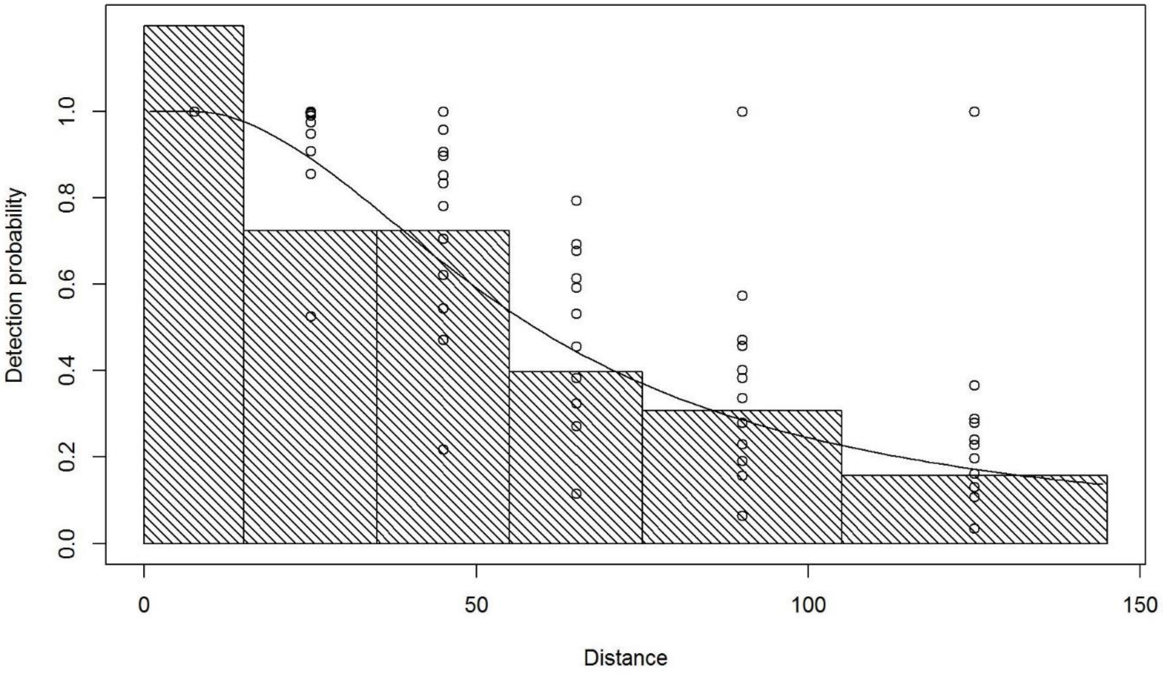

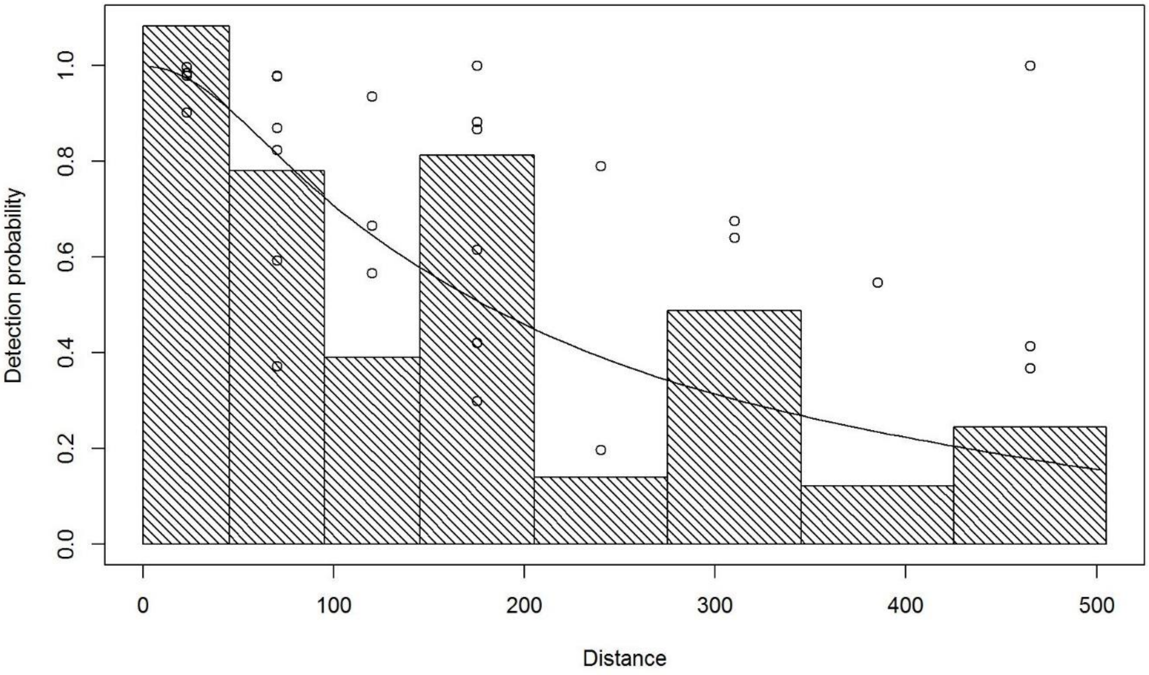
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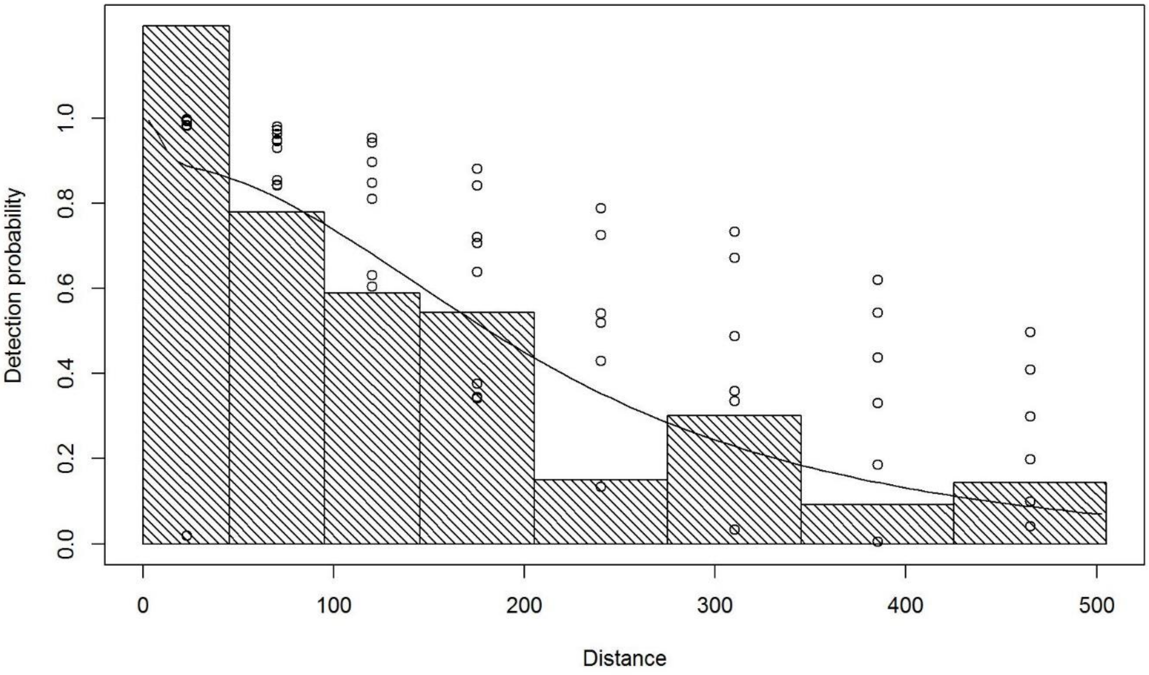
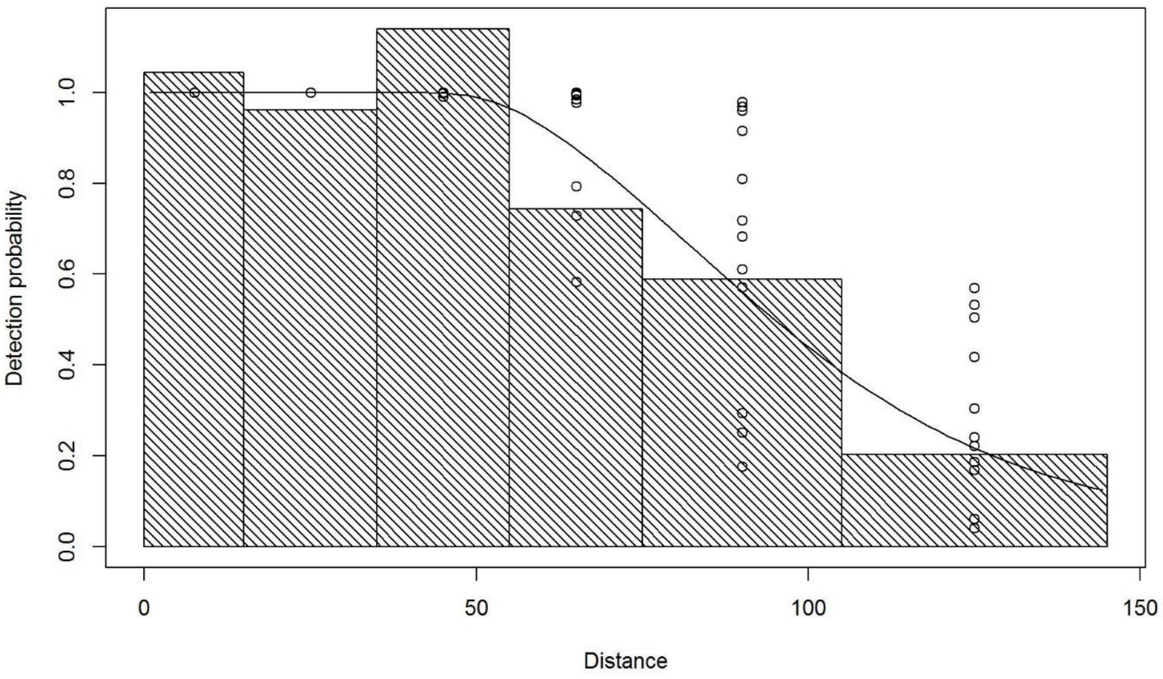
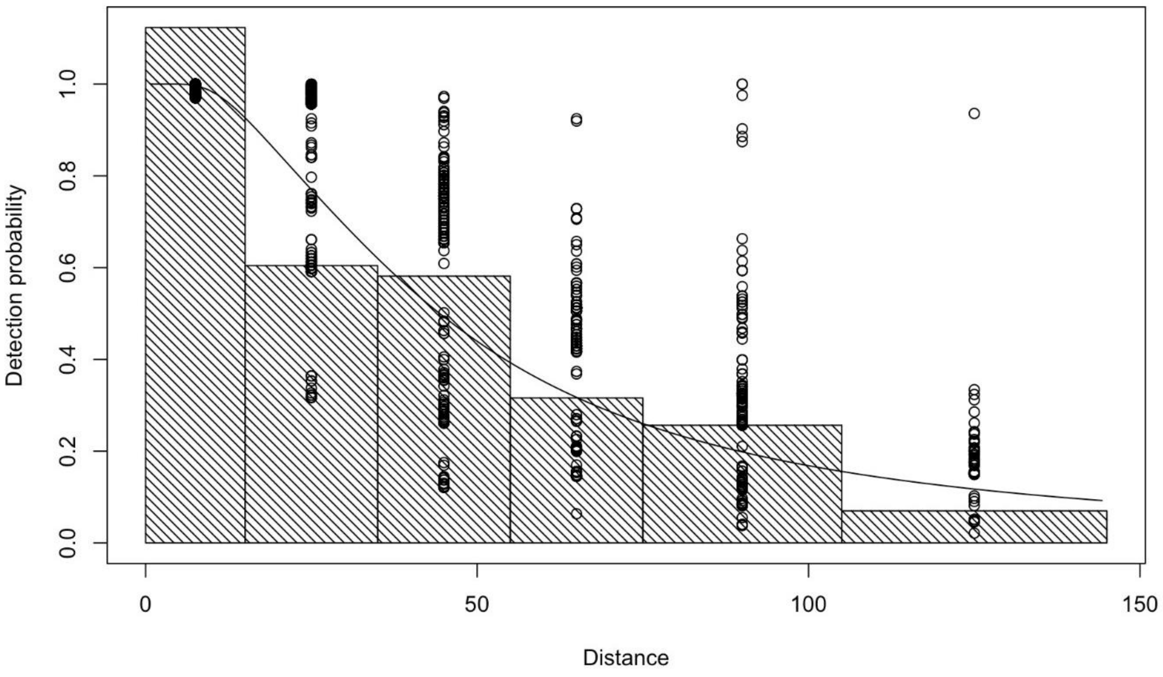

Brown Falcon

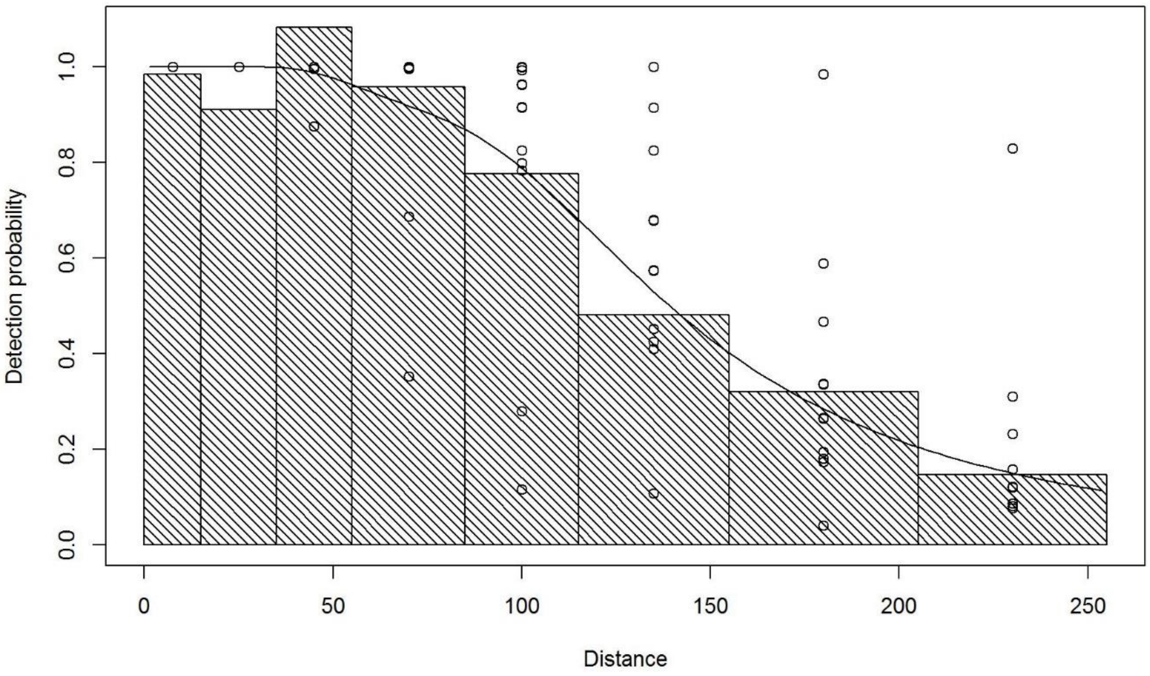
Brown Songlark



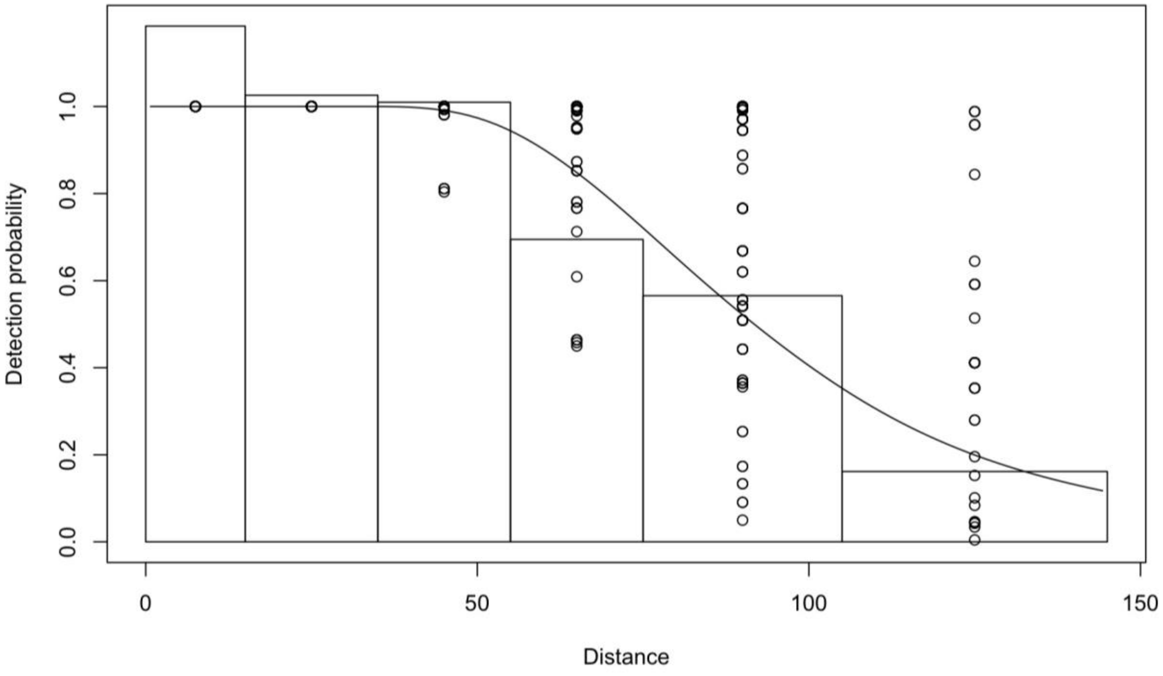
Budgerigar

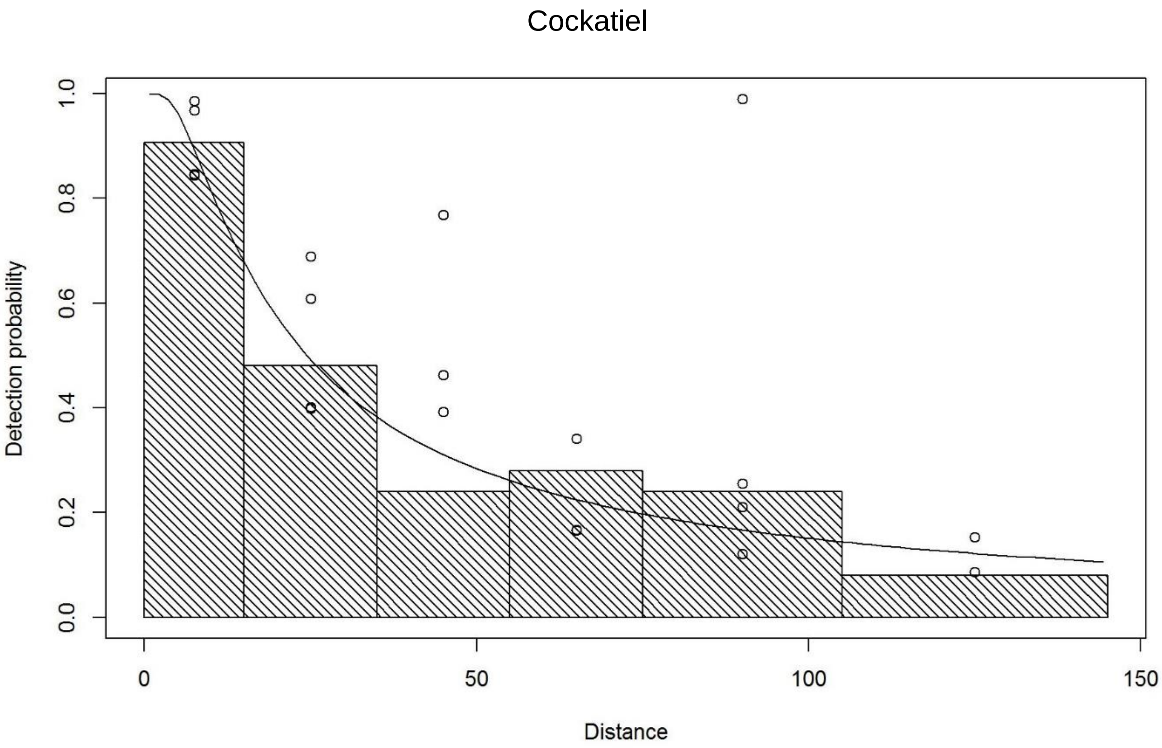


Chirruping Wedgebill*



Cinnamon Quail-thrush

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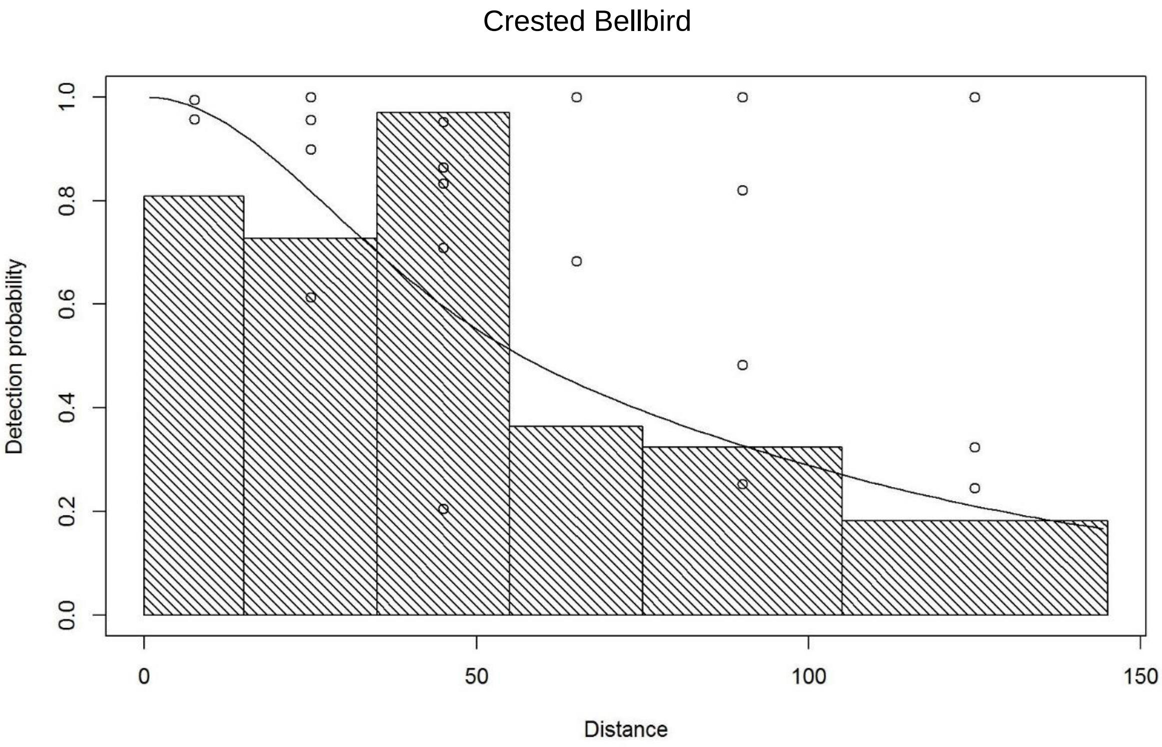
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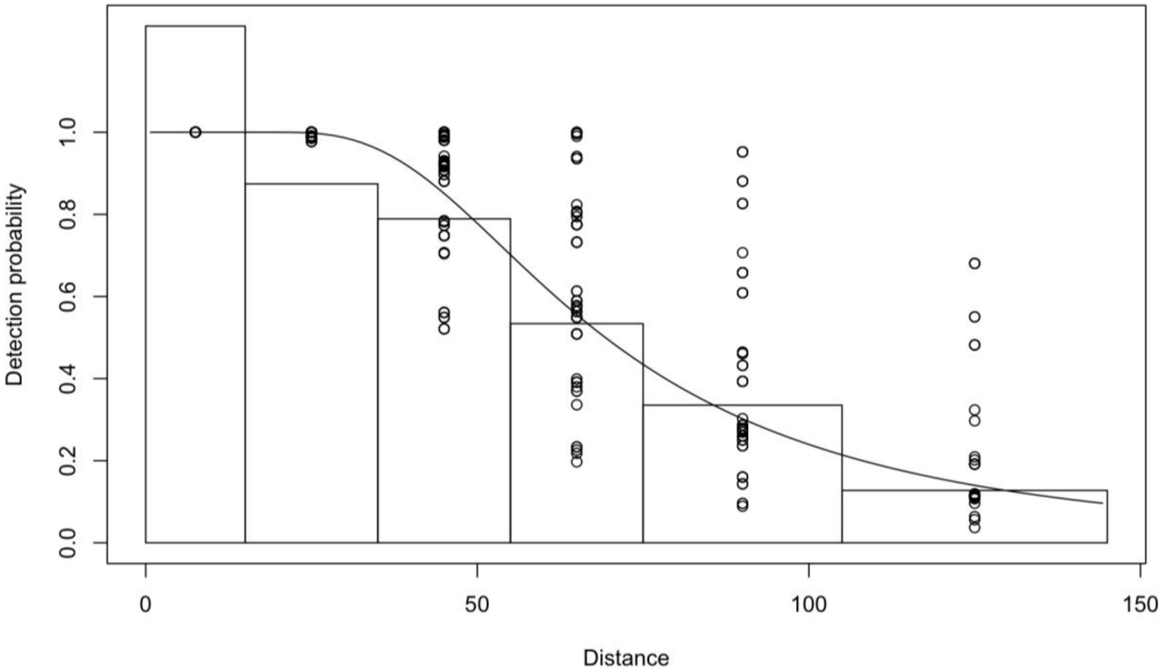

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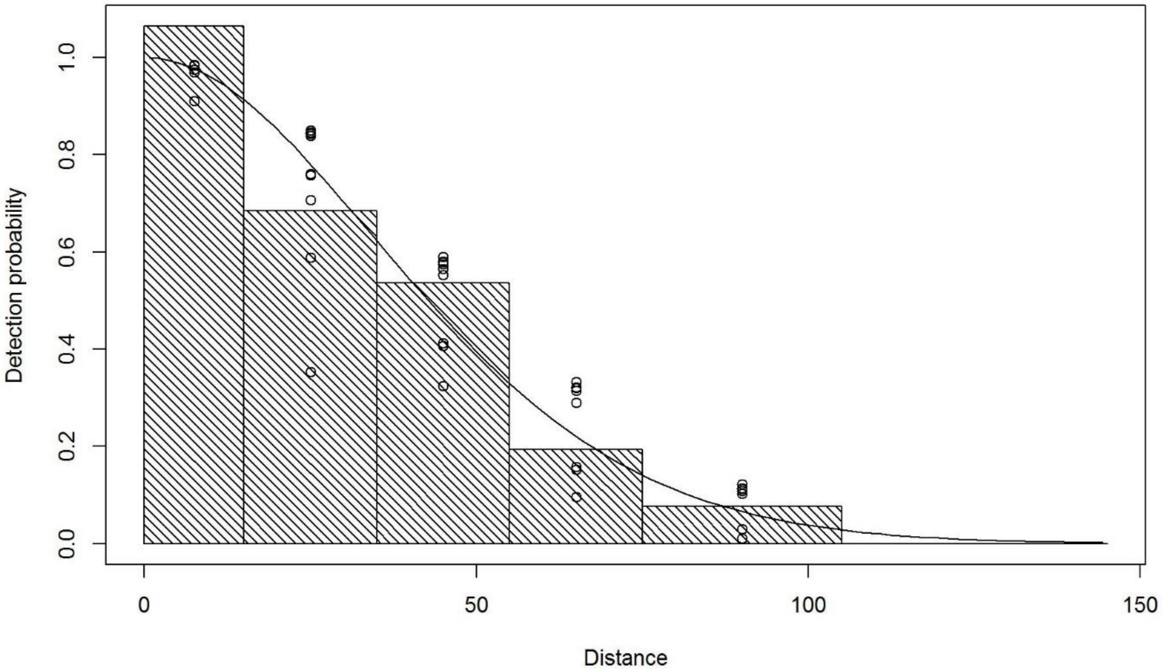
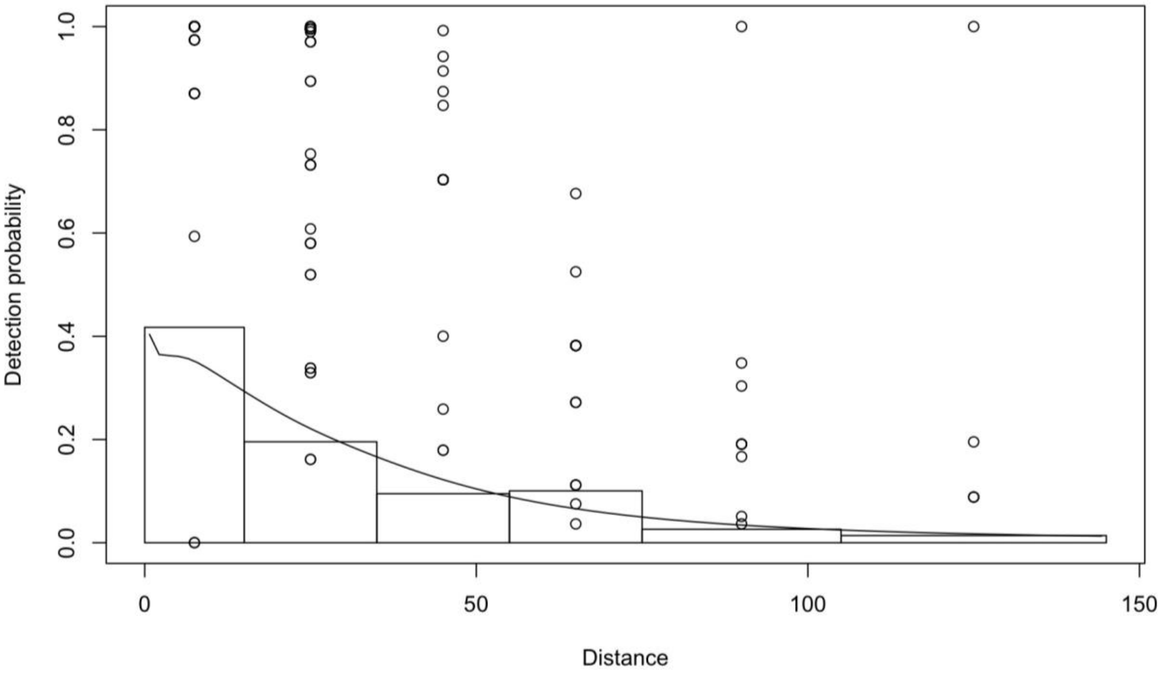


Crimson Chat

Diamond Dove*



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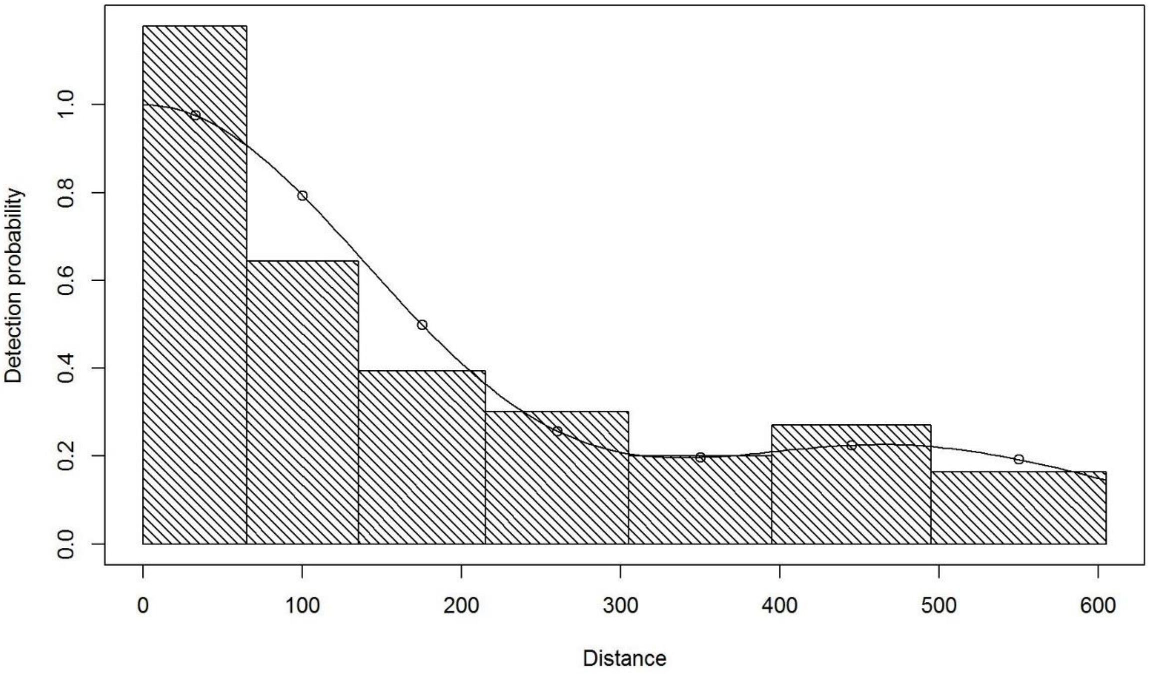

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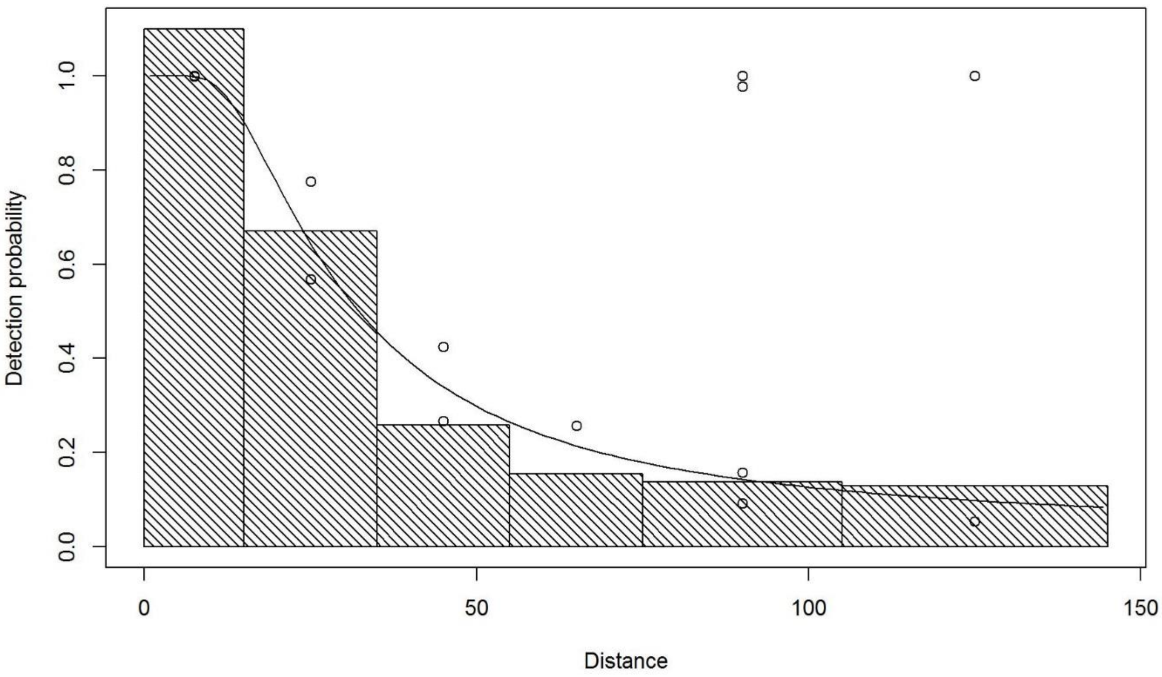

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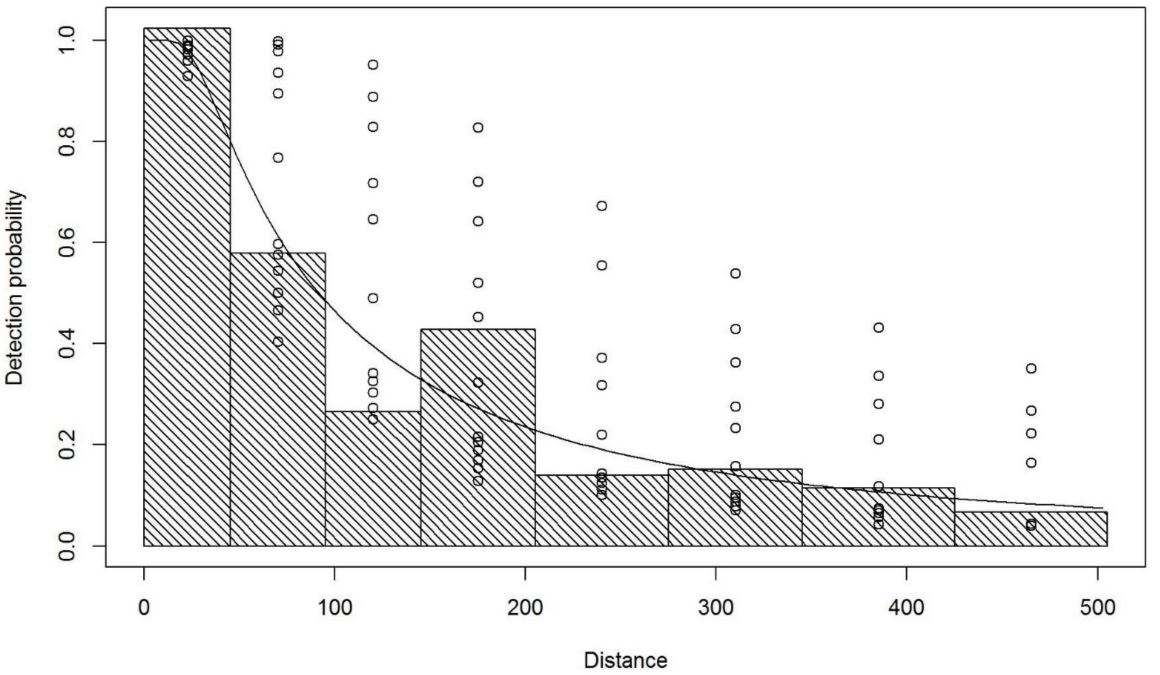
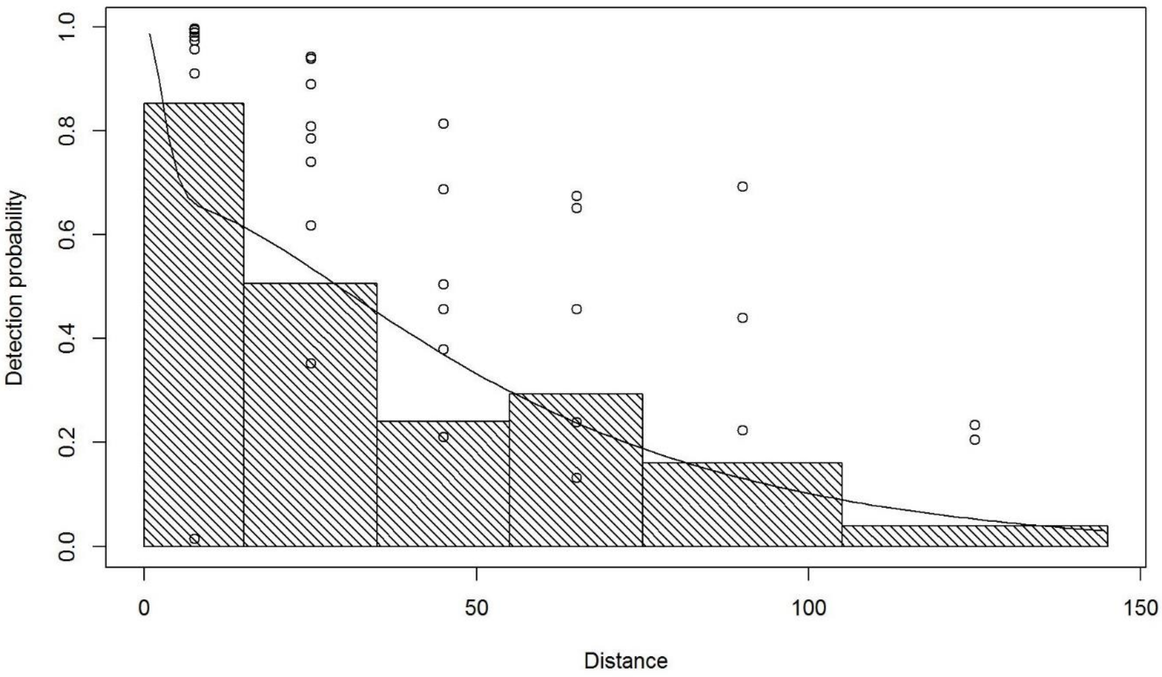


Gibberbird



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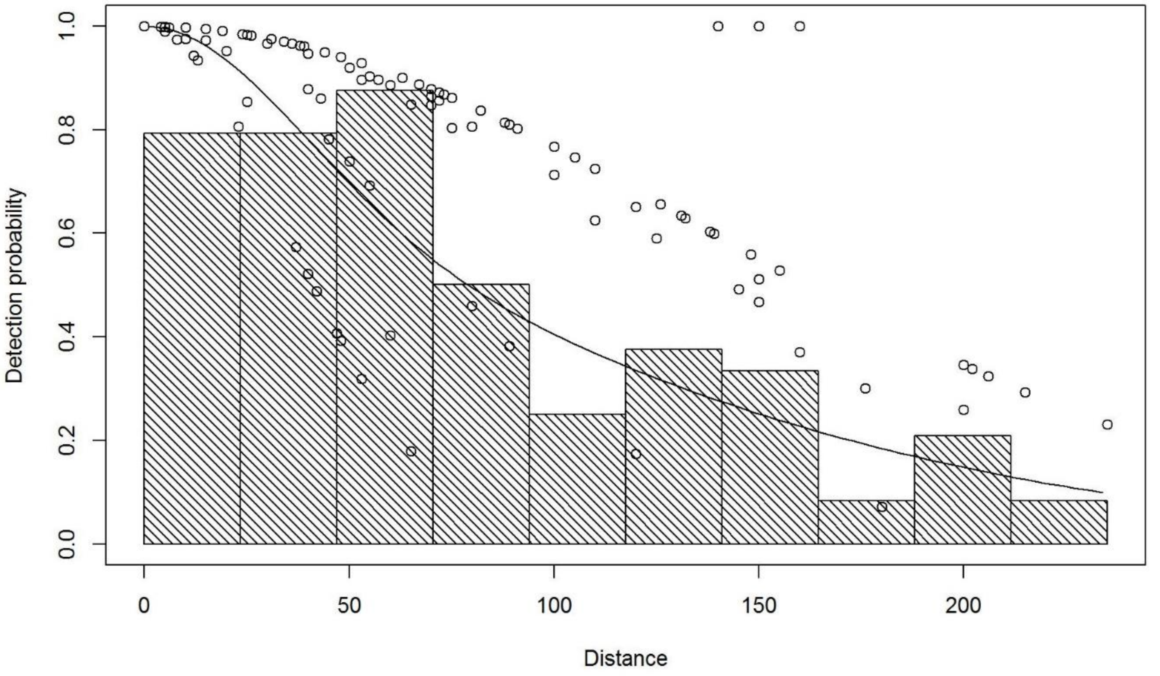

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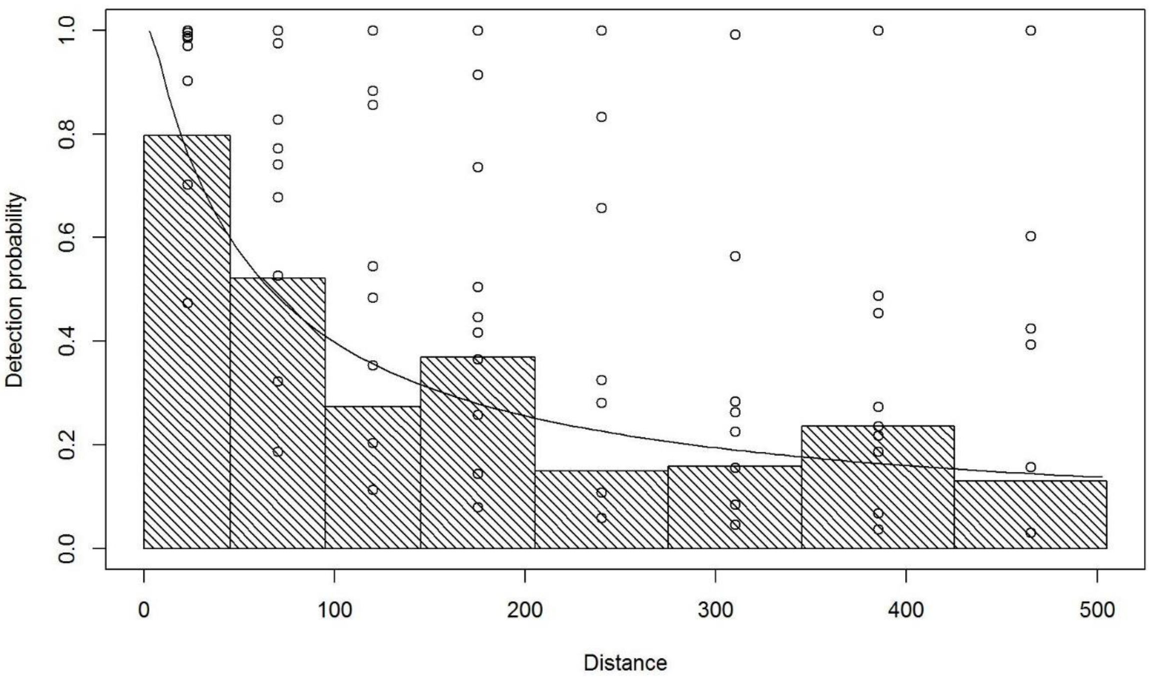

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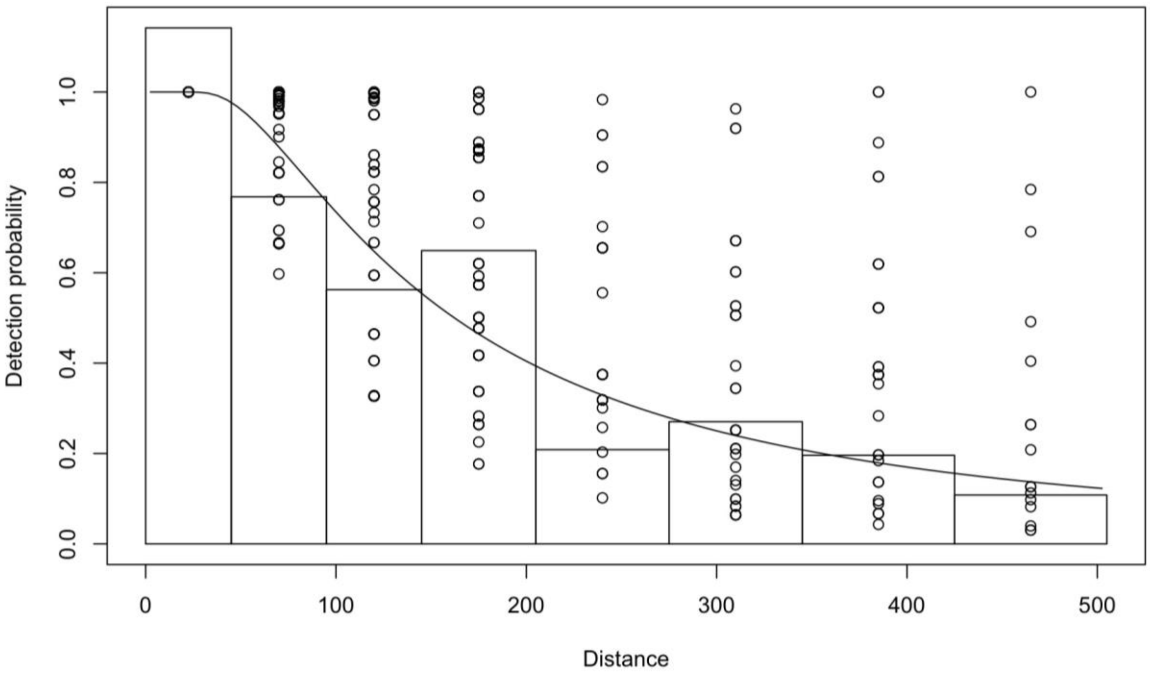

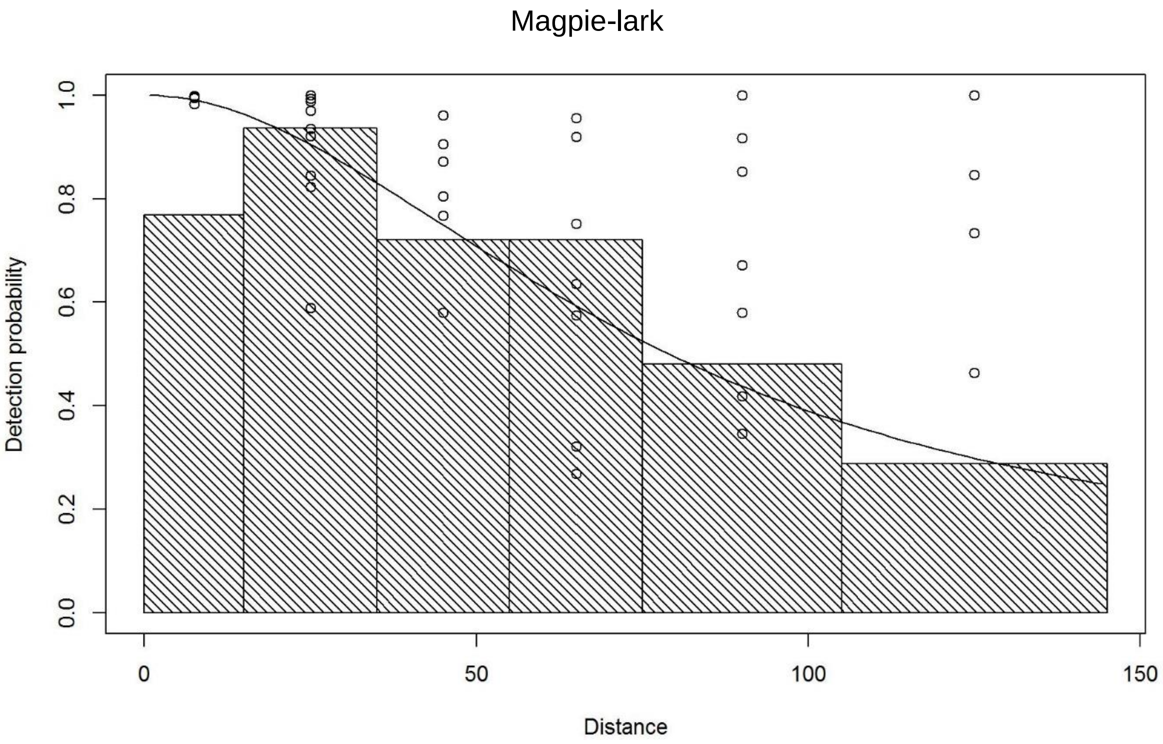
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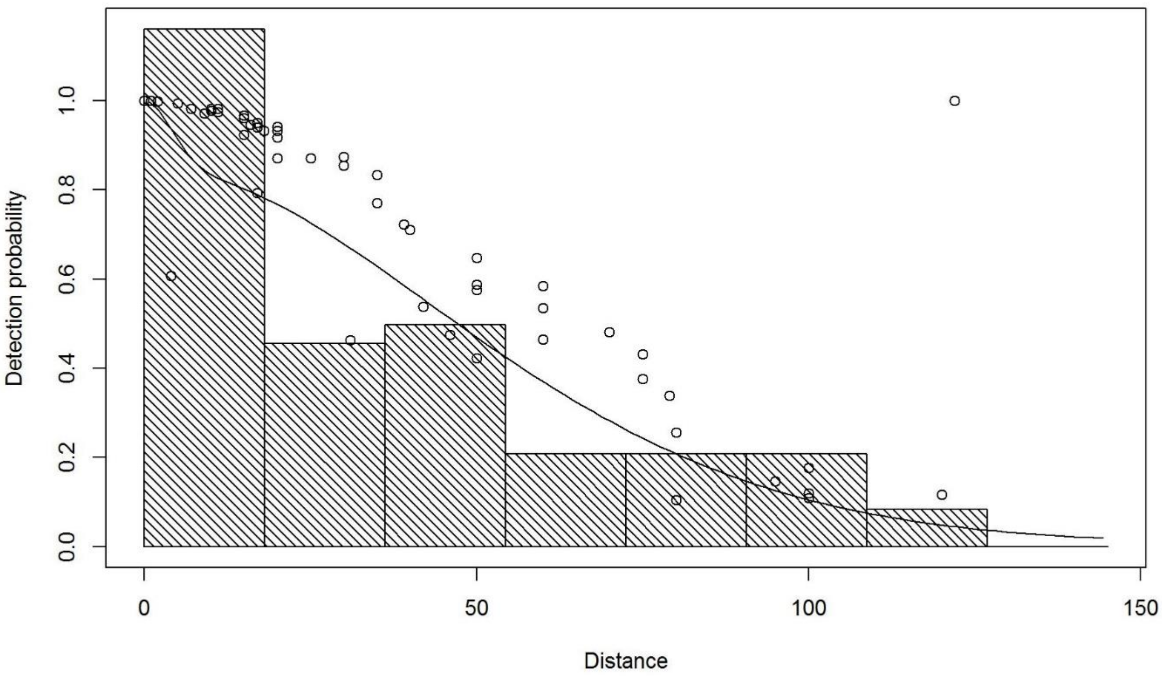

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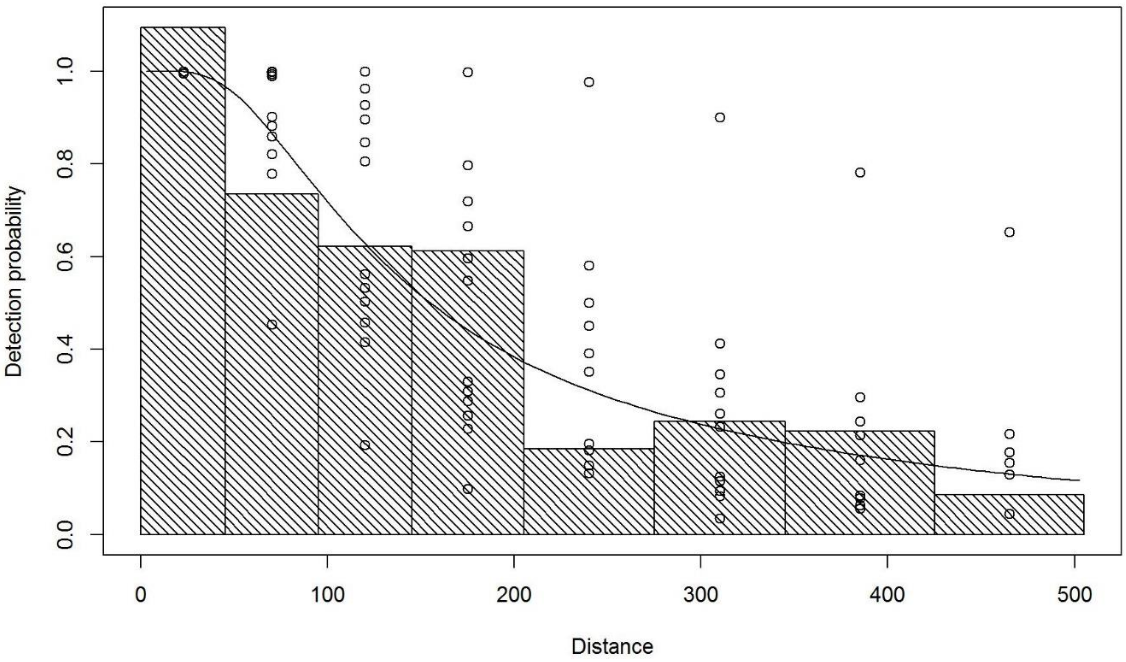

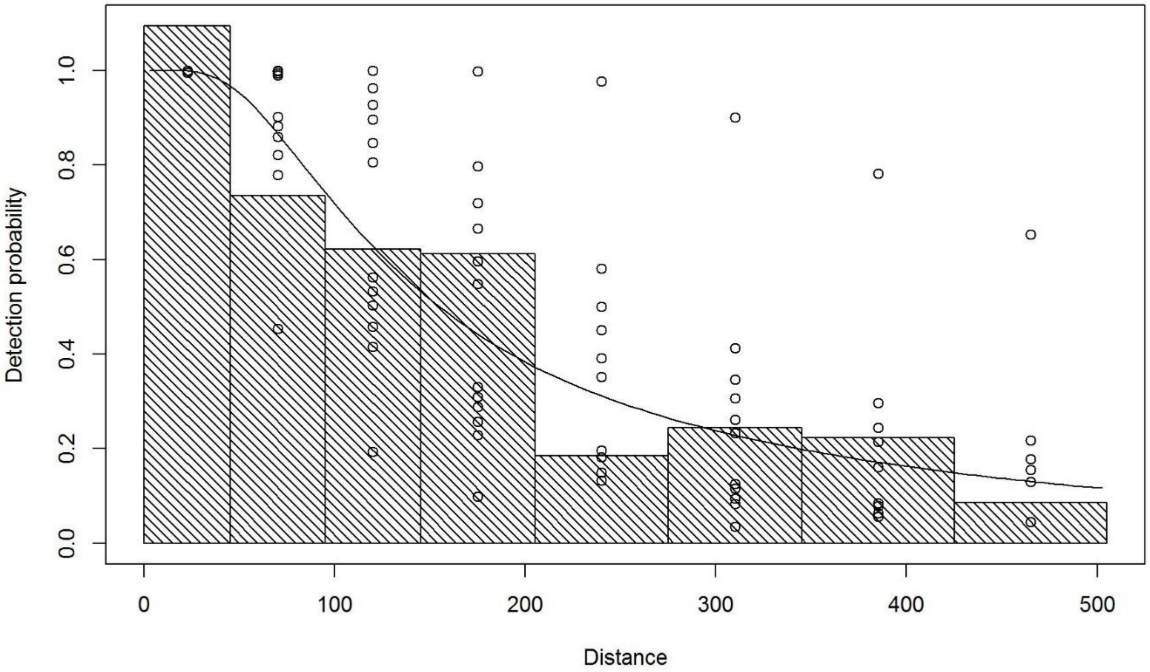
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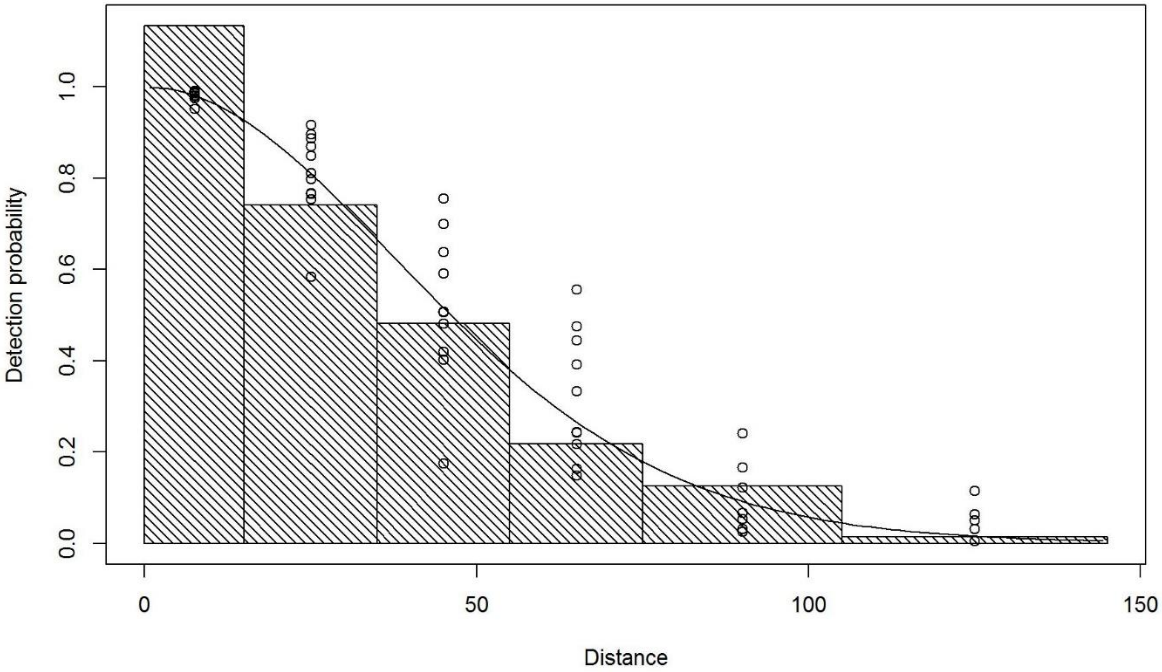
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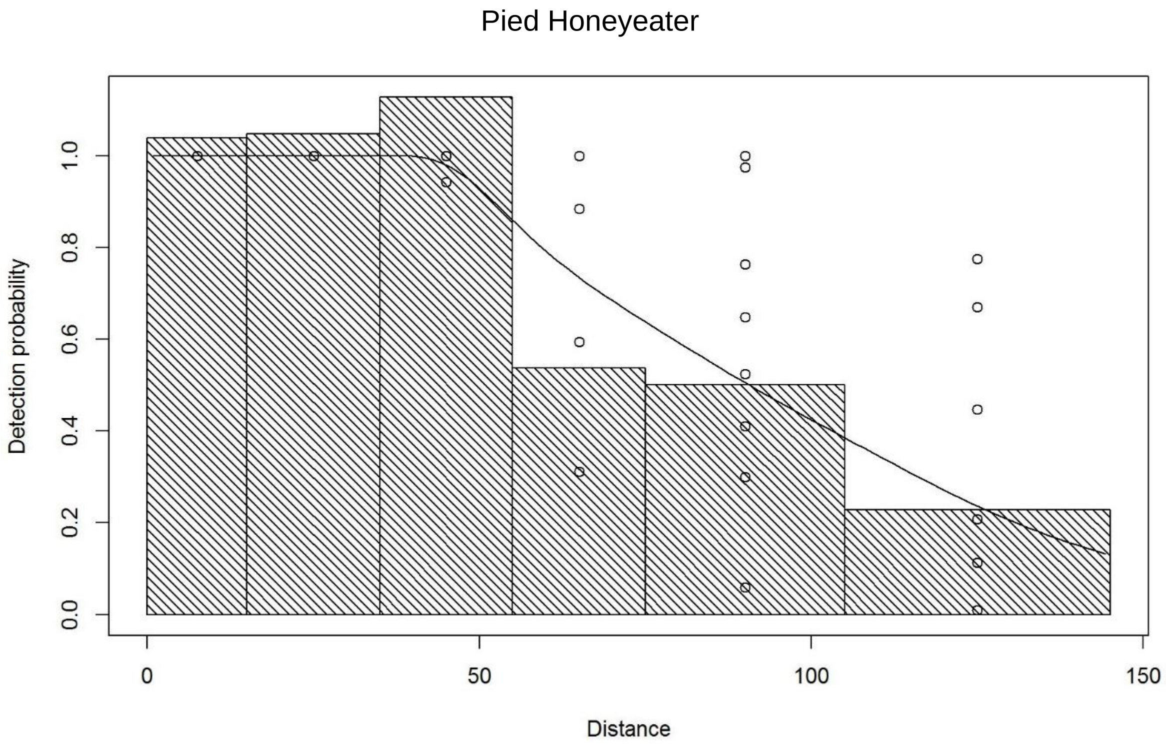
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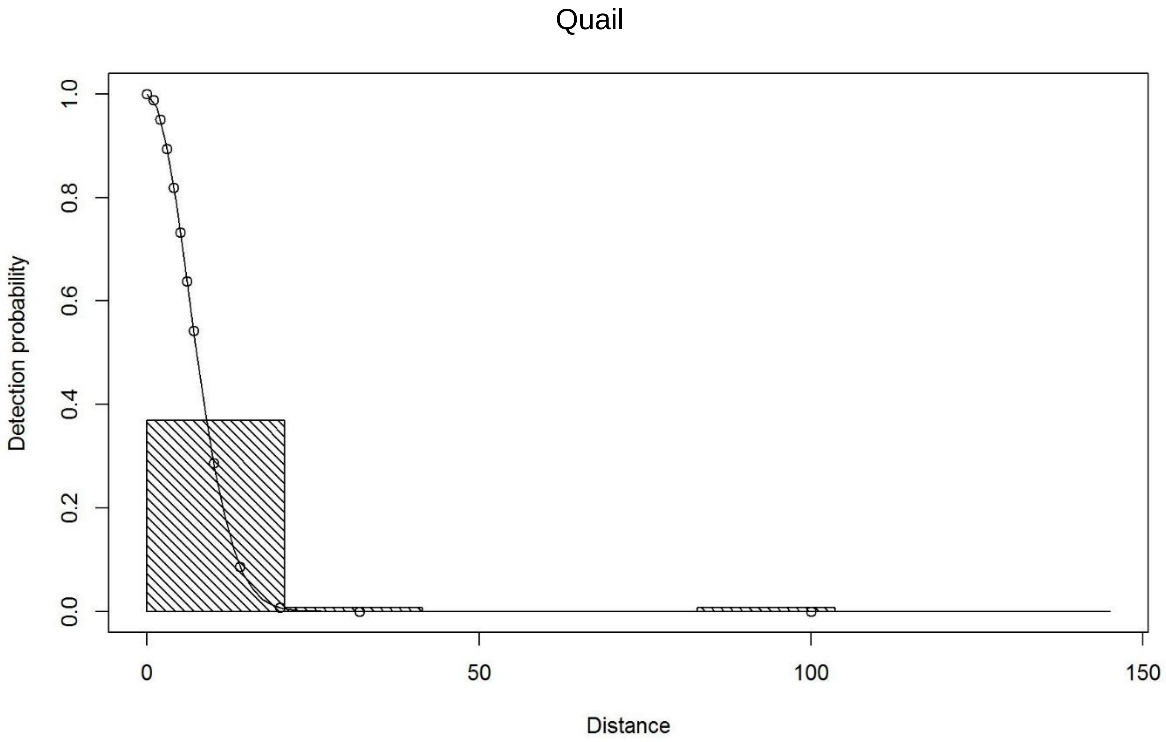
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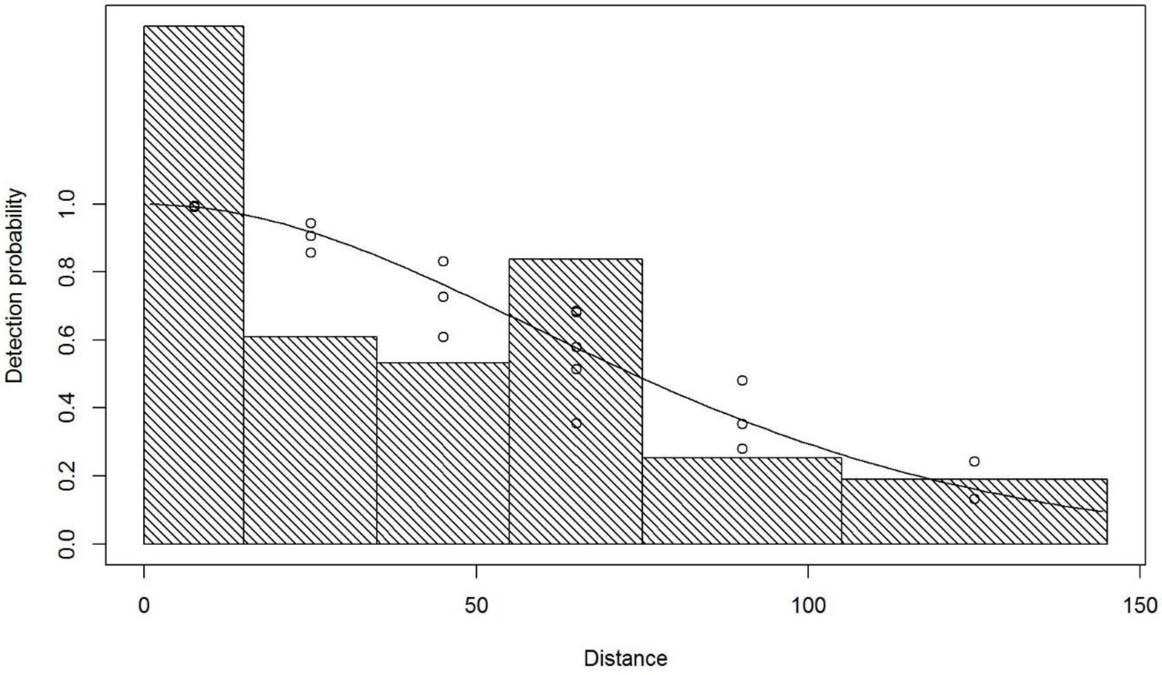

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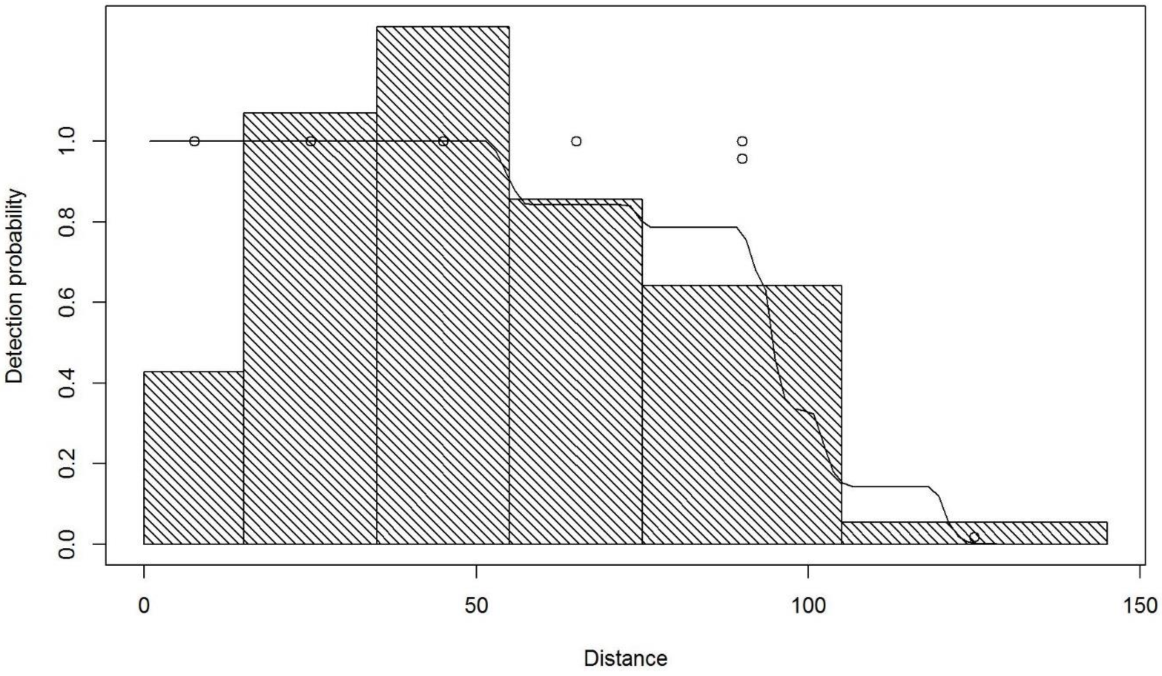
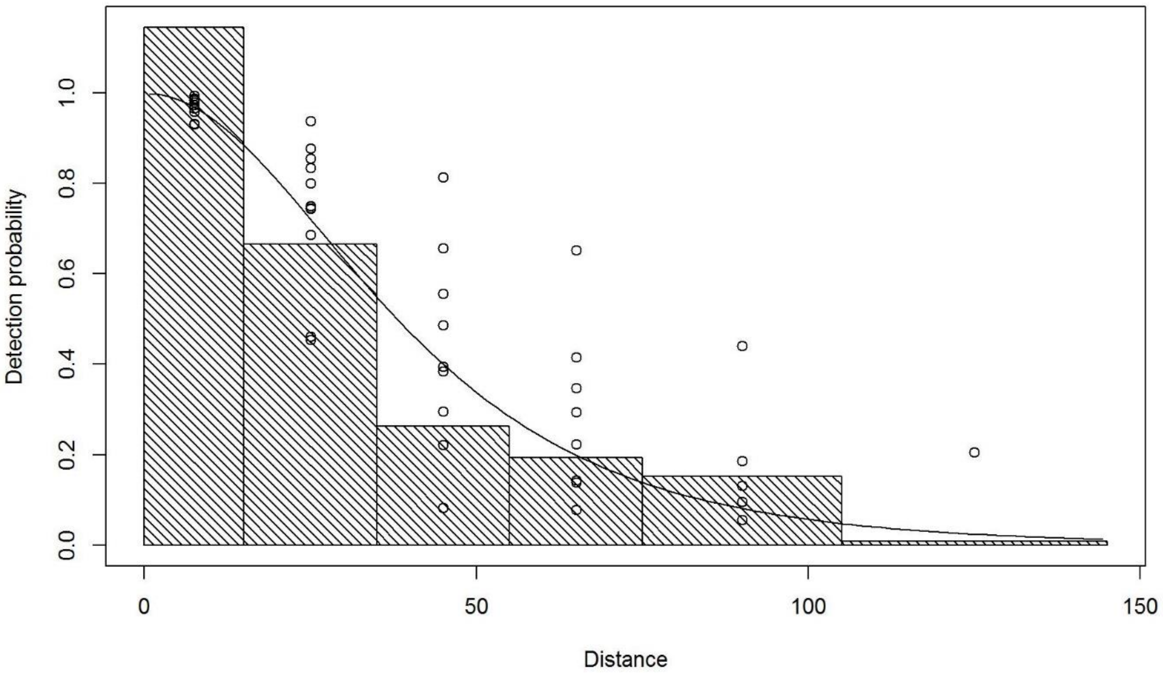
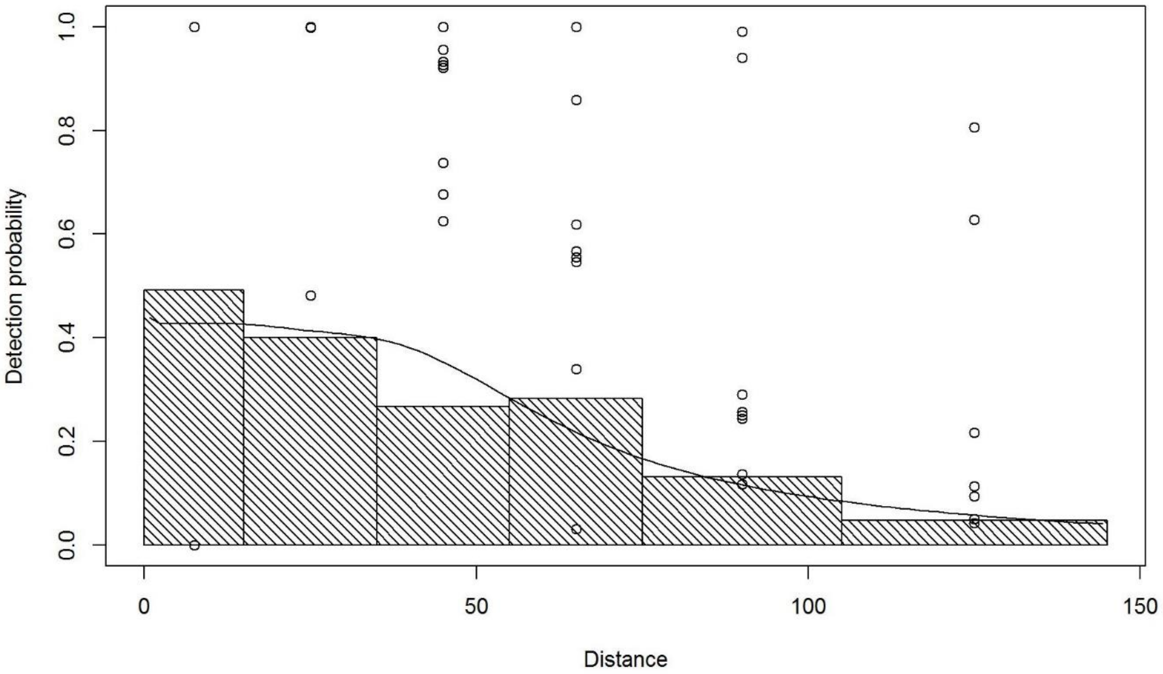
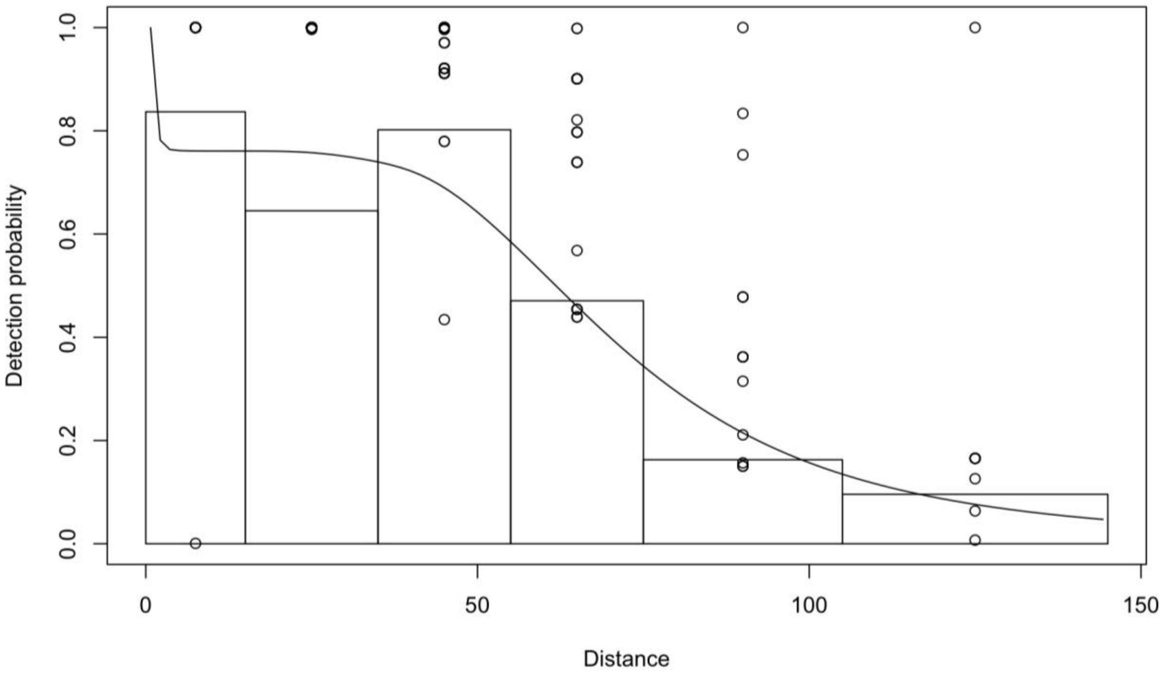


Red-capped Robin

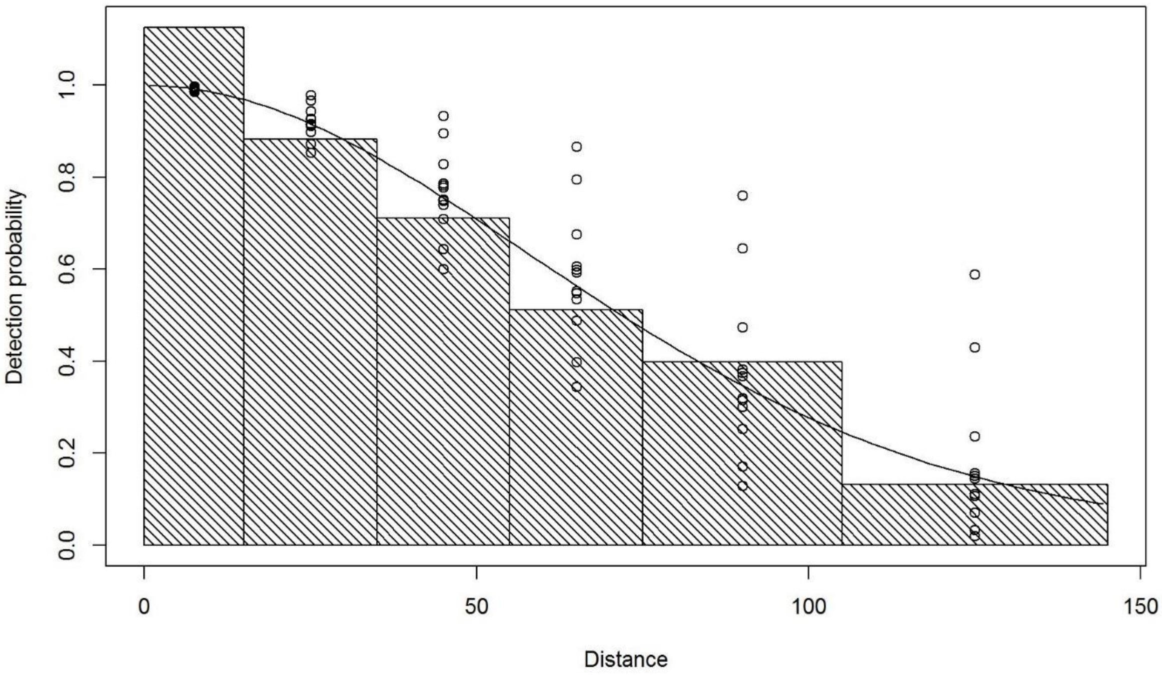


Rufous Fieldwren*



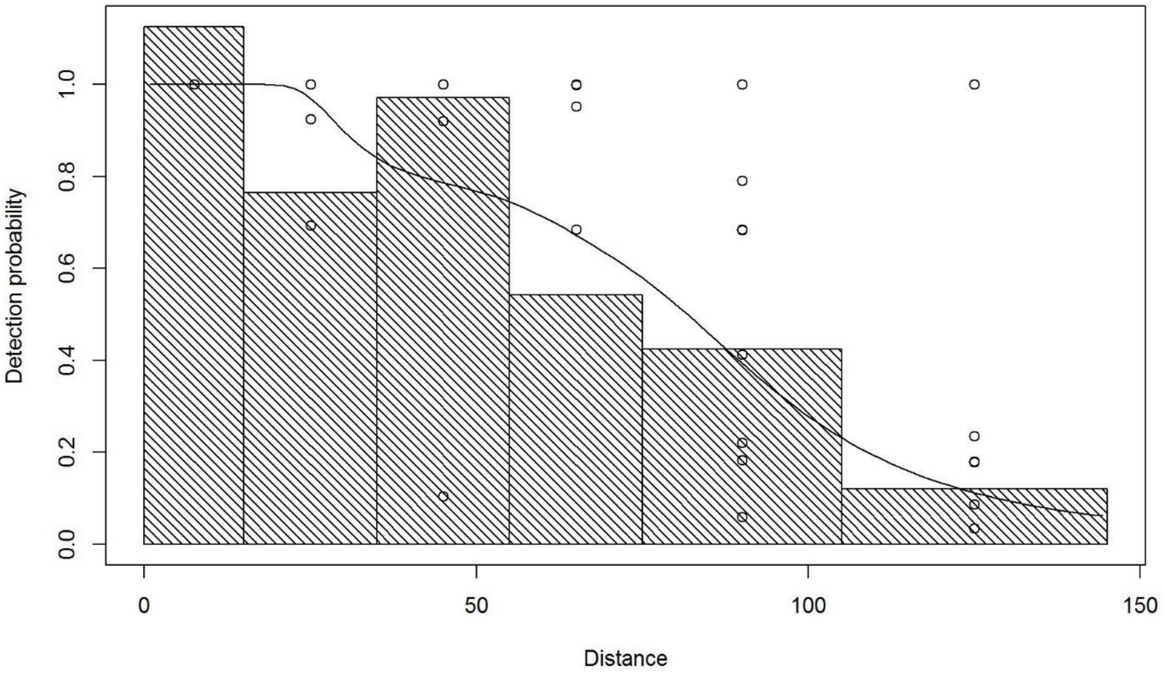


Rufous Songlark*

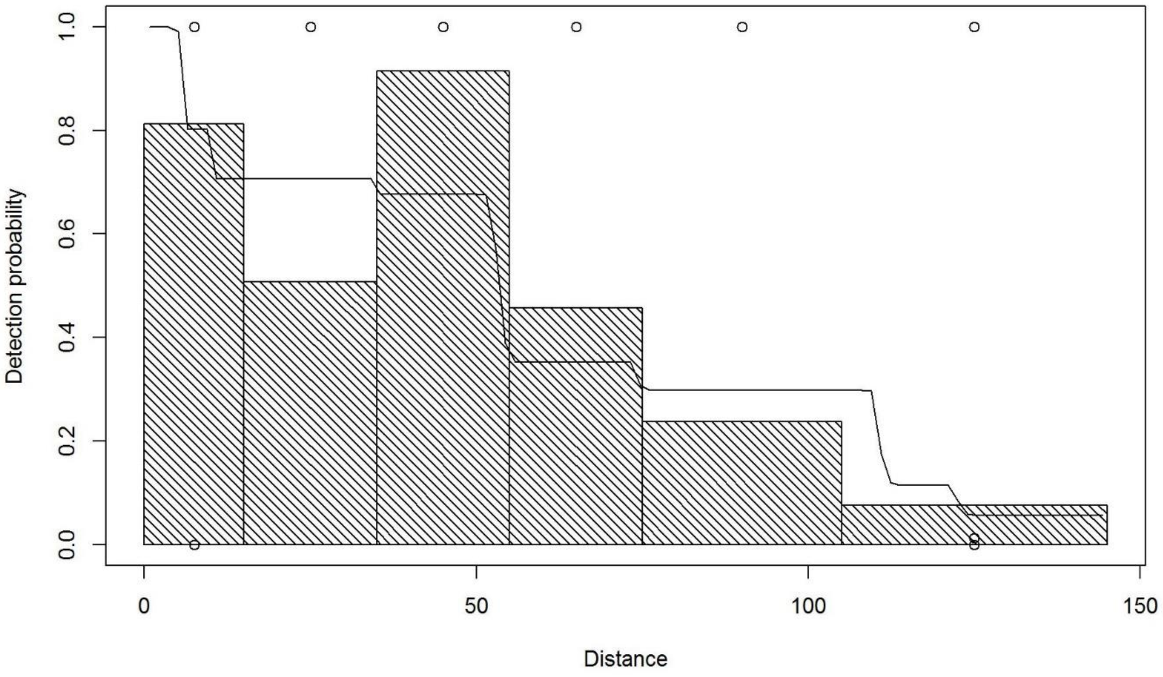


Singing Honeyeater

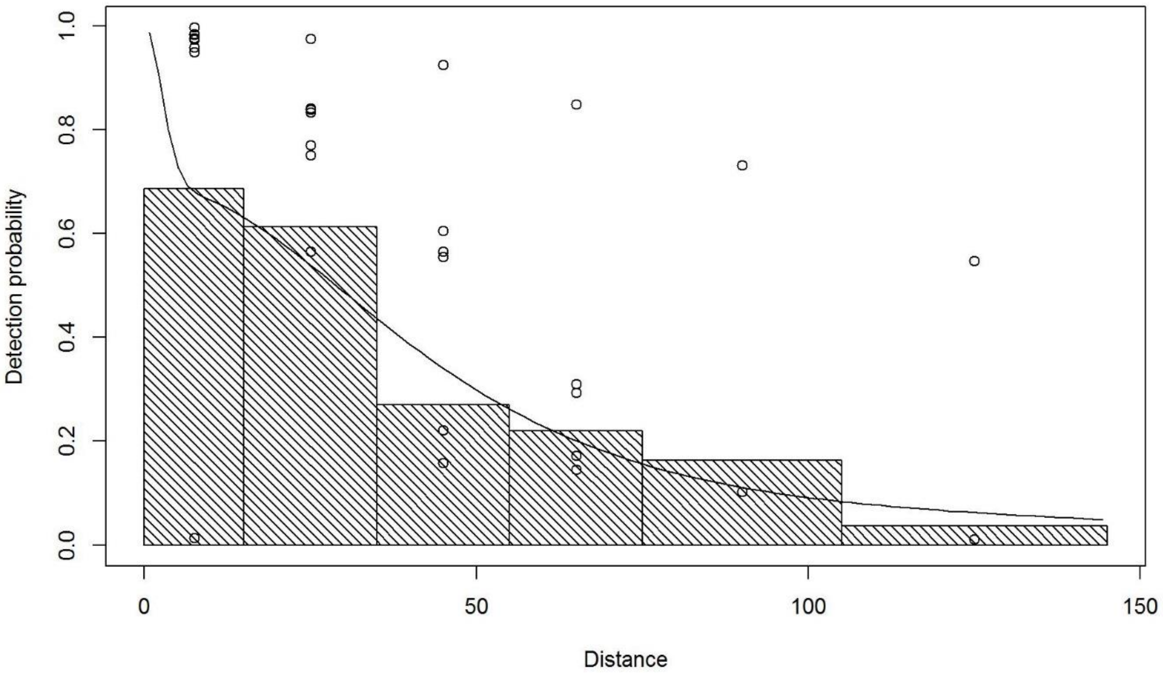
Spiny-cheeked Honeyeater



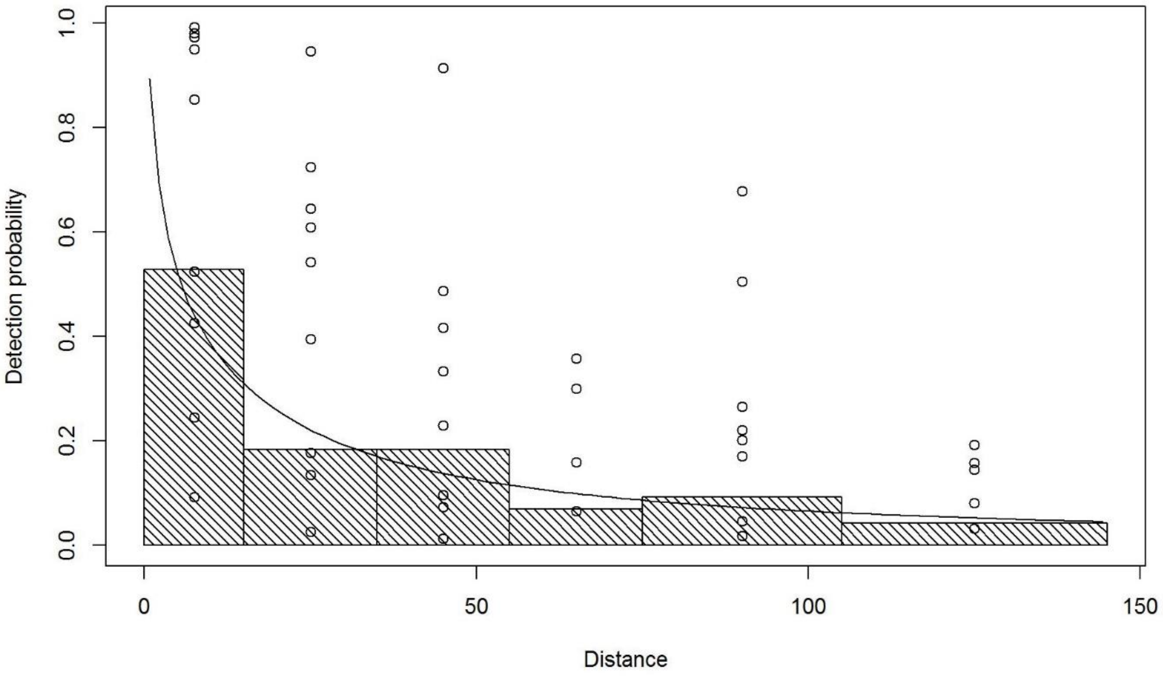
Striated Pardalote

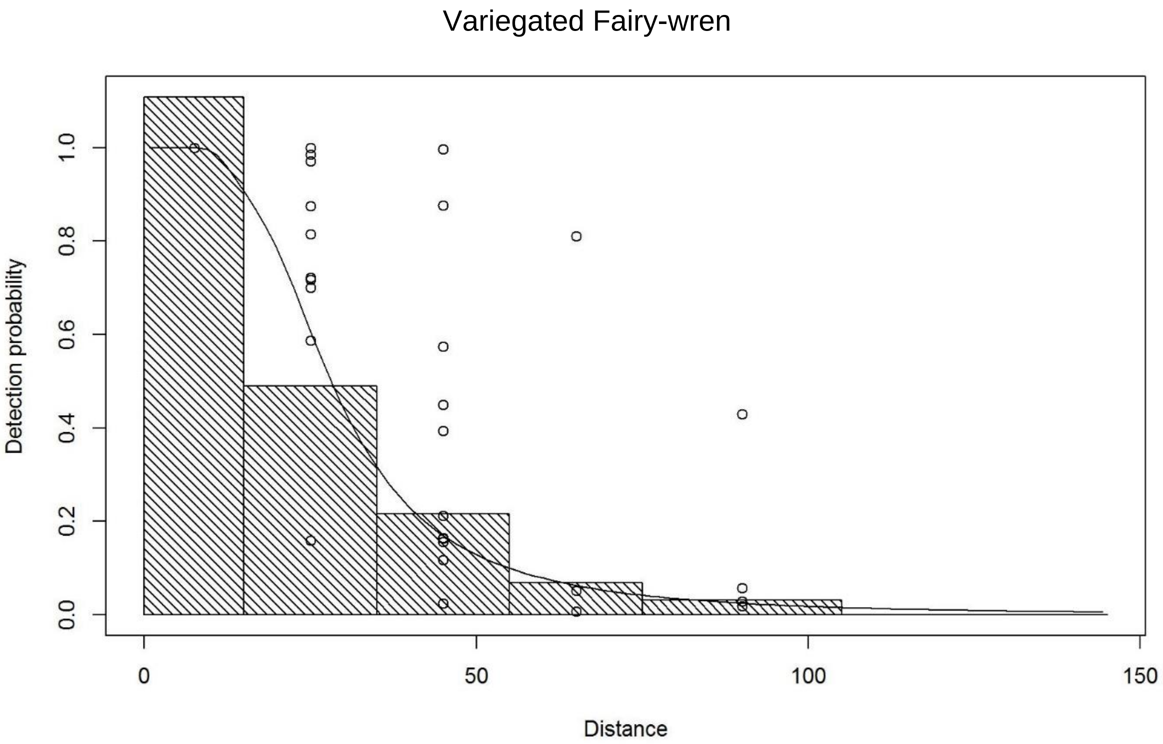


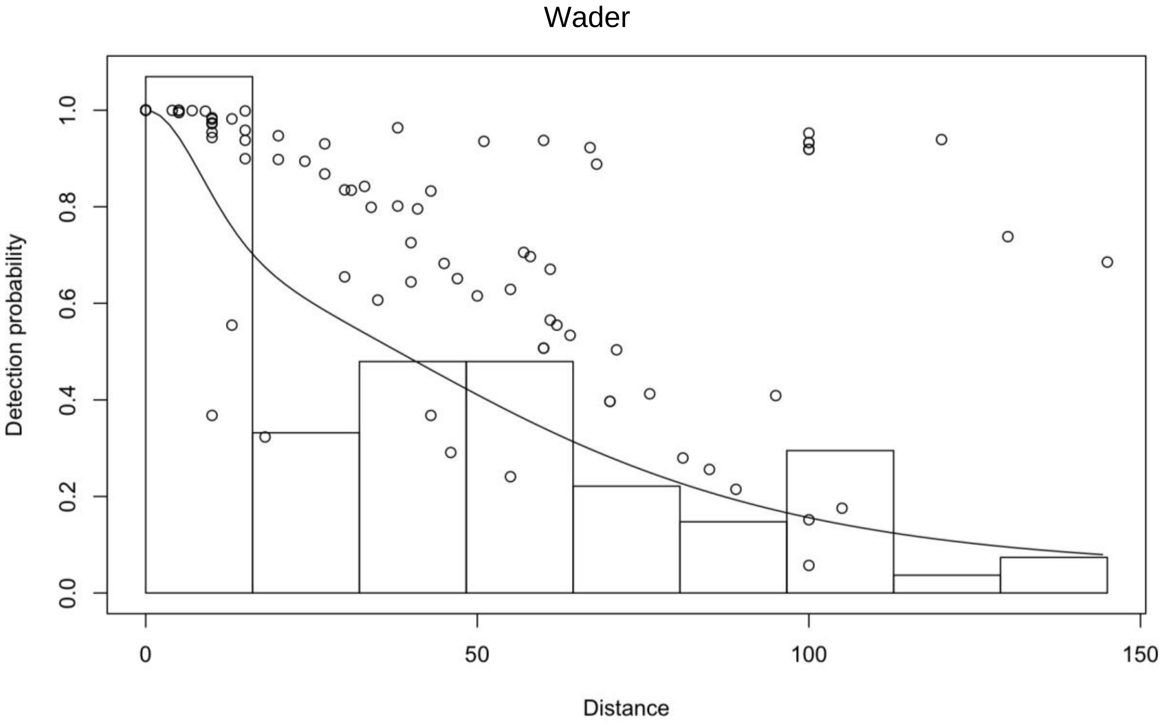
Thick-billed Grasswren*



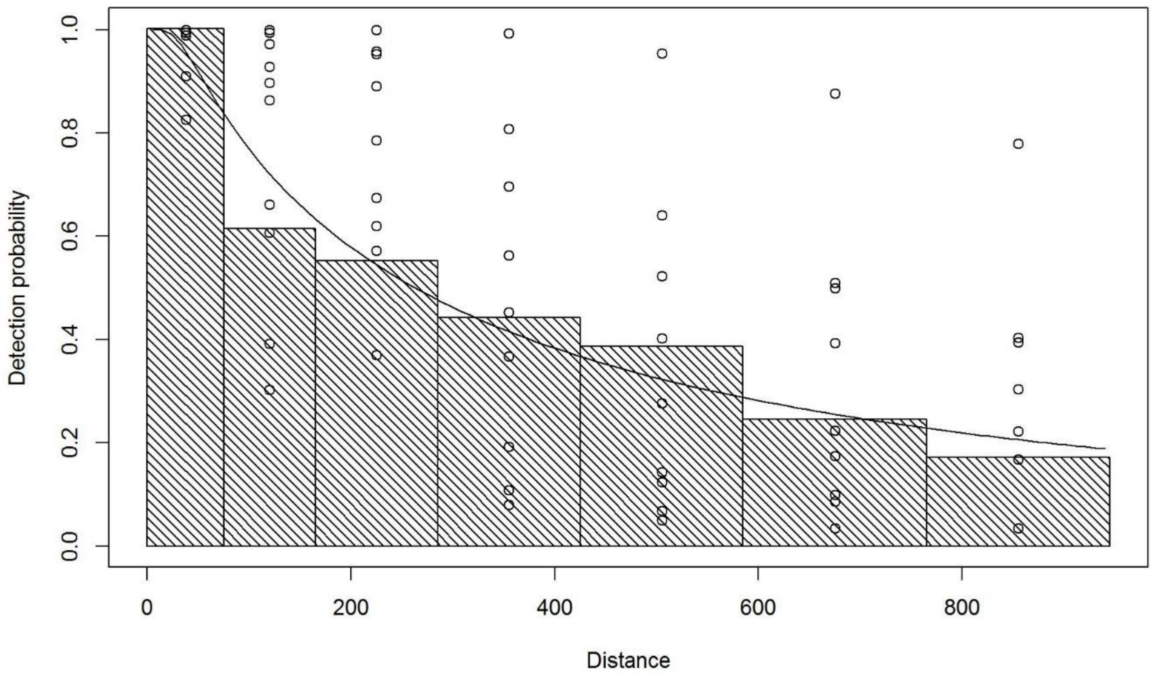
Tree Martin*



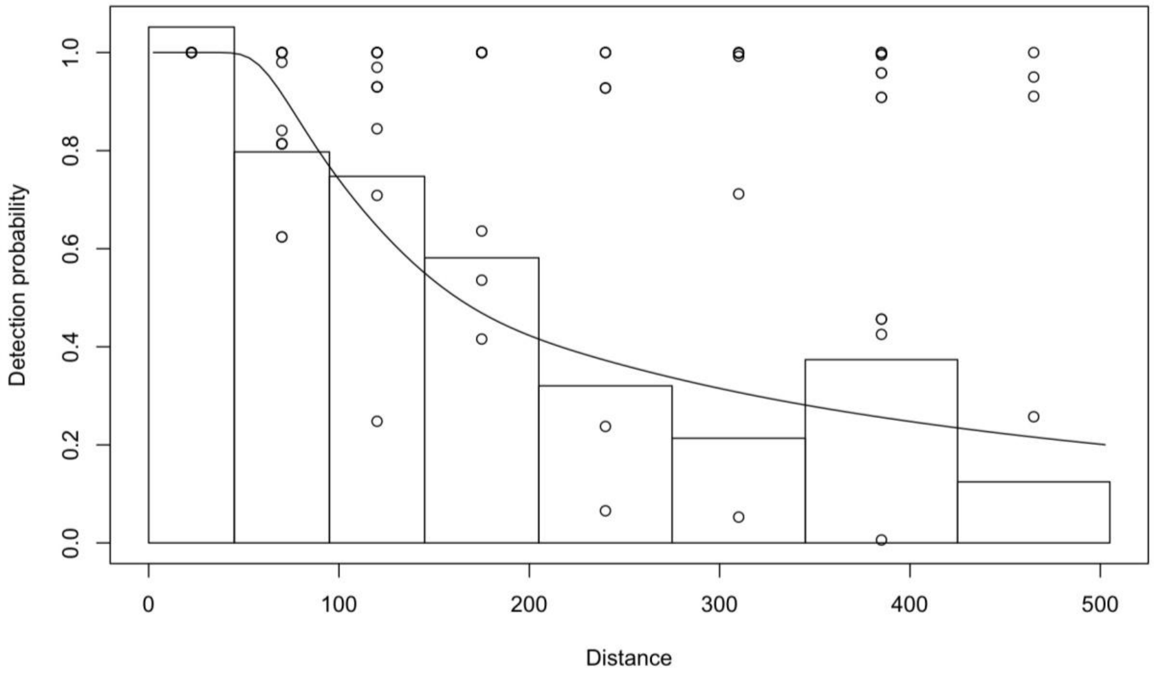

Variegated Fairy-wren

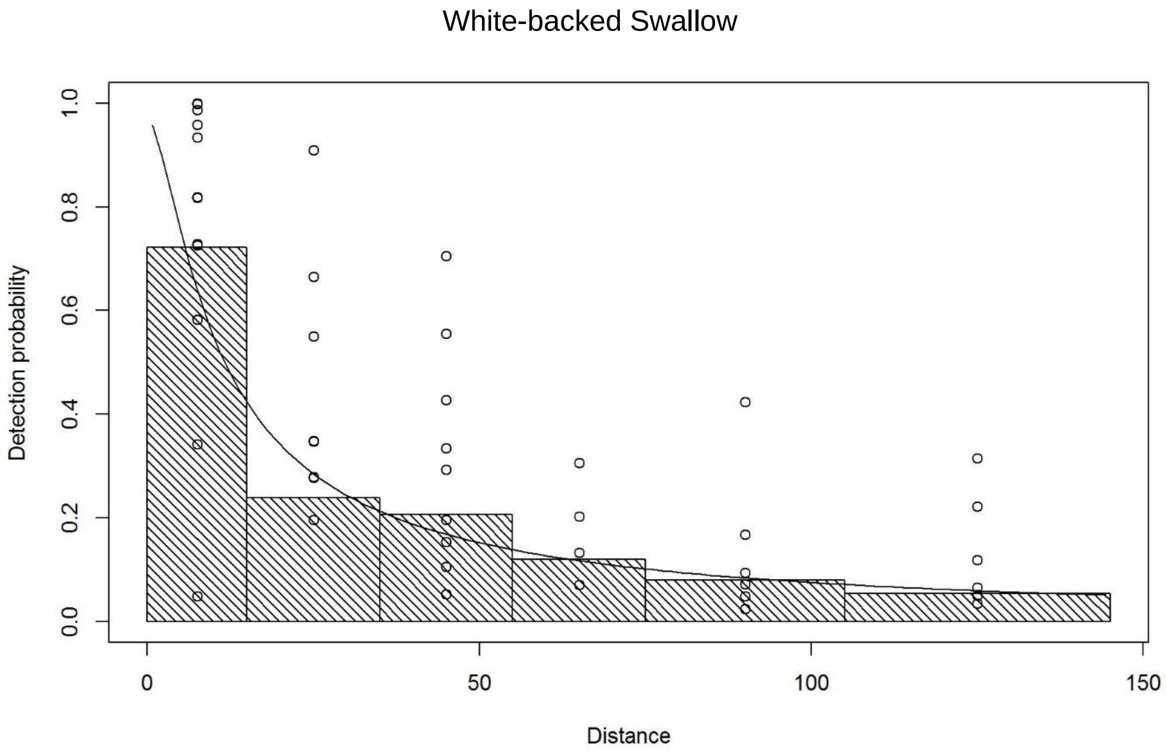

Wader

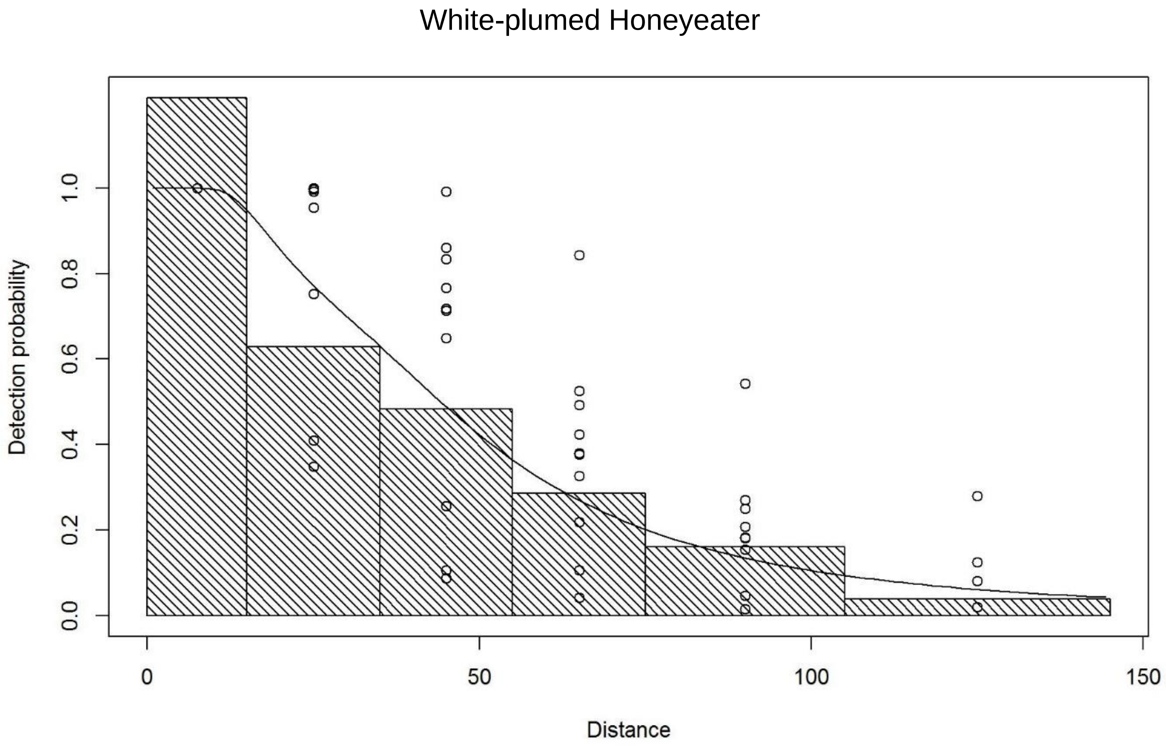
Wedge-tailed Eagle*

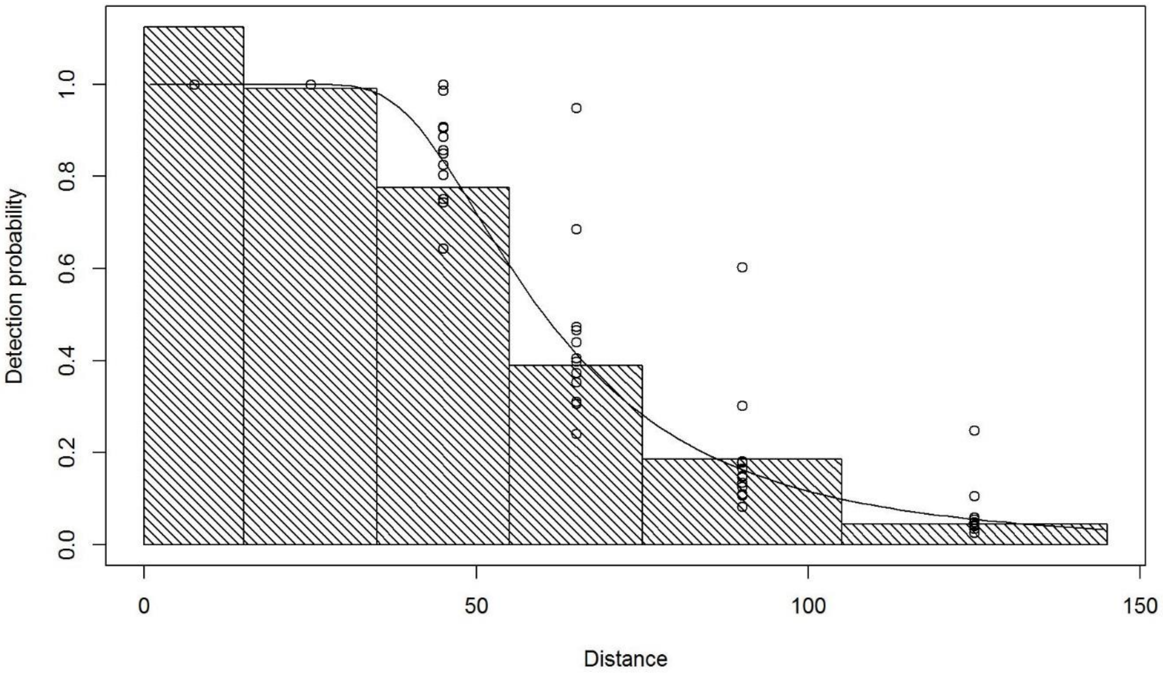


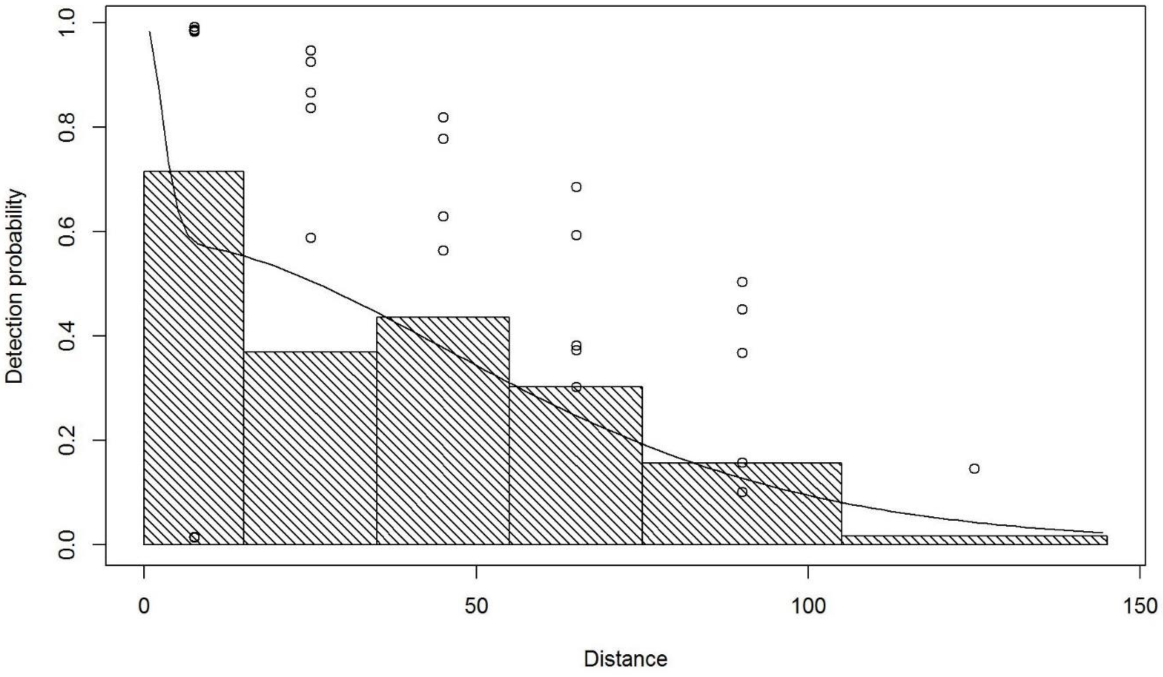
Whistling Kite

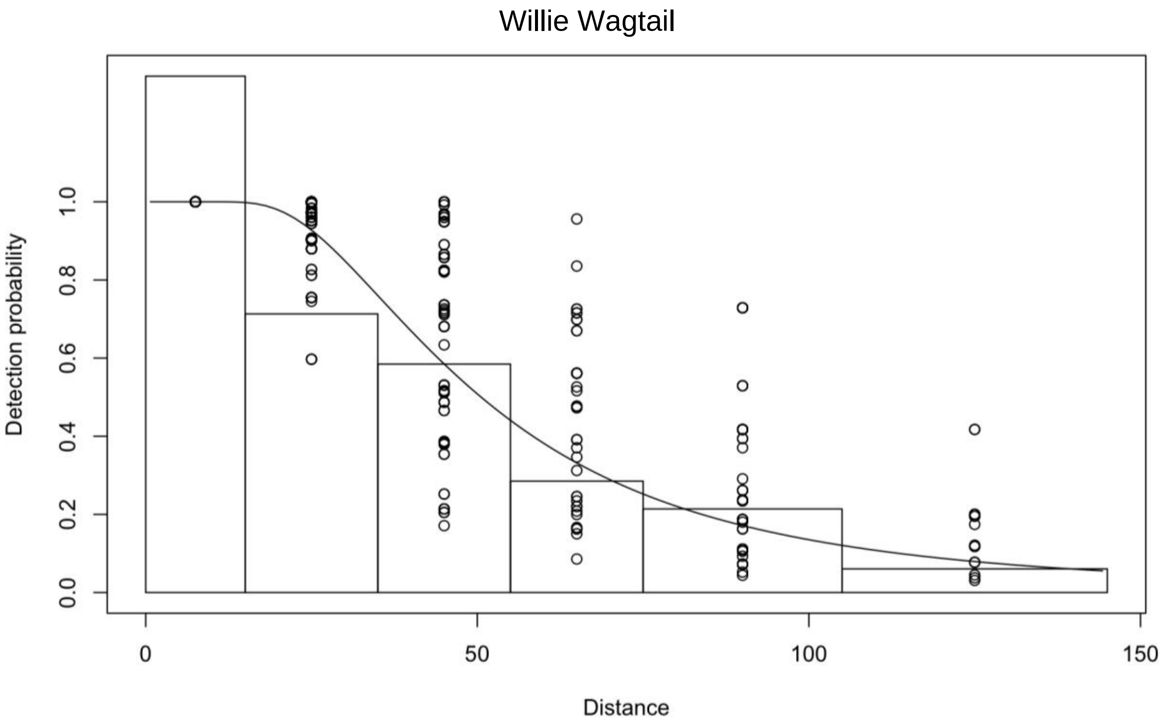


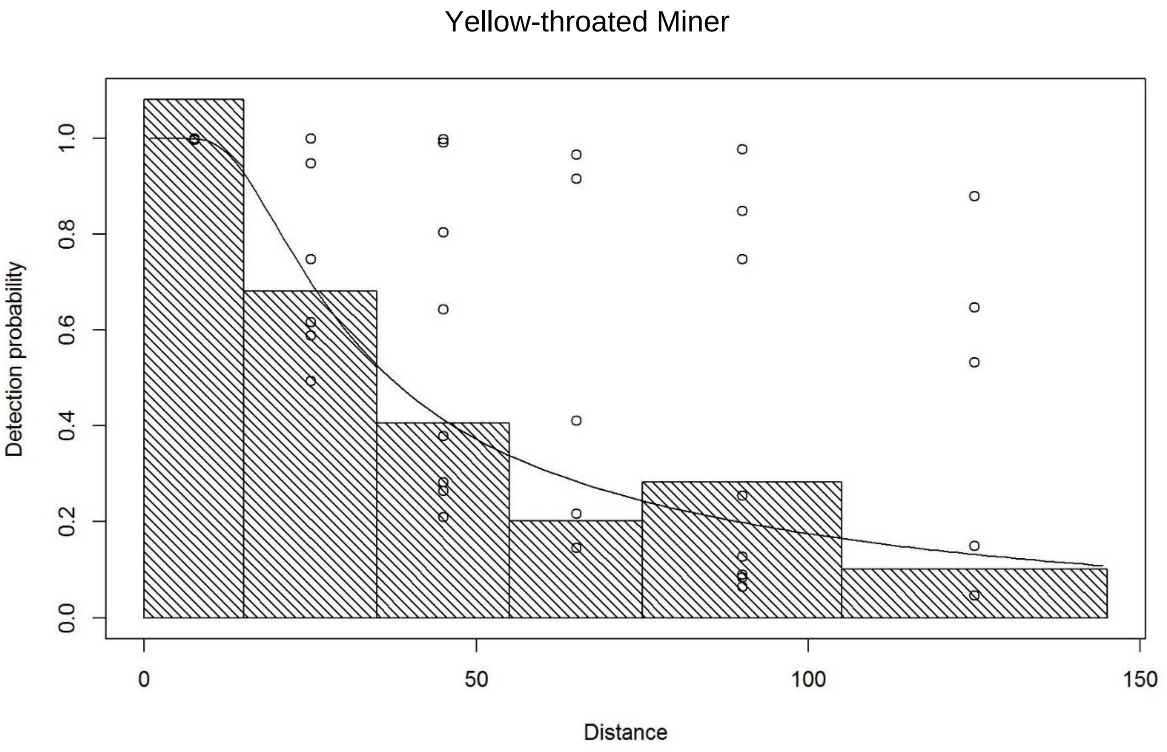

White-backed Swallow
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
Distance


White-plumed Honeyeater
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
Distance


White-winged Fairy-wren


White-winged Triller


Willie Wagtail
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
Distance


Yellow-throated Miner
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
Distance

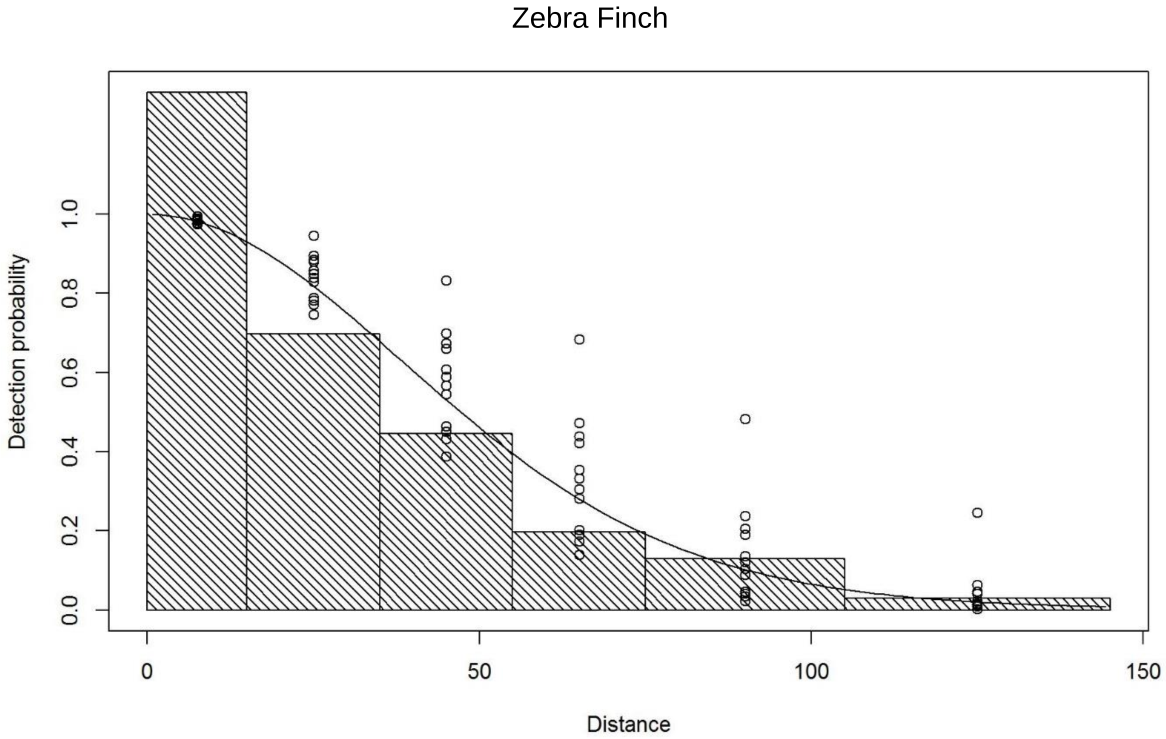
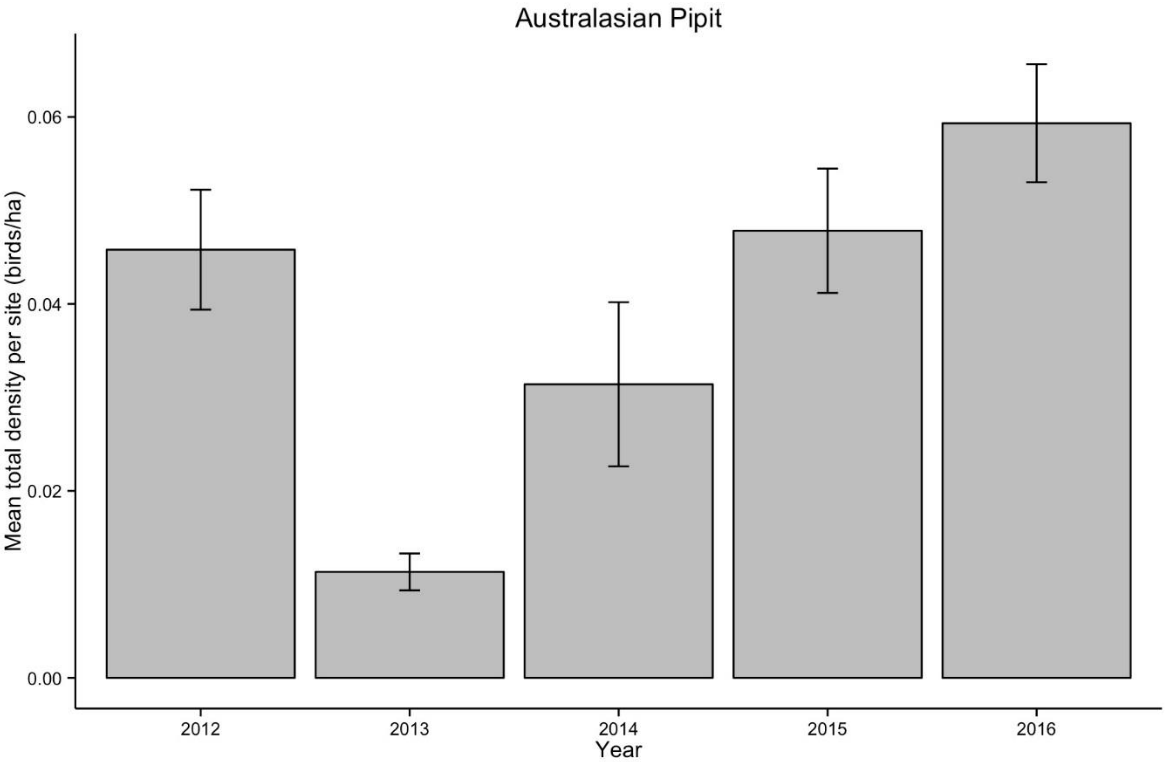
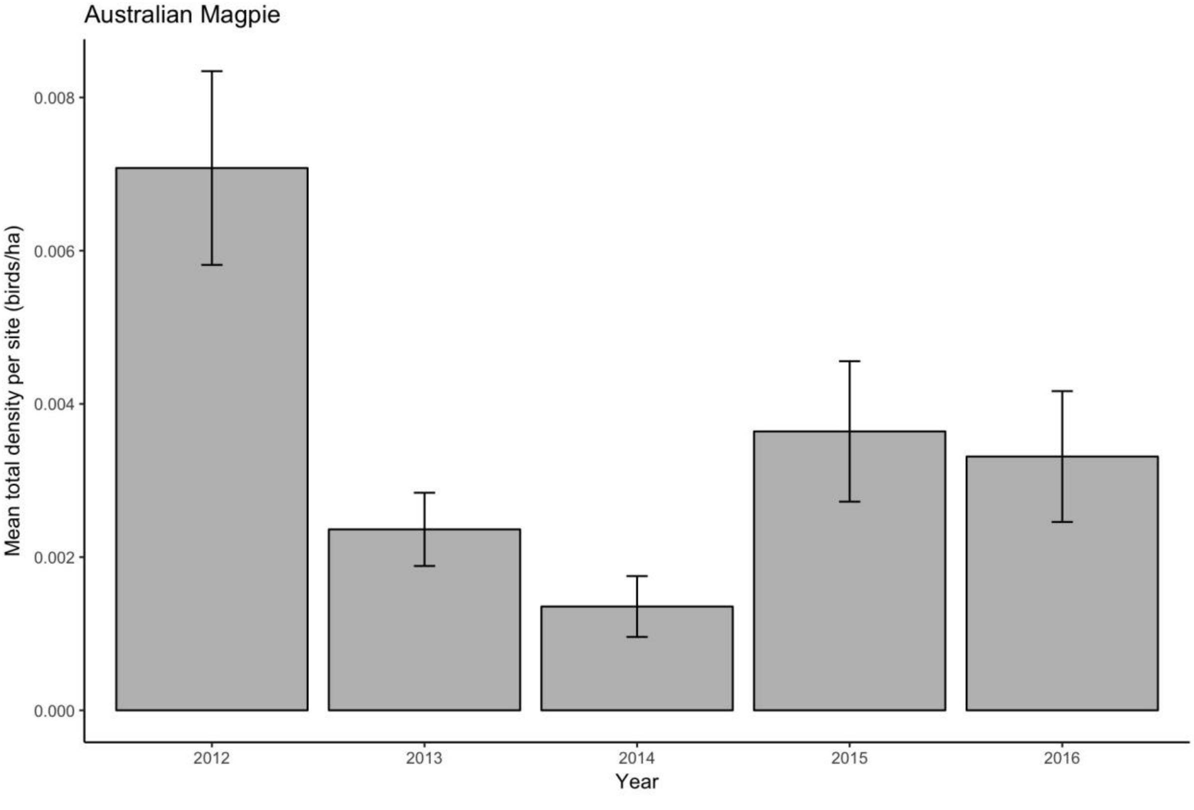
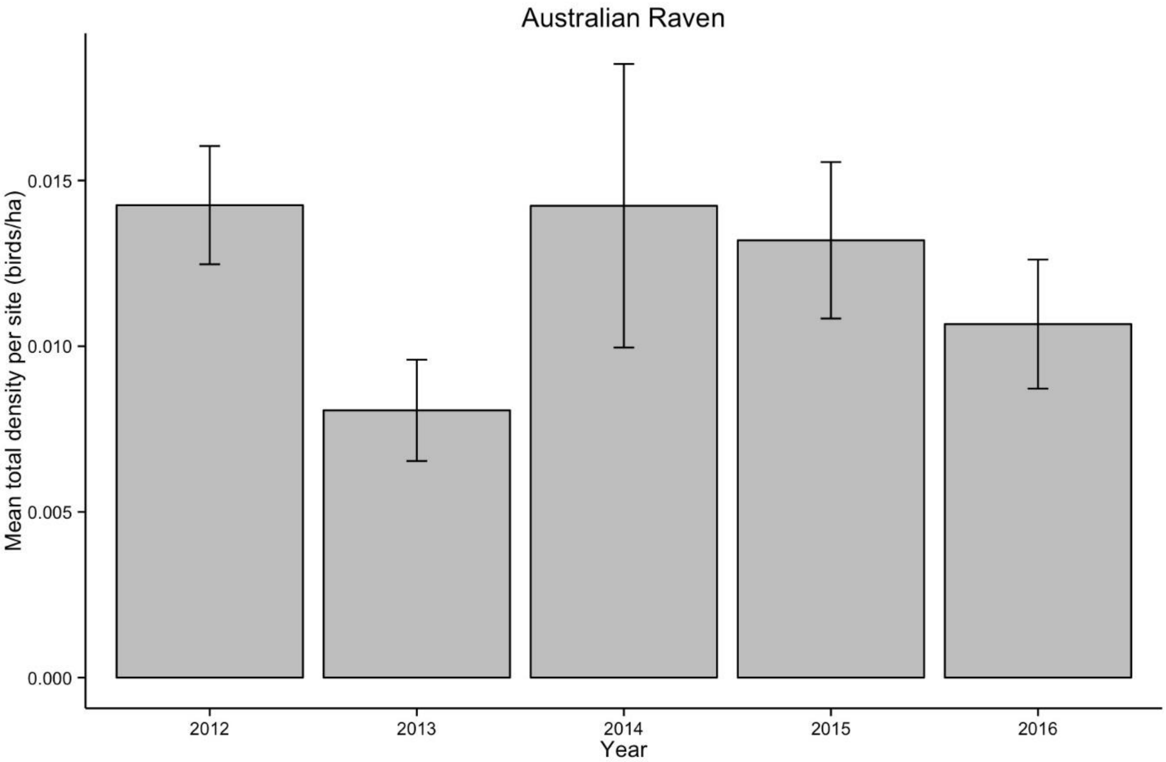
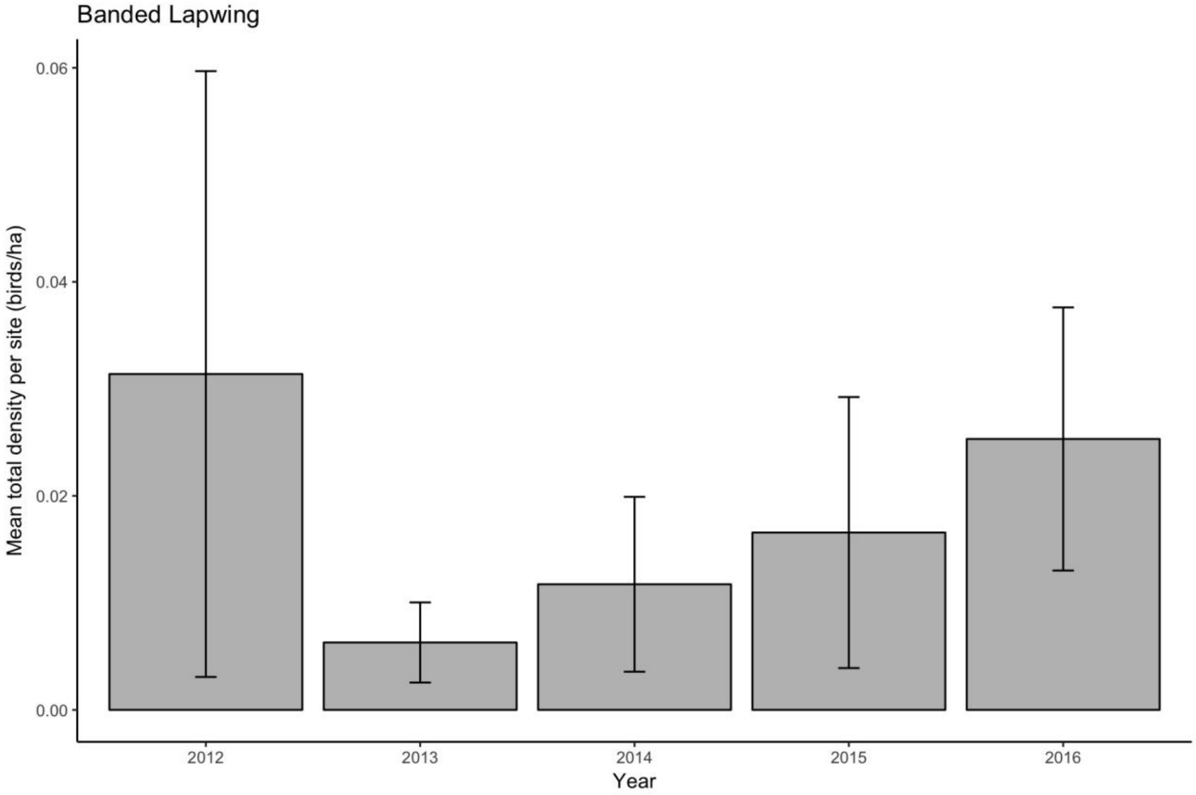


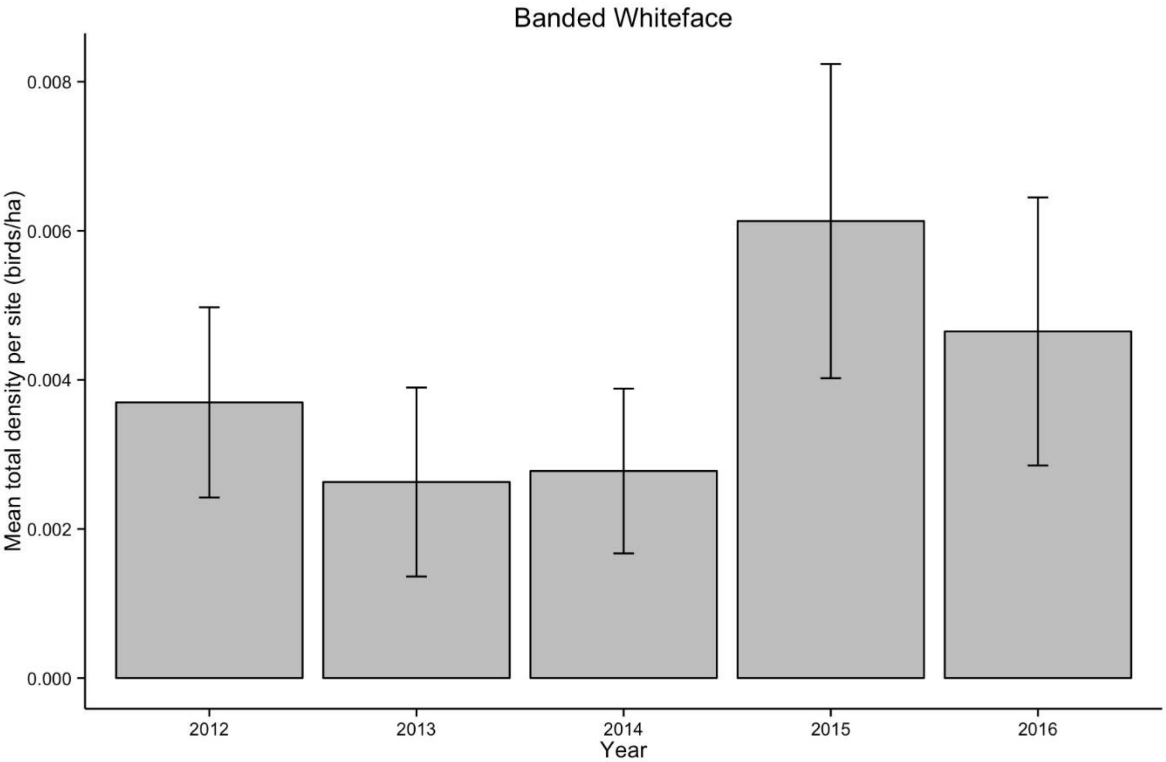
Figure S1. Species detection functions that model detection probability of species and species' composites (from Chapter 2, Table 2.4) as a function of distance from the transect line. Observer team was included as a covariate to account for variable detection abilities among teams (open circles). Time of day was included as an additional covariate when it improved detection function model fit for a species as indicated by AIC (plots with clear bars; see Chapter 2 Methods); a best fit detection function line is shown that best fits the variable team detections. *Species' densities were manually calculated when automated detection function models could not be fitted.

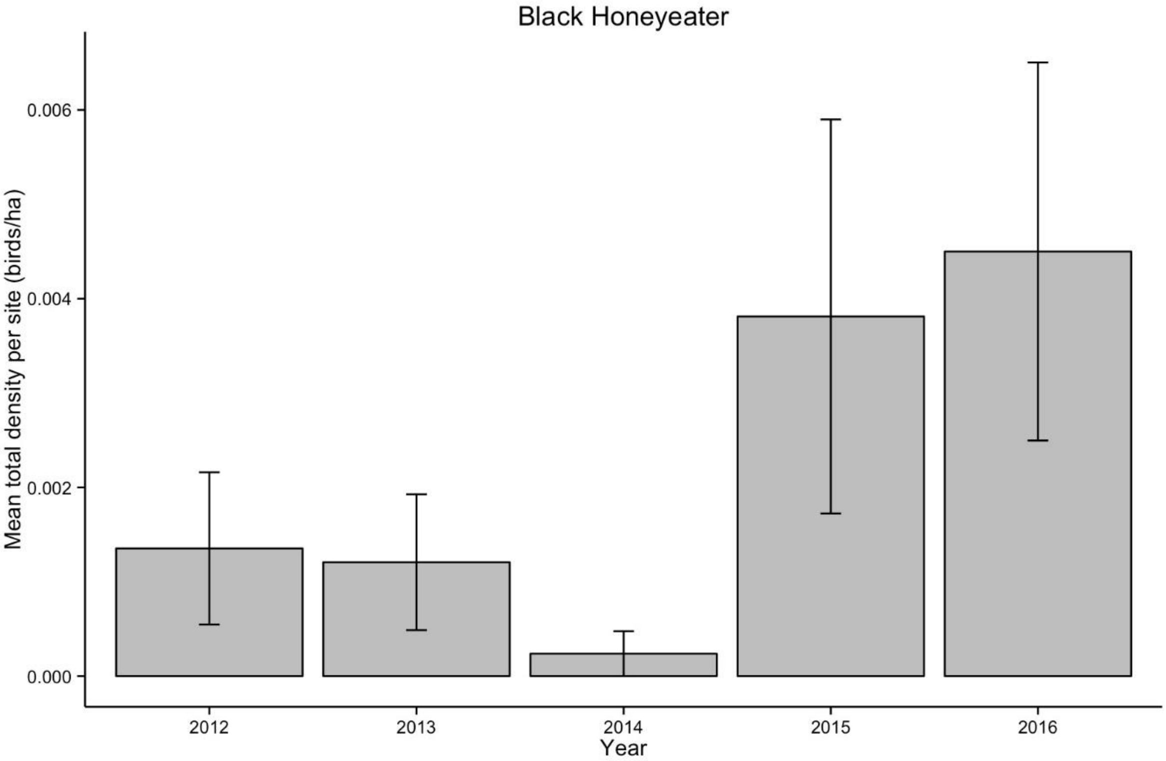

Australasian Pipit
Mean total density per site (birds/ha)
0.06
0.04
0.02
0.00
2012
2013
2014
2015
2016
Year

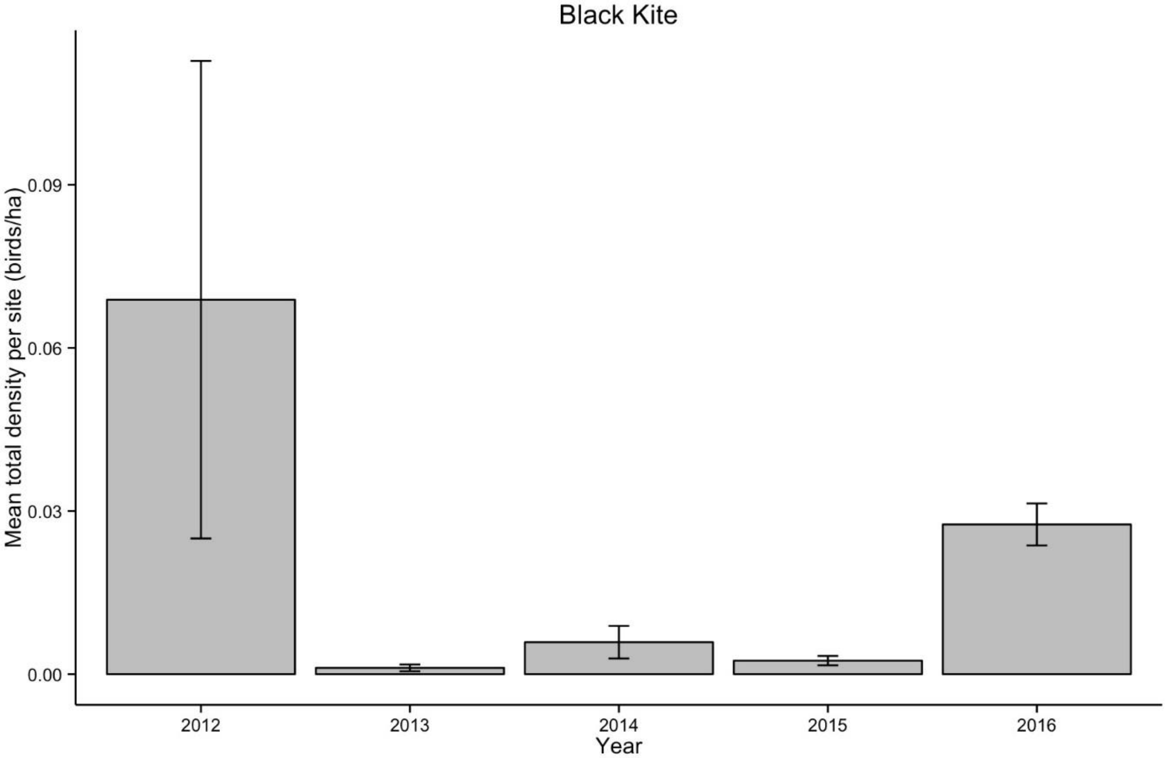

Australian Magpie
Mean total density per site (birds/ha)
0.008
0.006
0.004
0.002
0.000
2012
2013
2014
2015
2016
Year

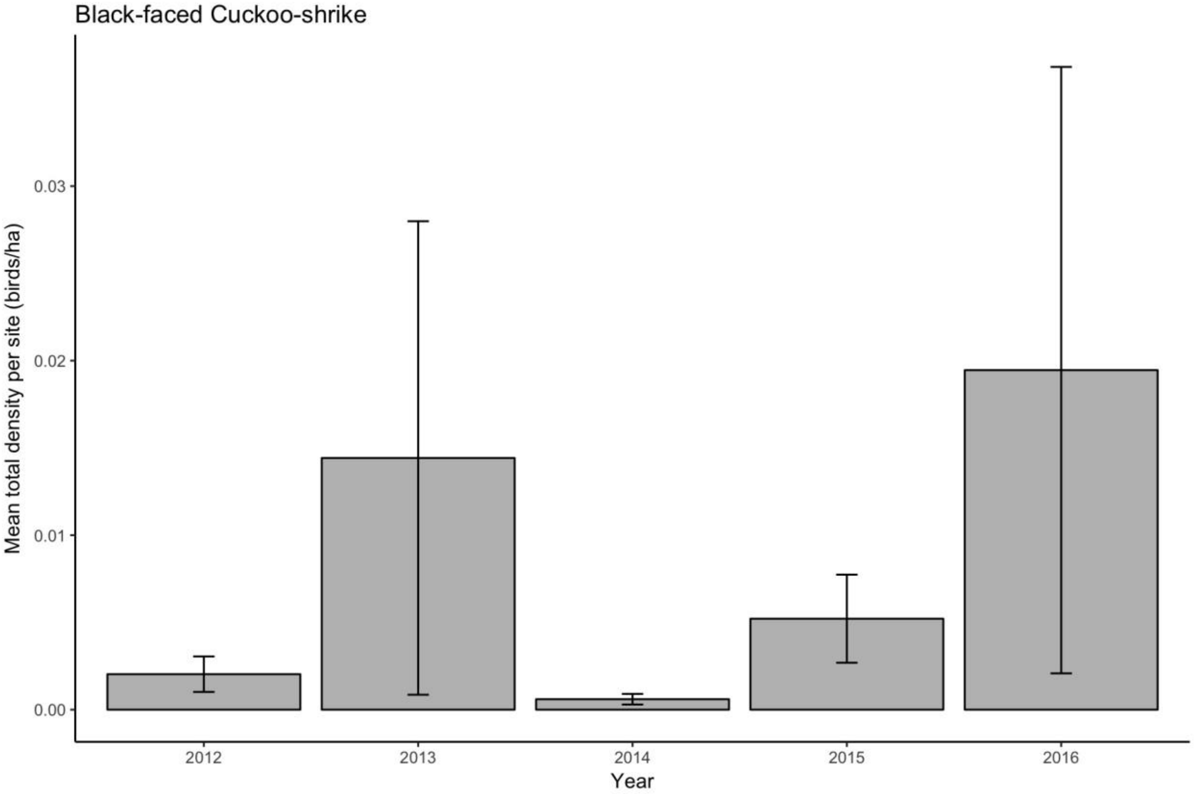

Australian Raven

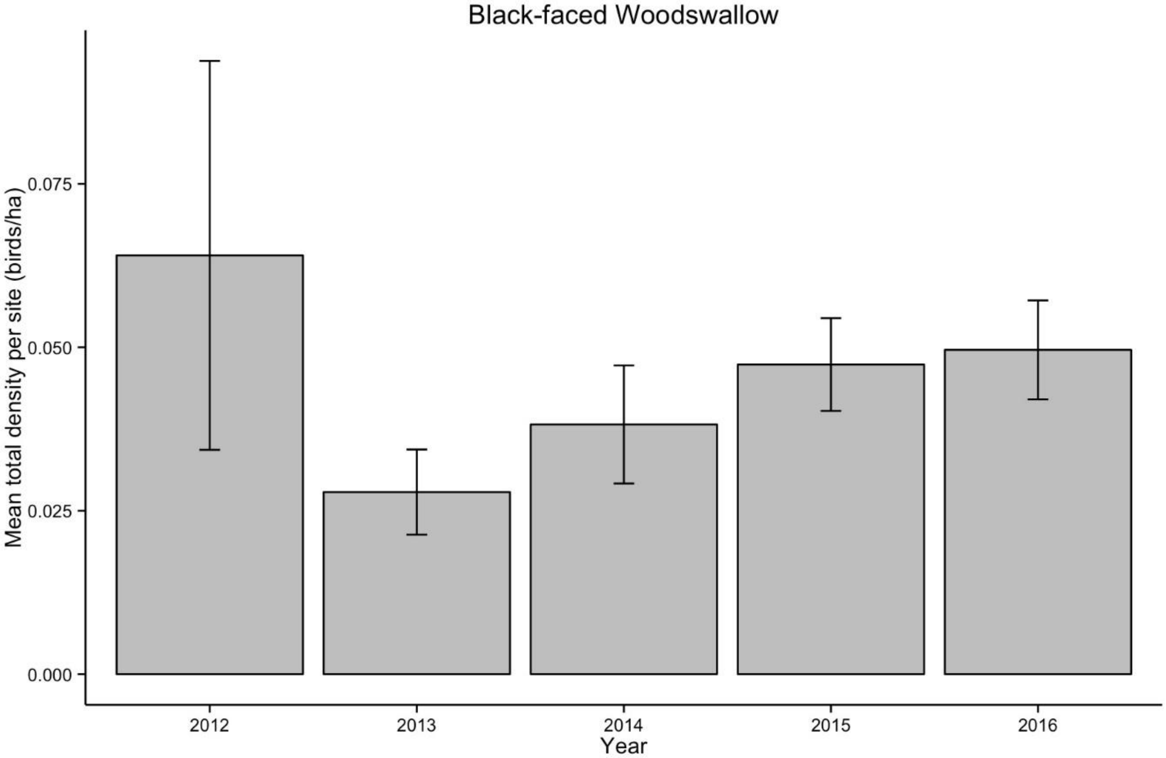

Banded Lapwing

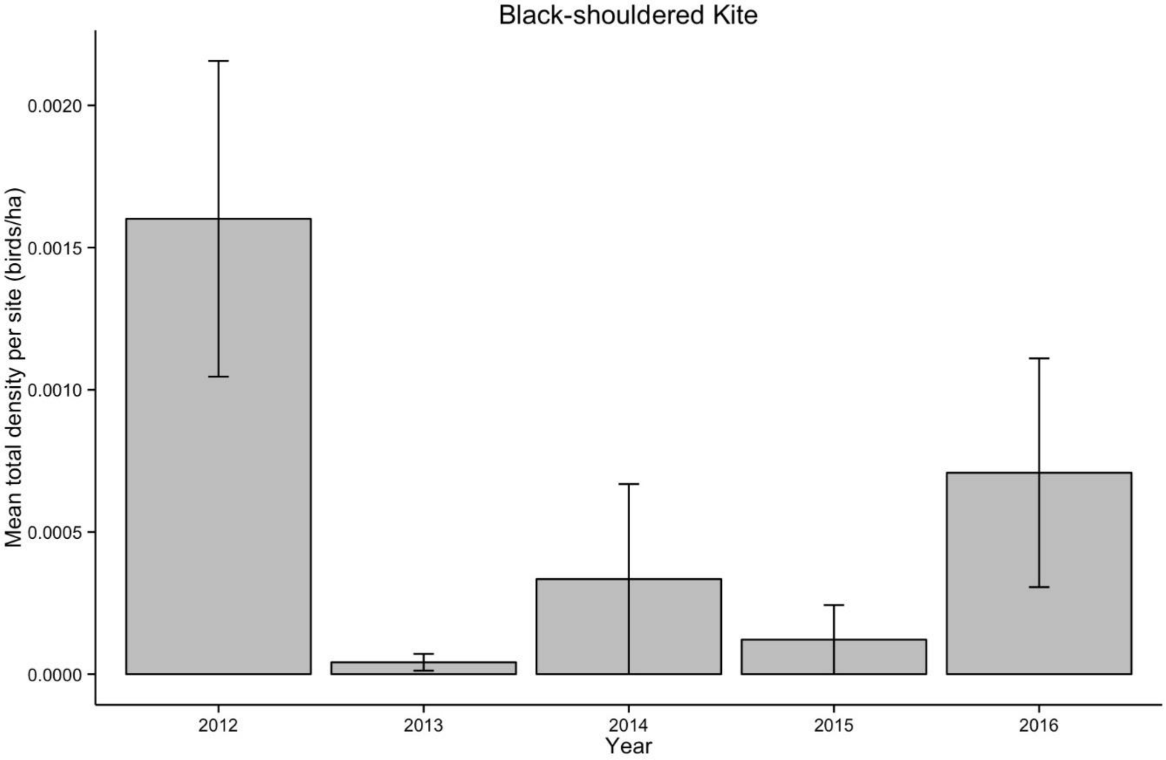

Banded Whiteface
Mean total density per site (birds/ha)
0.008
0.006
0.004
0.002
0.000
2012
2013
2014
2015
2016
Year

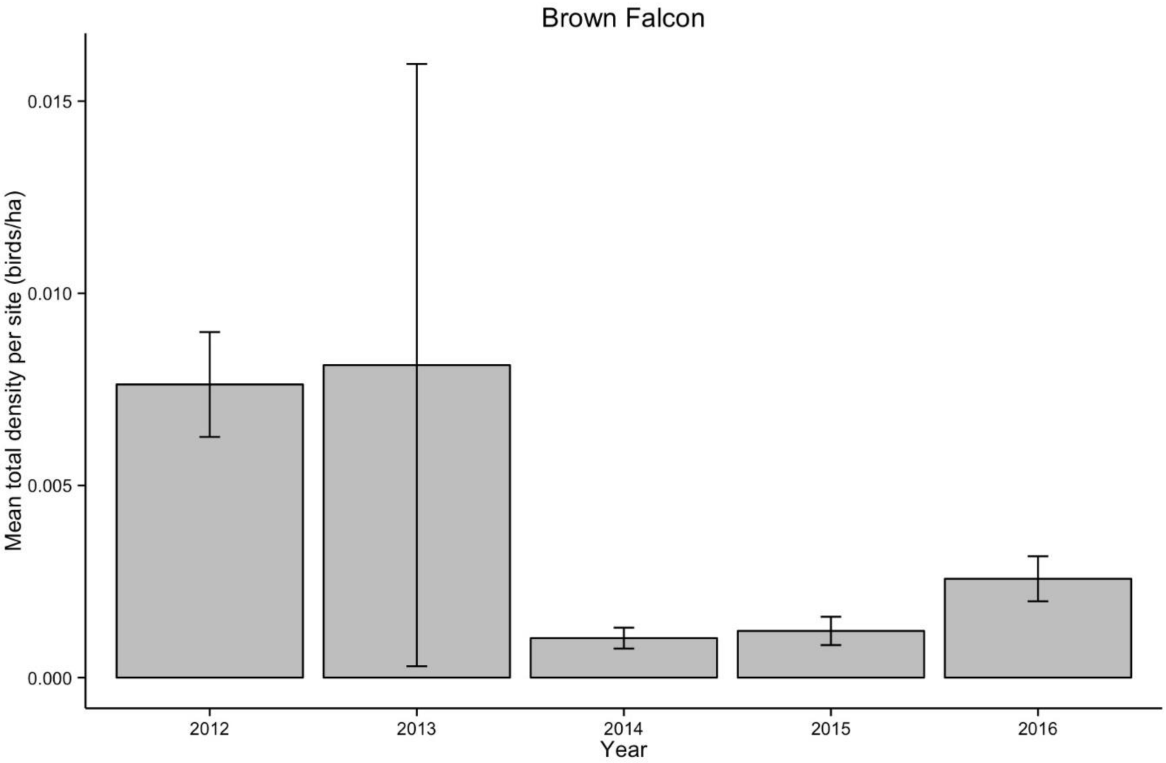

Black Honeyeater
Mean total density per site (birds/ha)
0.006
0.004
0.002
0.000
2012
2013
2014
2015
2016
Year

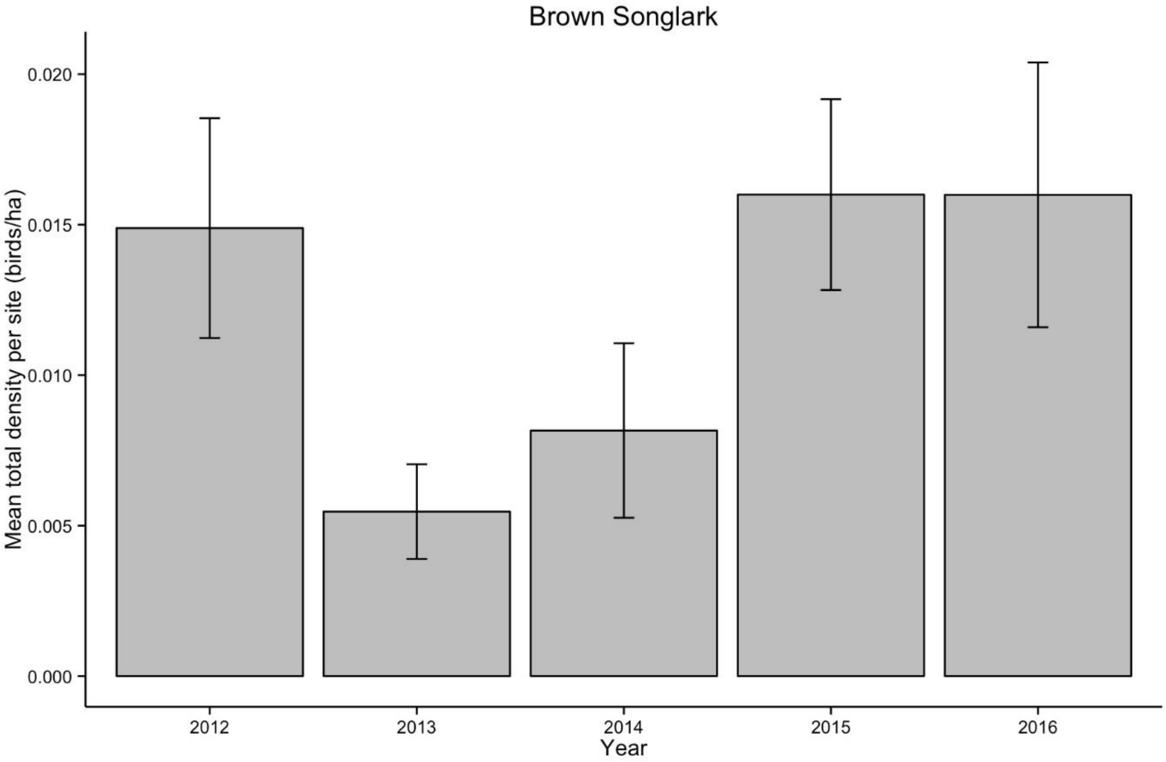

Black Kite
Mean total density per site (birds/ha)
0.09
0.06
0.03
0.00
2012
2013
2014
2015
2016
Year

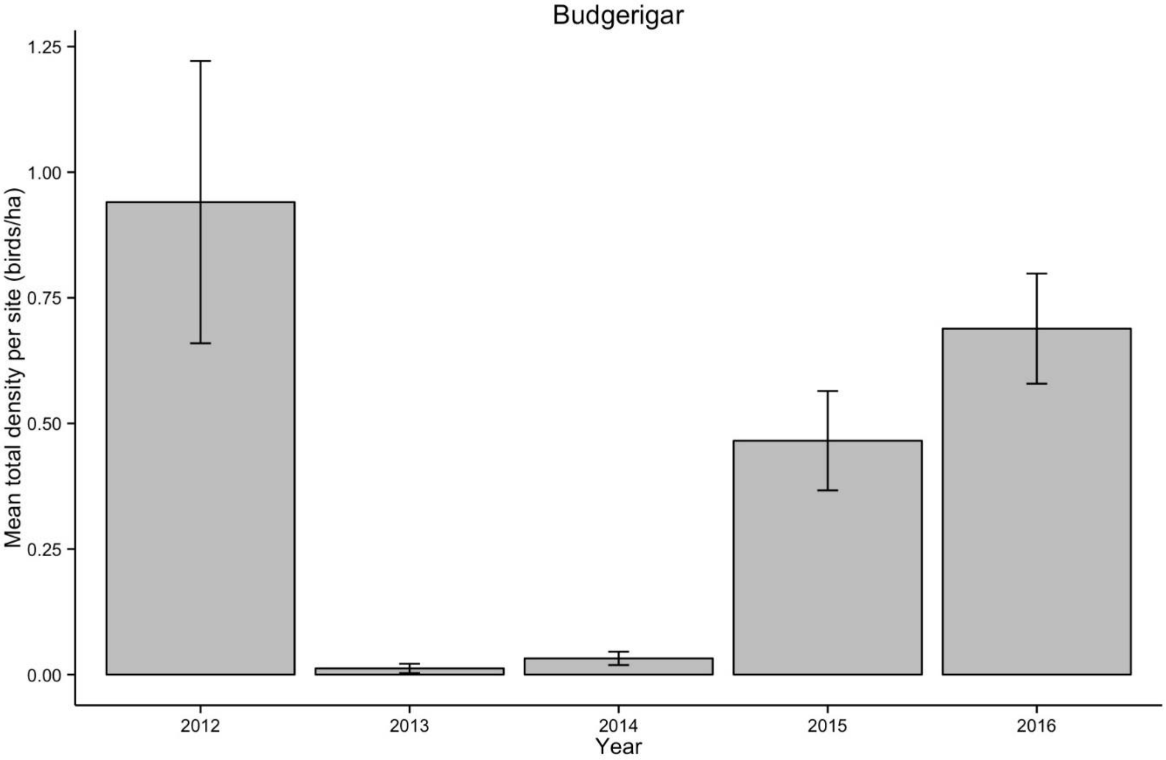

Black-faced Cuckoo-shrike
Mean total density per site (birds/ha)
0.03
0.02
0.01
0.00
2012
2013
2014
2015
2016
Year

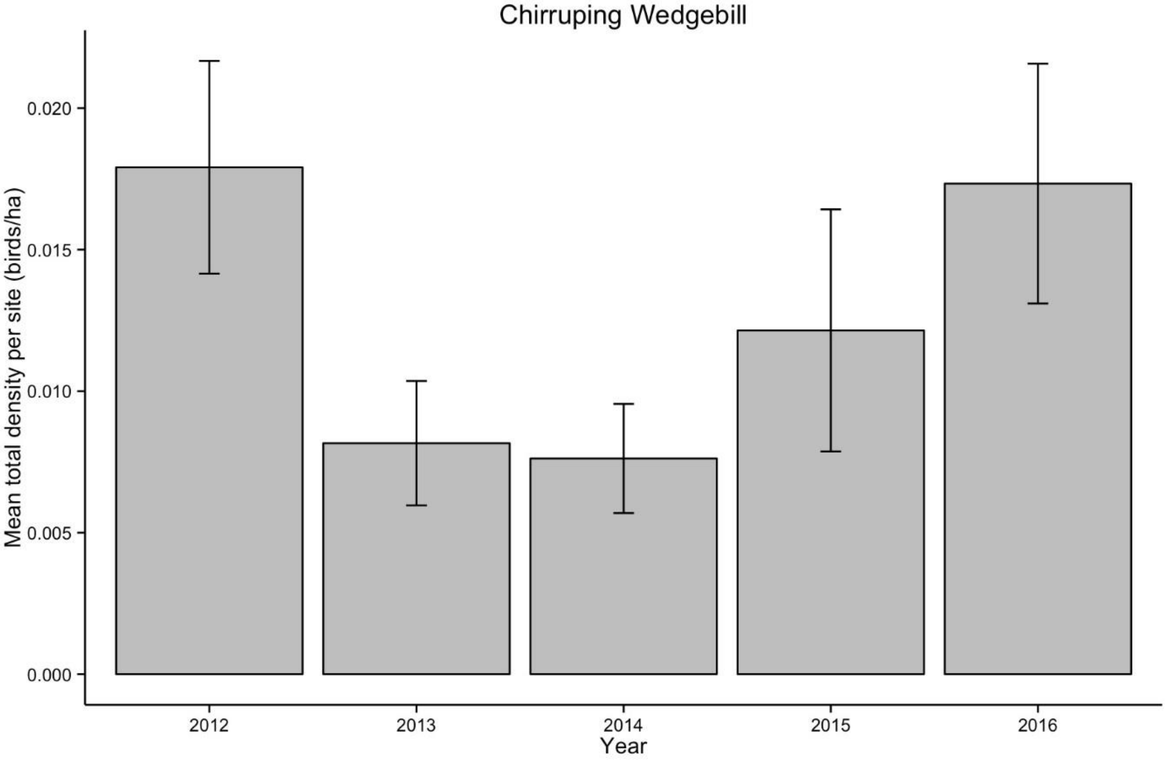

Black-faced Woodswallow
Mean total density per site (birds/ha)
0.000
0.025
0.050
0.075
2012
2013
2014
2015
2016
Year

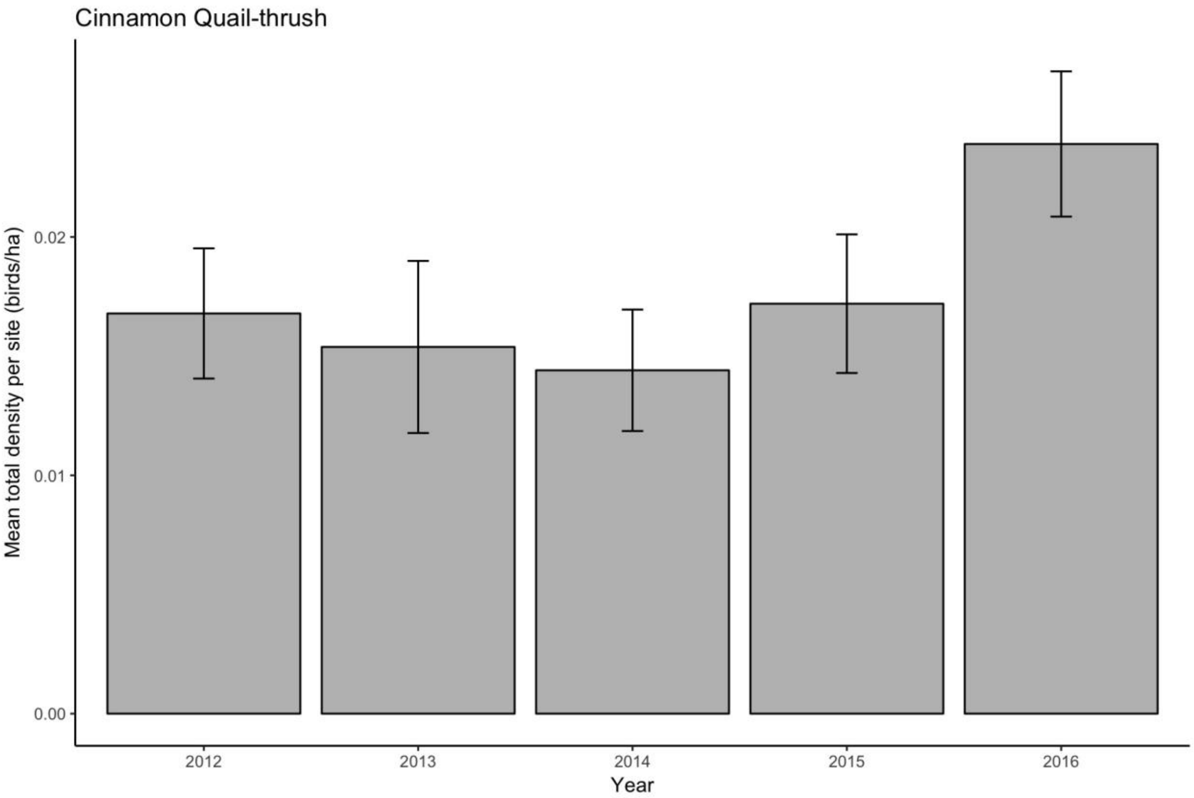

Black-shouldered Kite
Mean total density per site (birds/ha)
0.0000
0.0005
0.0010
0.0015
0.0020
2012
2013
2014
2015
2016
Year

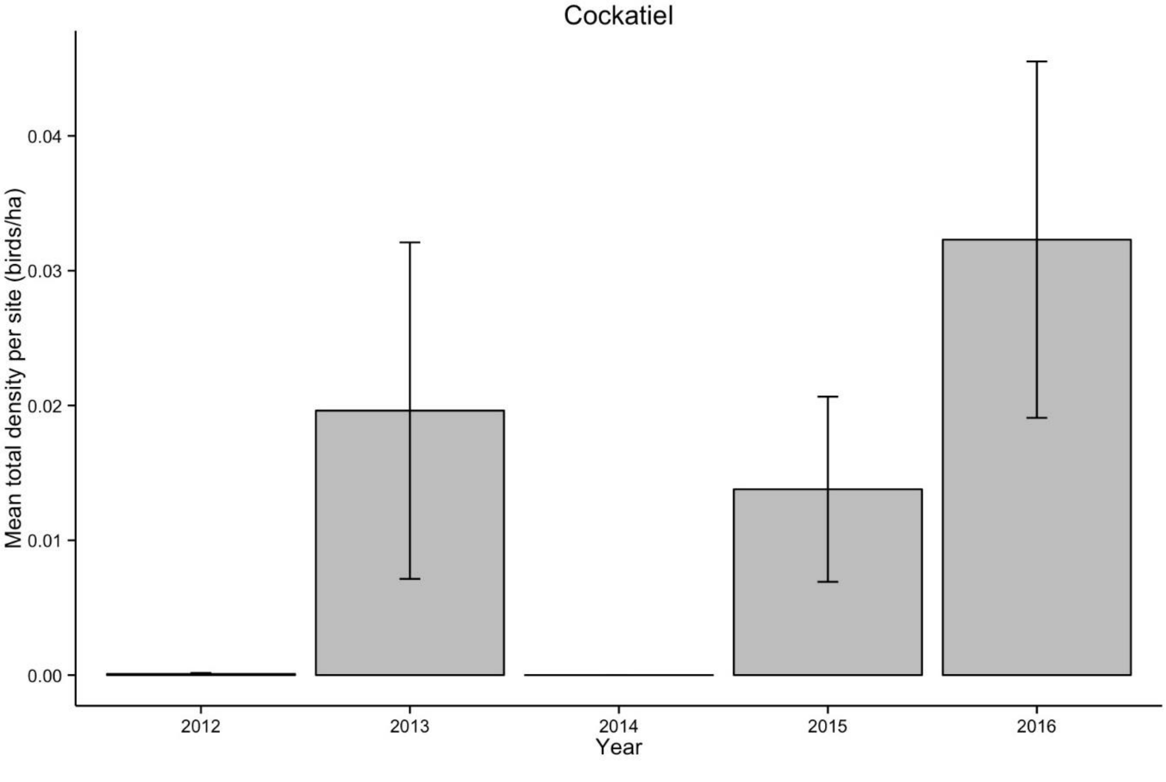

Brown Falcon

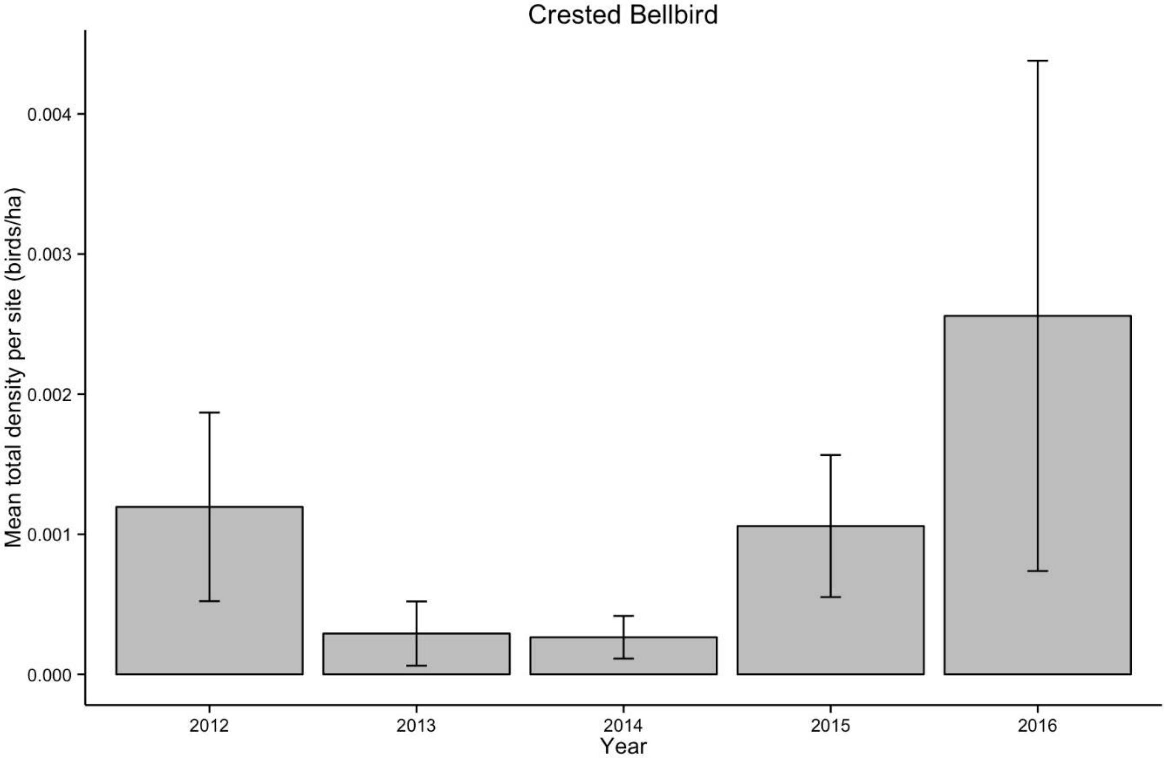

Brown Songlark

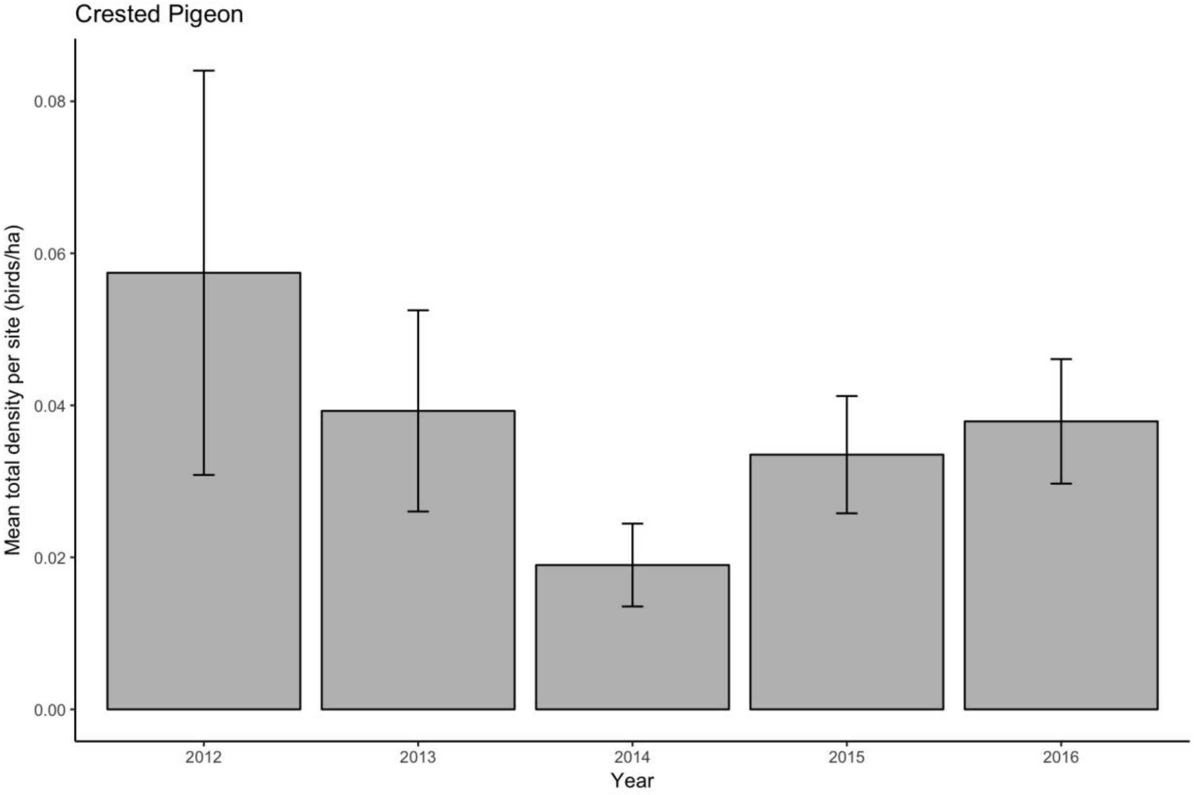

Budgerigar
Mean total density per site (birds/ha)
1.25
1.00
0.75
0.50
0.25
0.00
2012
2013
2014
2015
2016
Year

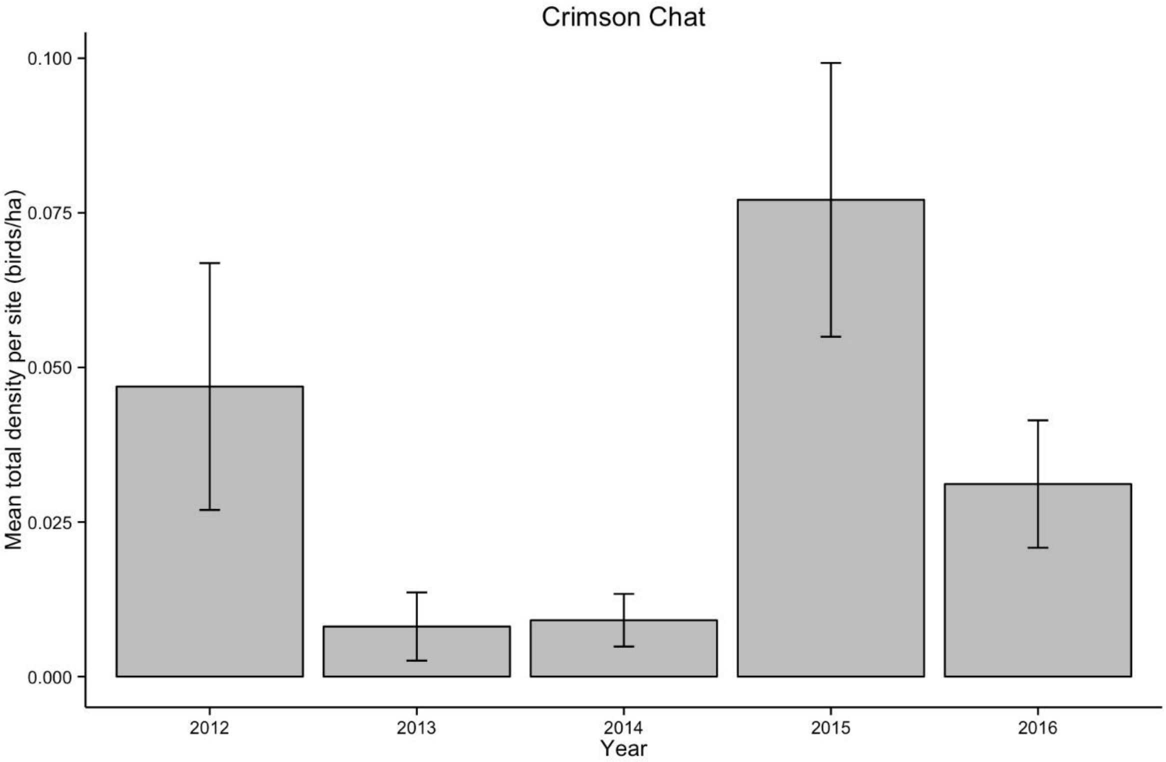

Chirruping Wedgebill
Mean total density per site (birds/ha)
0.020
0.015
0.010
0.005
0.000
2012
2013
2014
2015
2016
Year

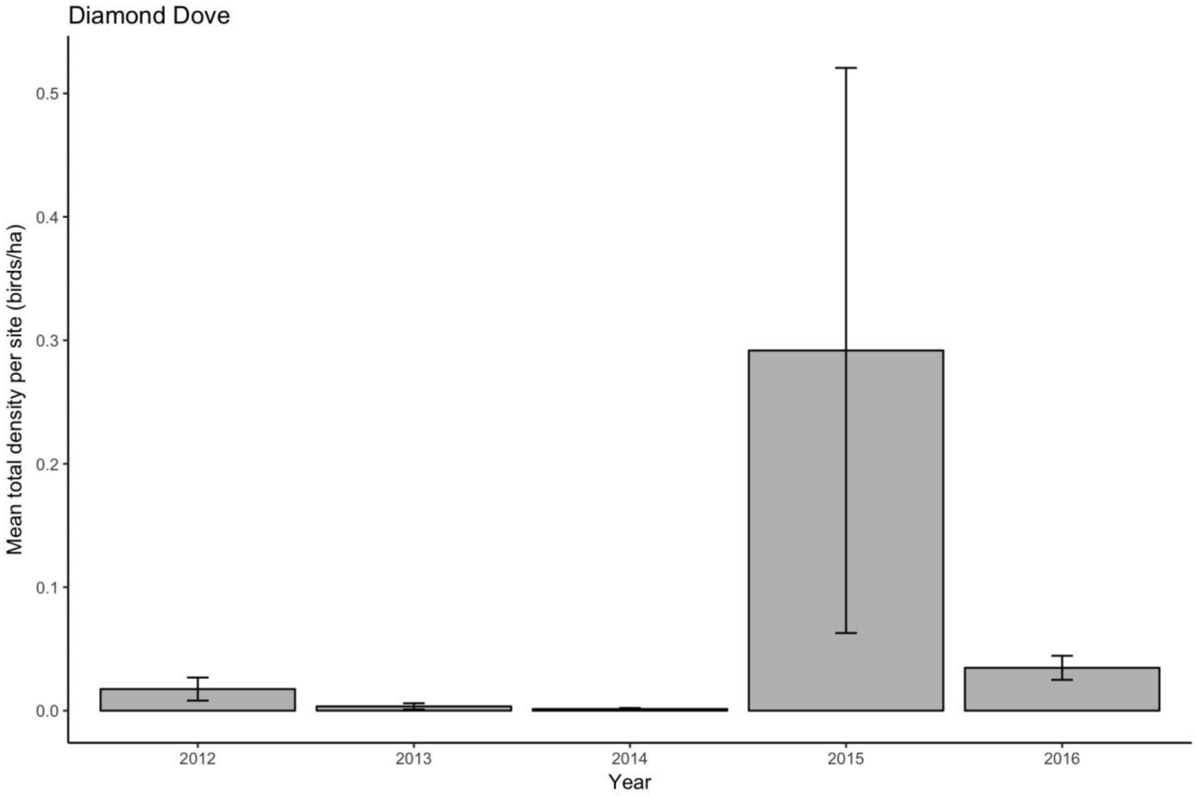

Cinnamon Quail-thrush
Mean total density per site (birds/ha)
0.00
0.01
0.02
2012
2013
2014
2015
2016
Year

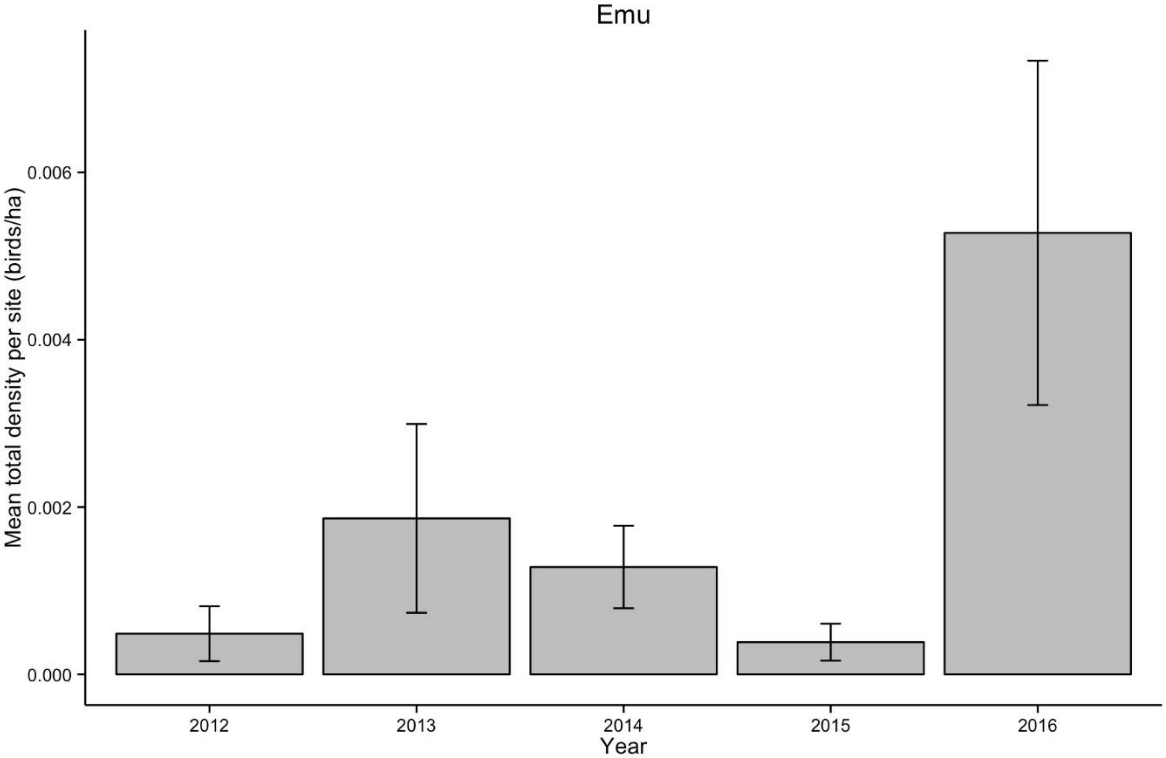

Cockatiel
Mean total density per site (birds/ha)
0.00
0.01
0.02
0.03
0.04
2012
2013
2014
2015
2016
Year

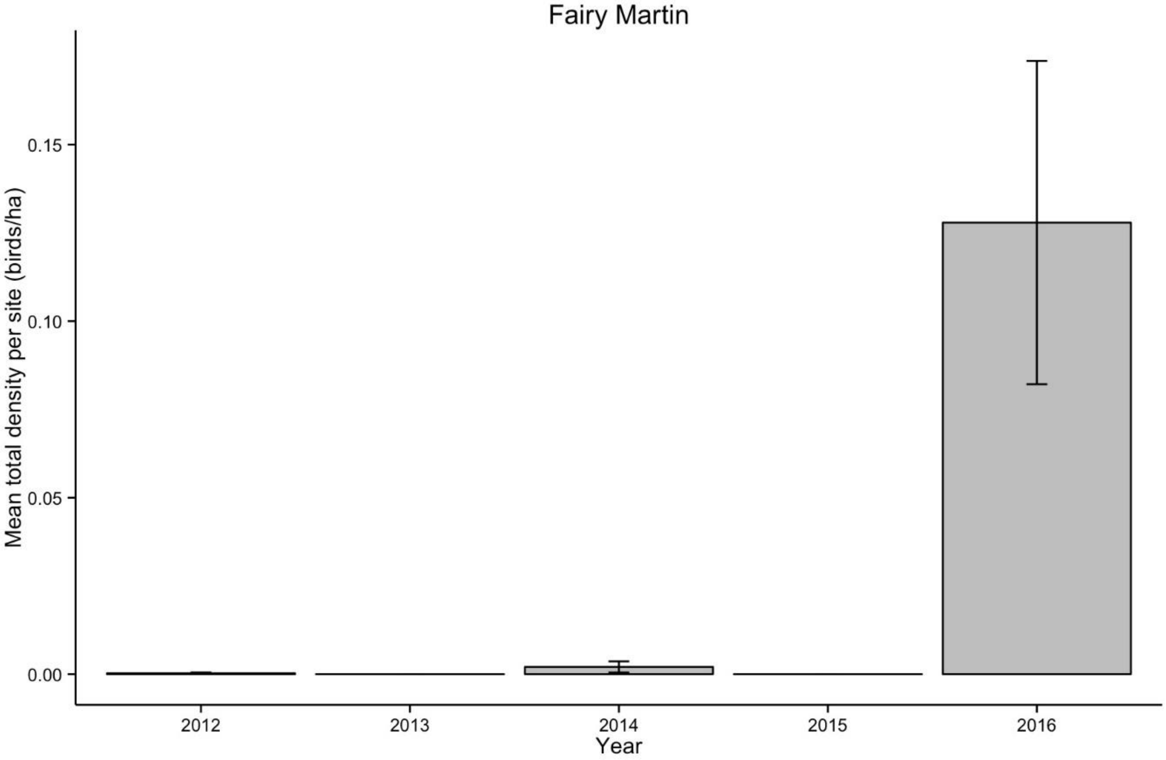

Crested Bellbird
Mean total density per site (birds/ha)
0.004
0.003
0.002
0.001
0.000
2012
2013
2014
2015
2016
Year

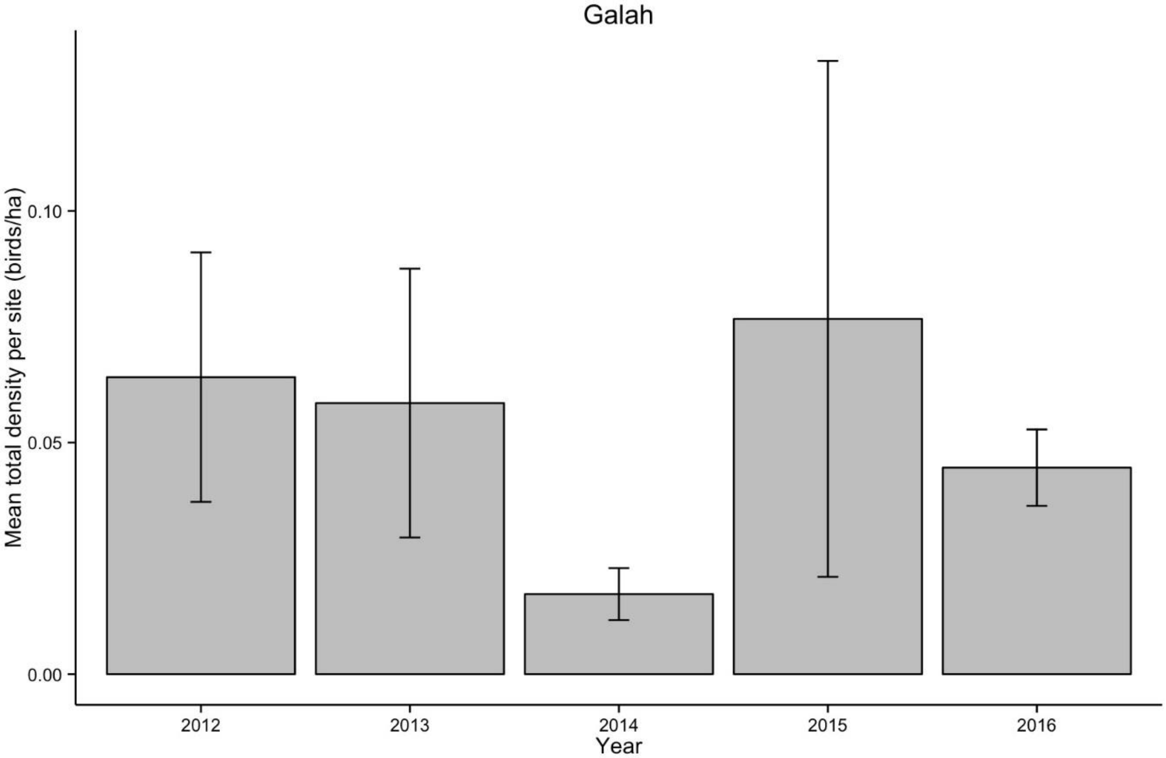

Crested Pigeon
Mean total density per site (birds/ha)
0.08
0.06
0.04
0.02
0.00
2012
2013
2014
2015
2016
Year

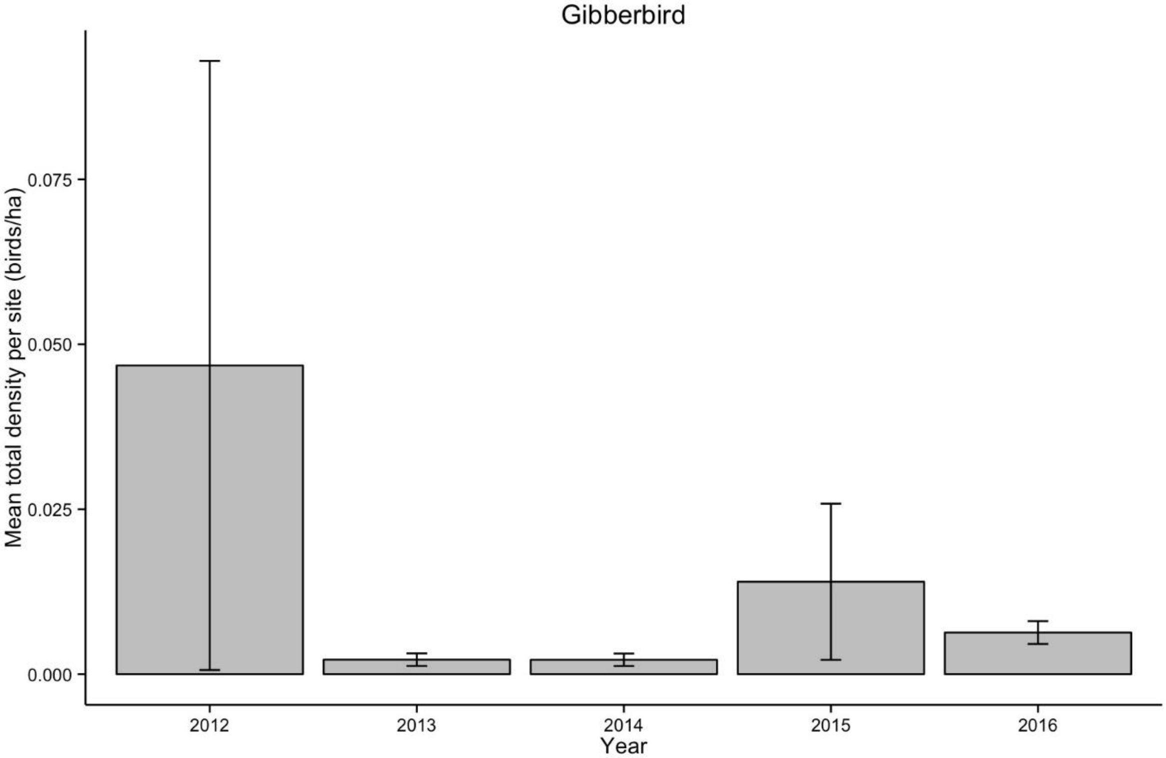

Crimson Chat
Mean total density per site (birds/ha)
0.100
0.075
0.050
0.025
0.000
2012
2013
2014
2015
2016
Year

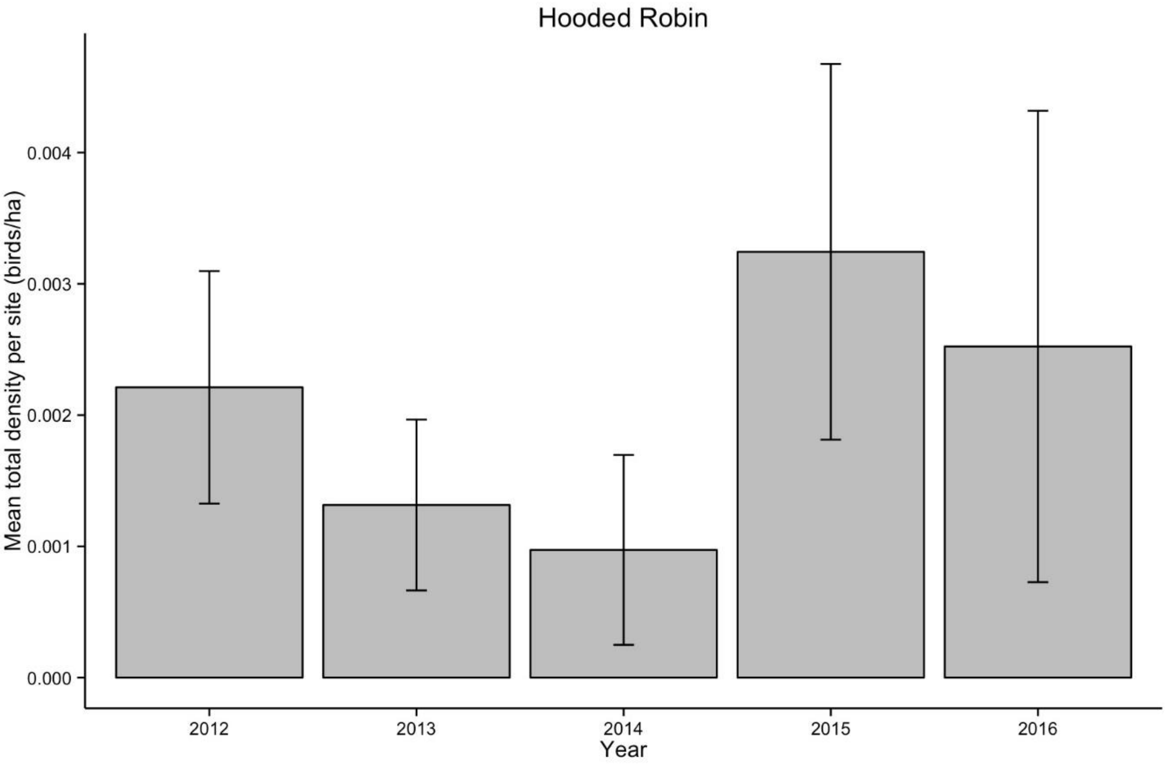

Diamond Dove
Mean total density per site (birds/ha)
0.5
0.4
0.3
0.2
0.1
0.0
2012
2013
2014
2015
2016
Year

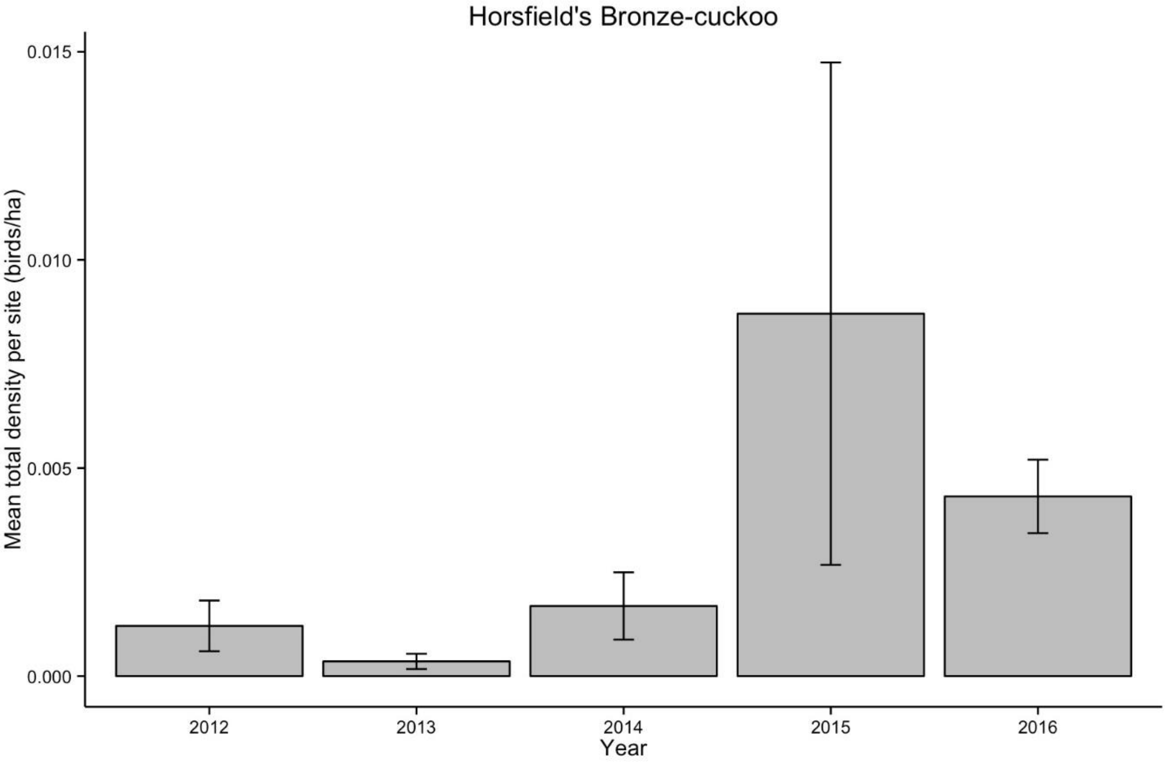

Emu
Mean total density per site (birds/ha)
0.006
0.004
0.002
0.000
2012
2013
2014
2015
2016
Year

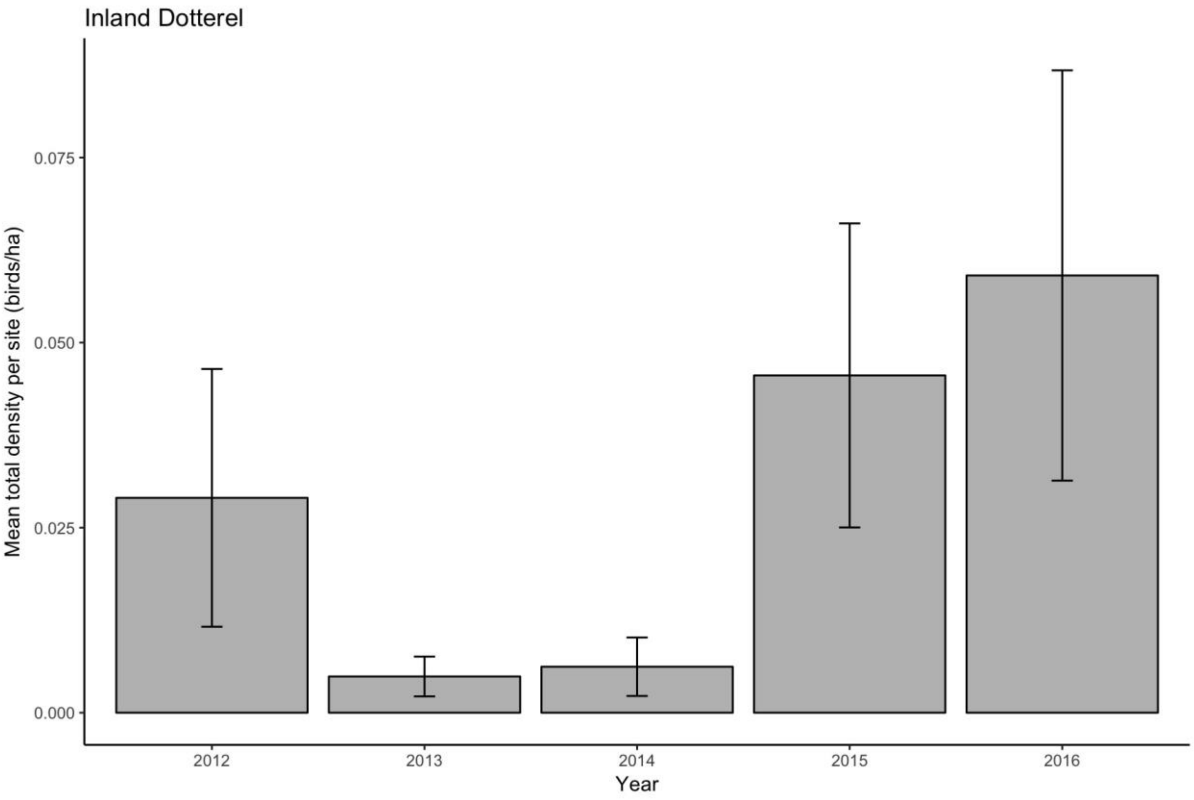

Fairy Martin
Mean total density per site (birds/ha)
0.15
0.10
0.05
0.00
2012
2013
2014
2015
2016
Year

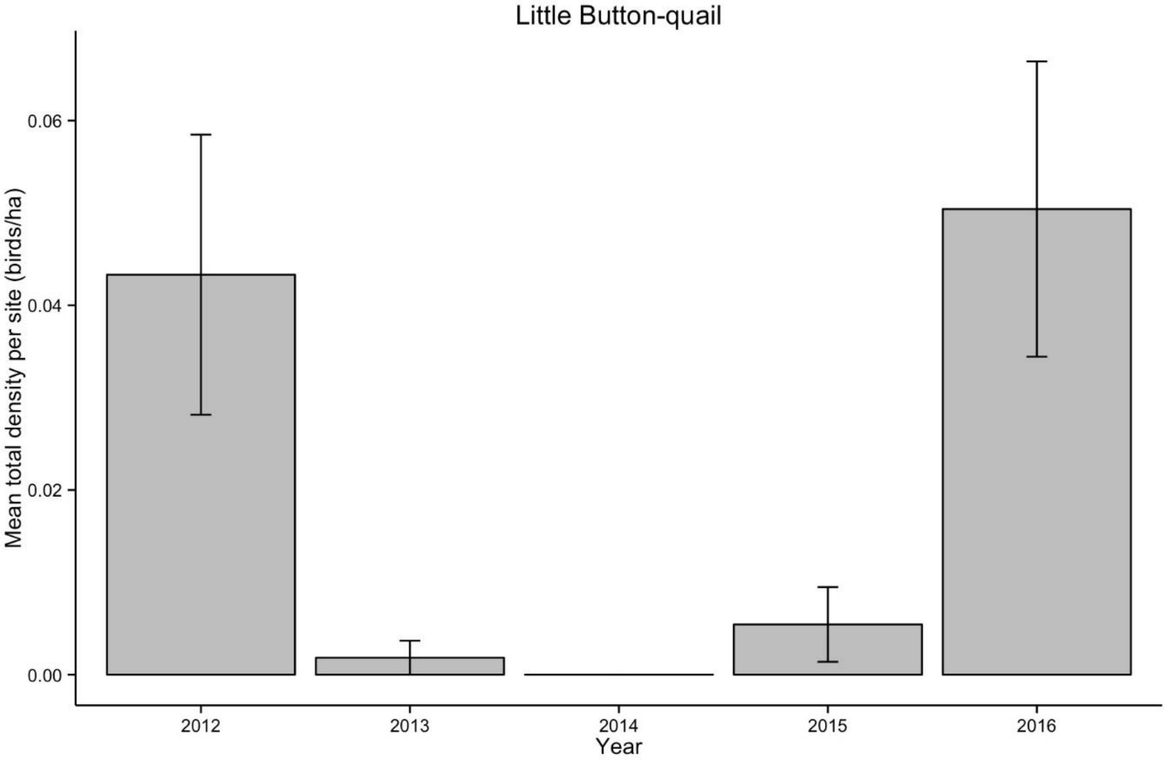

Galah
Mean total density per site (birds/ha)
0.10
0.05
0.00
2012
2013
2014
2015
2016
Year

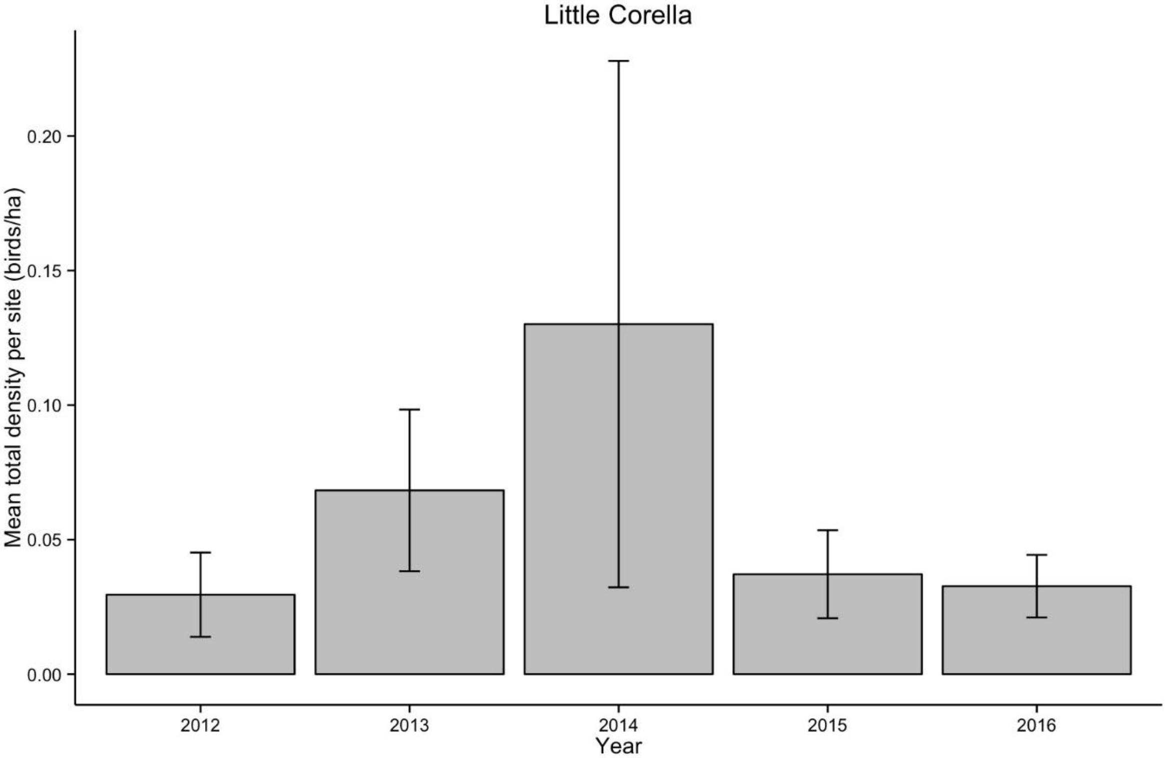

Gibberbird
Mean total density per site (birds/ha)
0.075
0.050
0.025
0.000
2012
2013
2014
2015
2016
Year

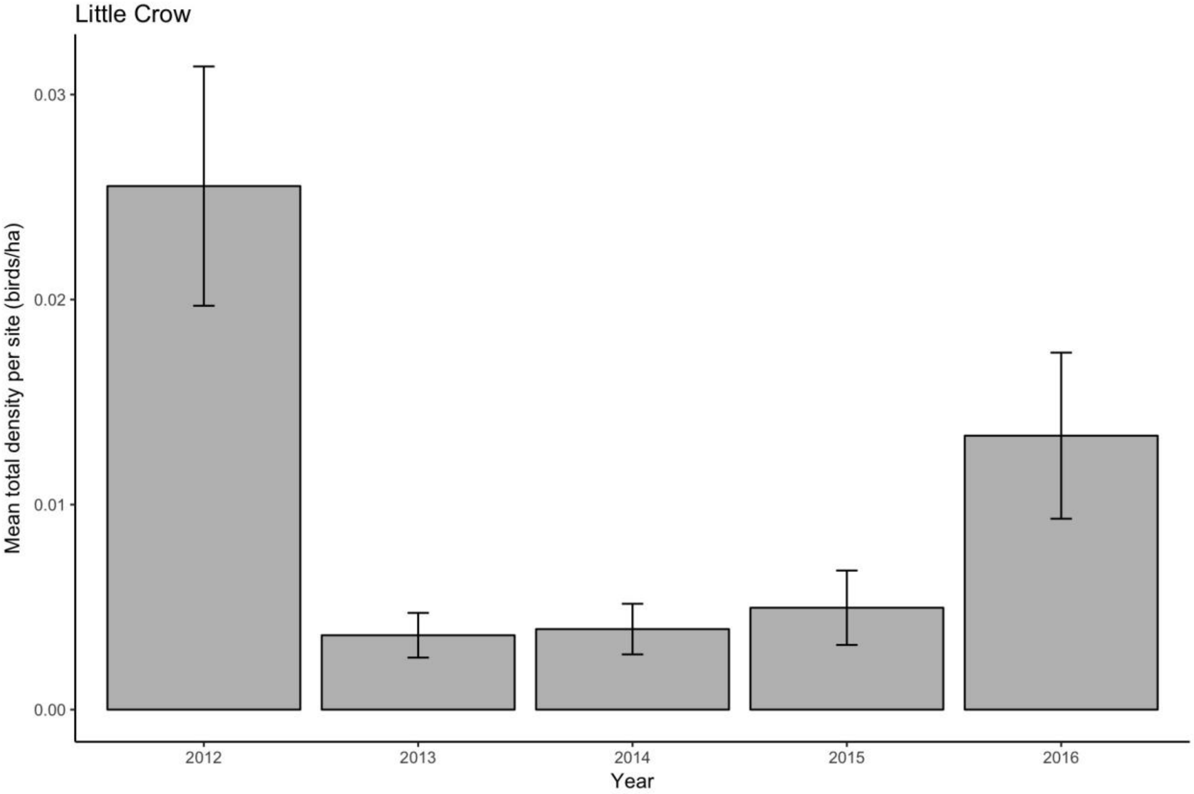

Hooded Robin
Mean total density per site (birds/ha)
0.000
0.001
0.002
0.003
0.004
2012
2013
2014
2015
2016
Year

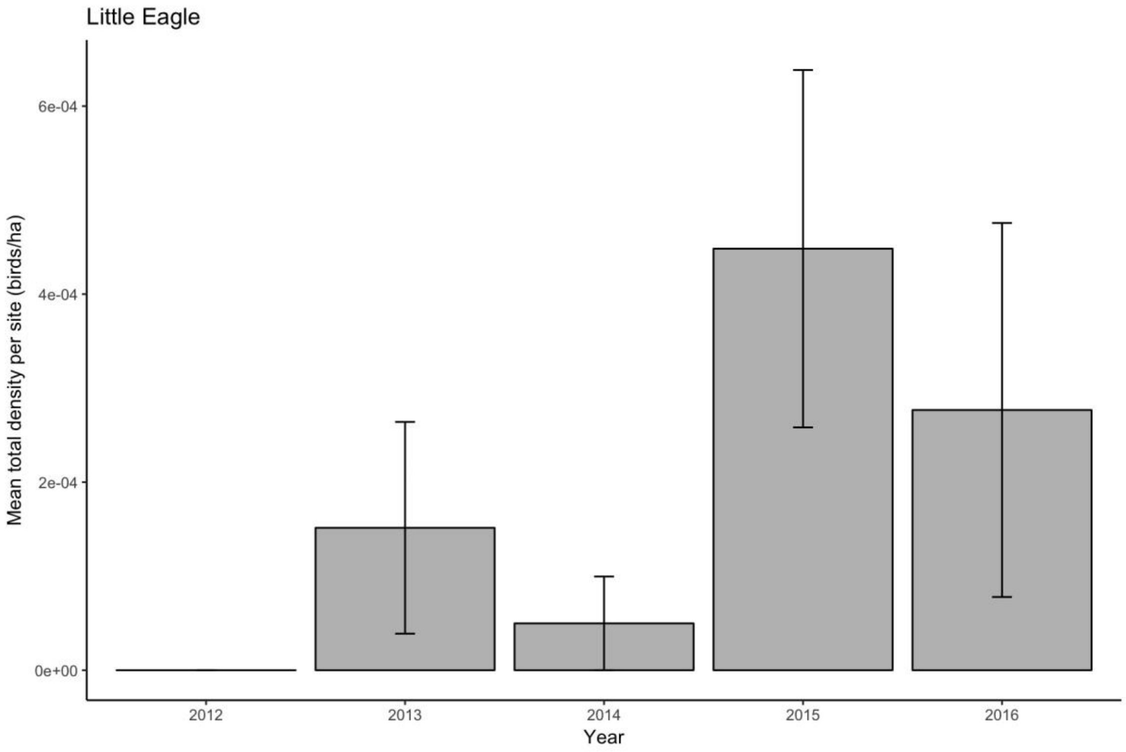

Horsfield's Bronze-cuckoo
Mean total density per site (birds/ha)
0.000
0.005
0.010
0.015
2012
2013
2014
2015
2016
Year

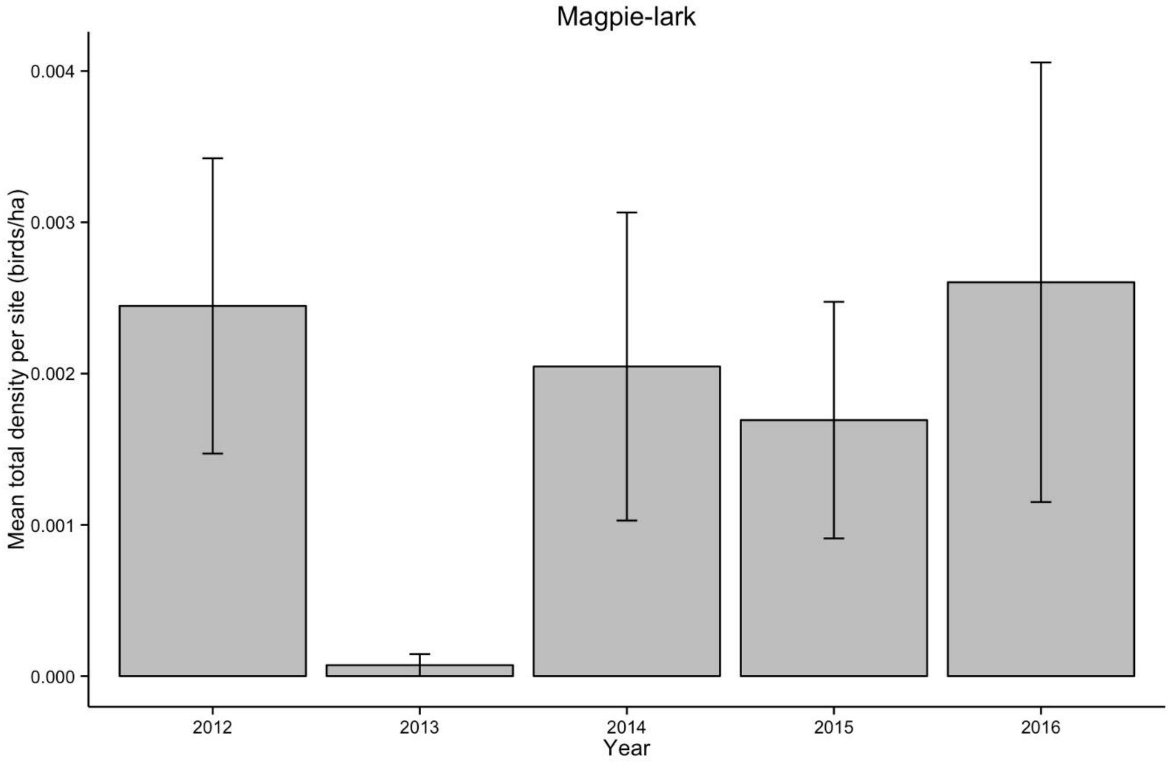

Inland Dotterel

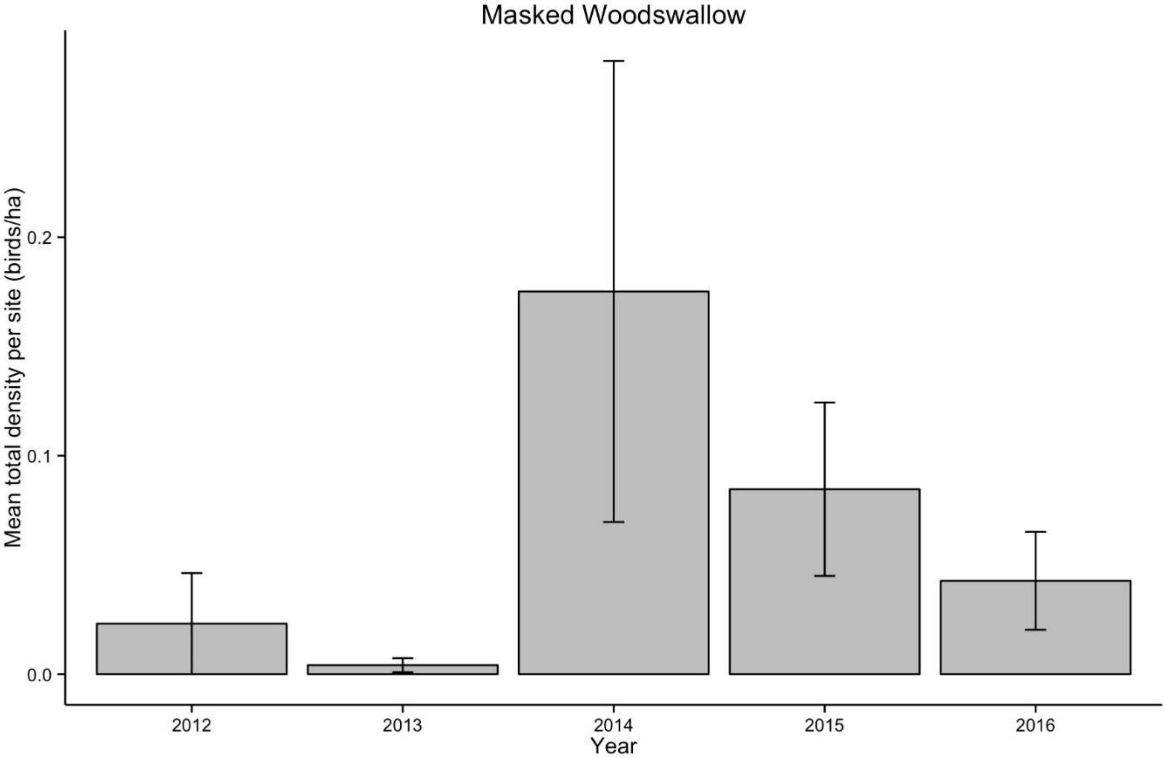

Little Button-quail

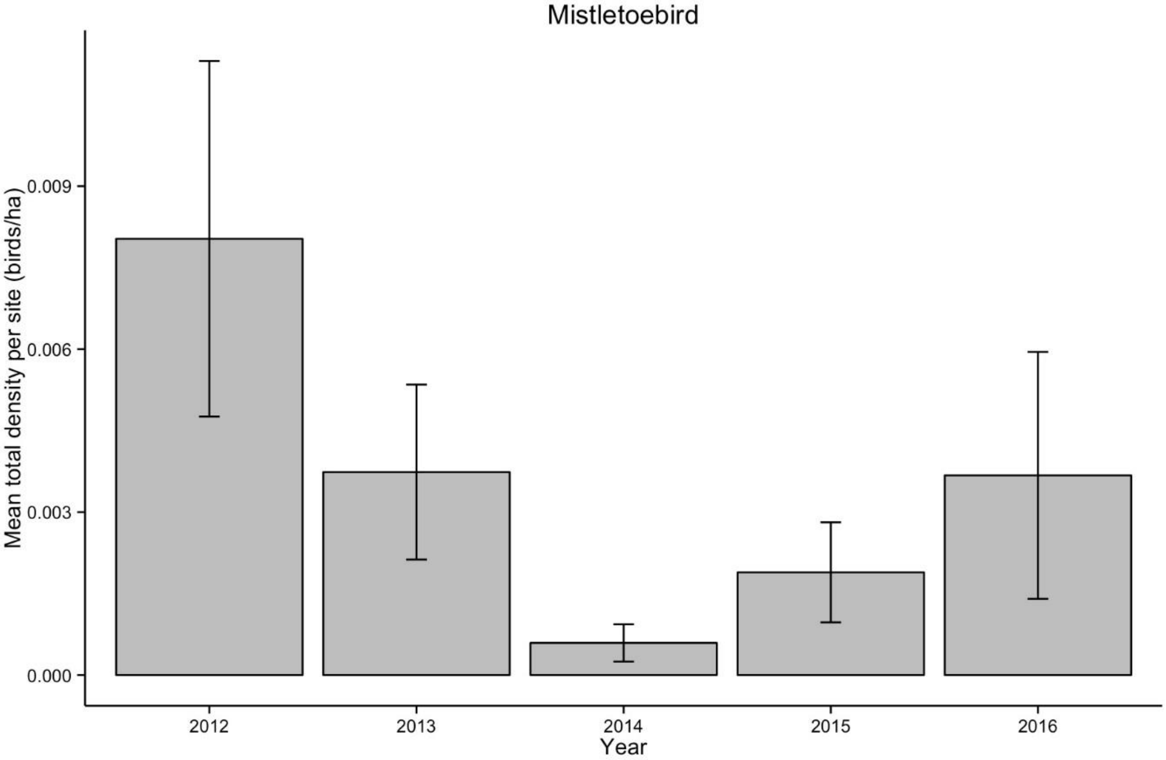

Little Corella
Mean total density per site (birds/ha)
0.00
0.05
0.10
0.15
0.20
2012
2013
2014
2015
2016
Year

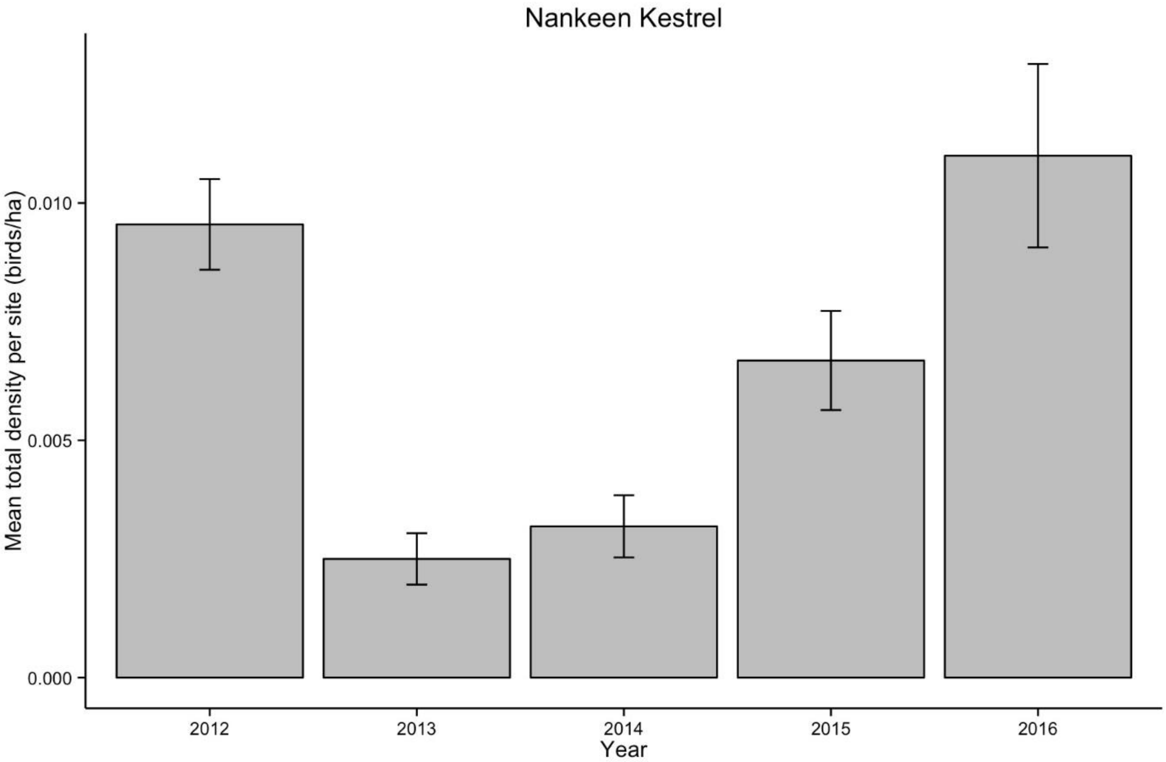

Little Crow
Mean total density per site (birds/ha)
0.00
0.01
0.02
0.03
2012
2013
2014
2015
2016
Year


Little Eagle
Mean total density per site (birds/ha)
6e-04
4e-04
2e-04
0e+00
2012
2013
2014
2015
2016
Year

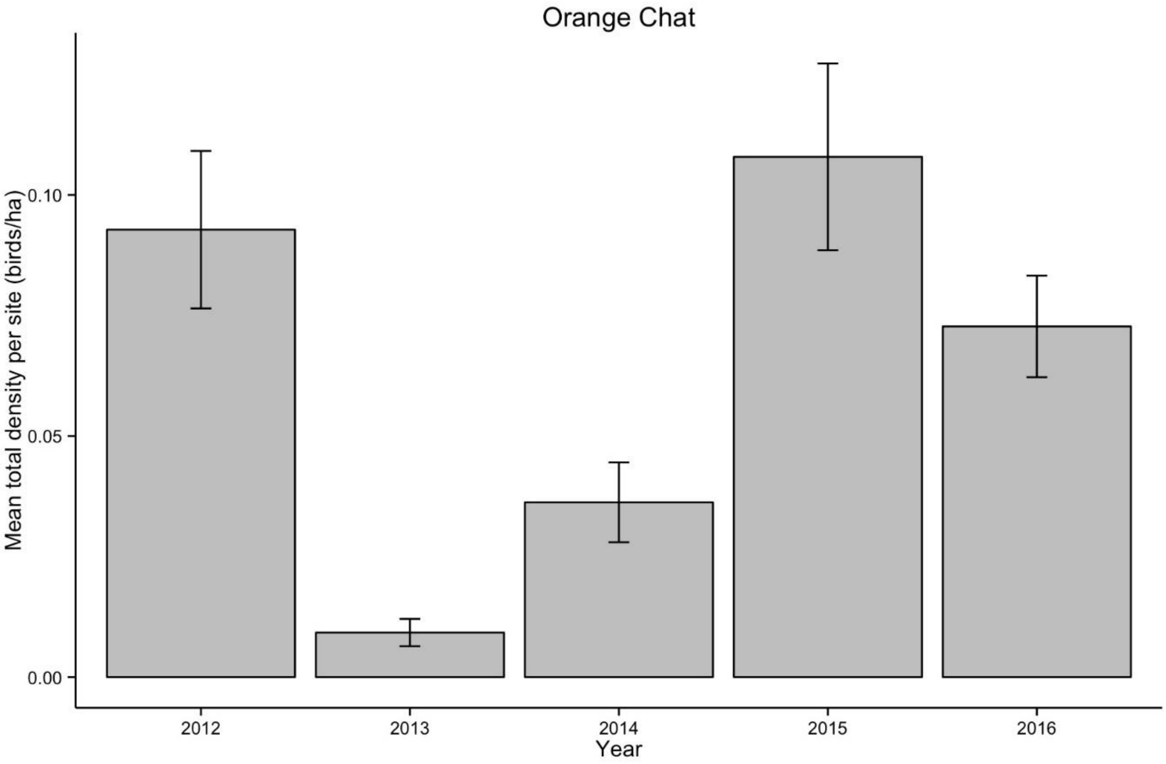

Magpie-lark
Mean total density per site (birds/ha)
0.004
0.003
0.002
0.001
0.000
2012
2013
2014
2015
2016
Year


Masked Woodswallow
Mean total density per site (birds/ha)
0.0
0.1
0.2
2012
2013
2014
2015
2016
Year

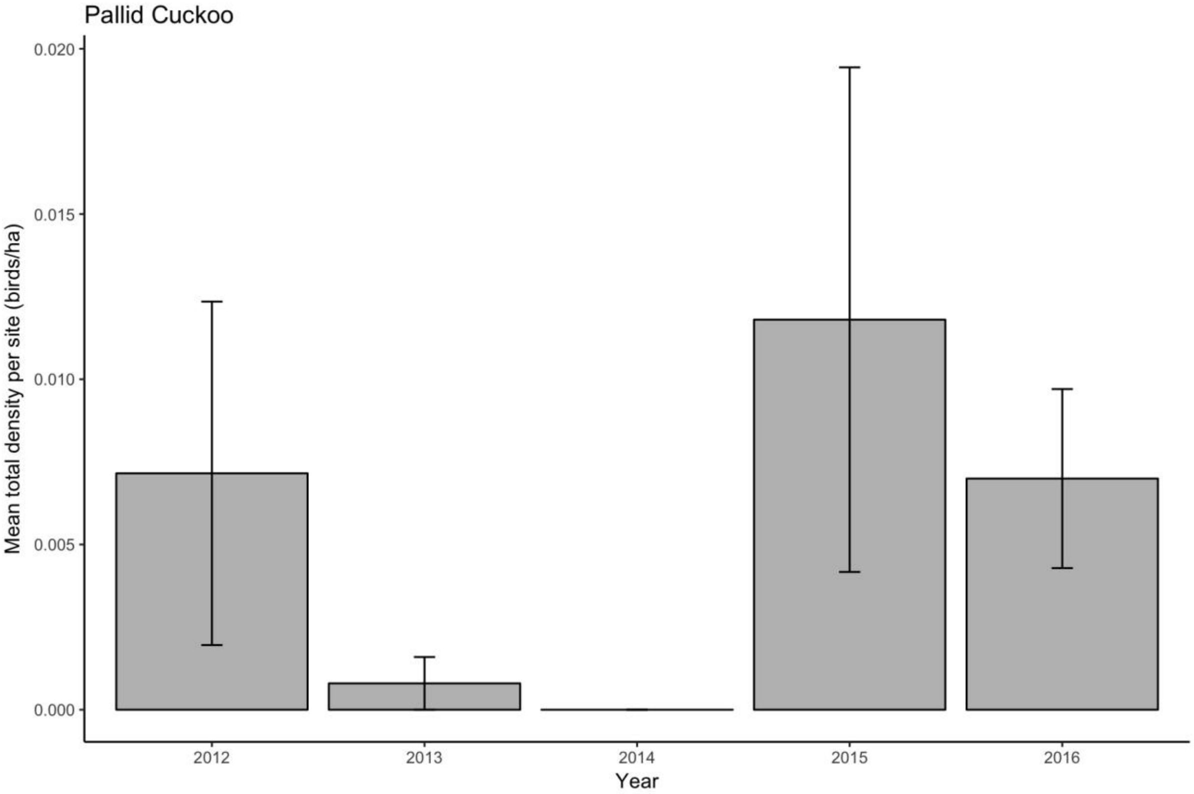

Mistletoebird
Mean total density per site (birds/ha)
0.000
0.003
0.006
0.009
2012
2013
2014
2015
2016
Year

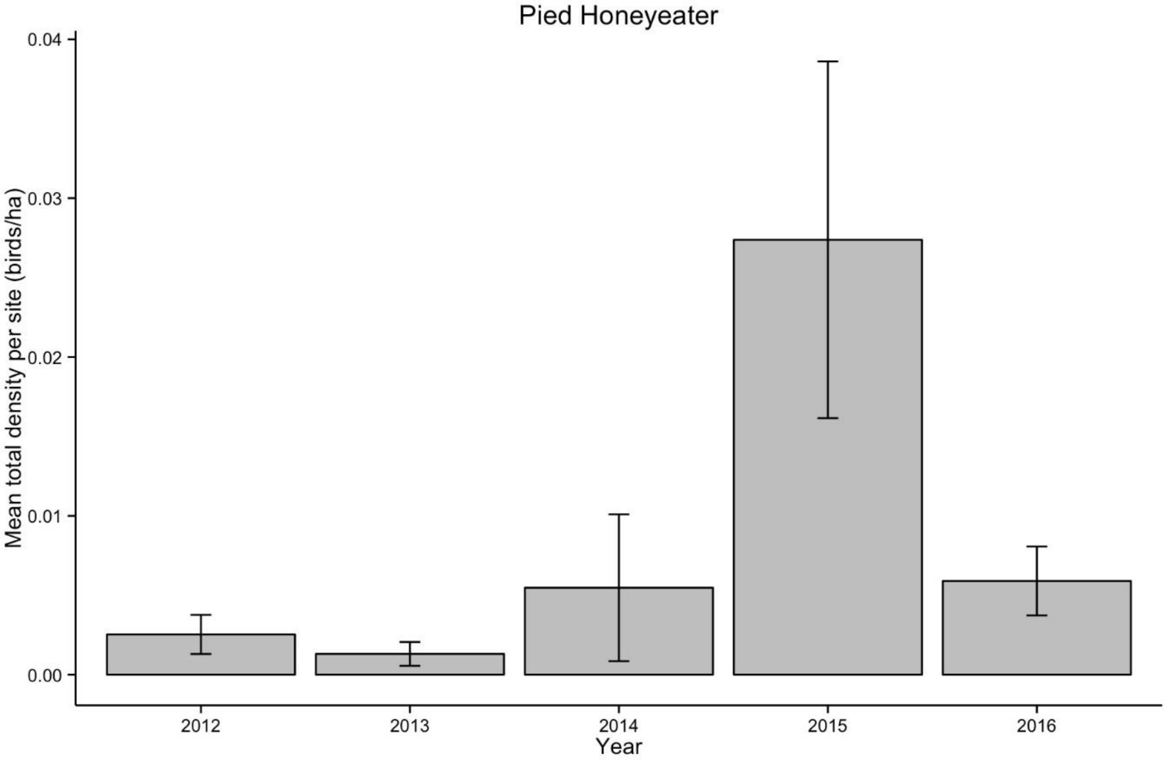


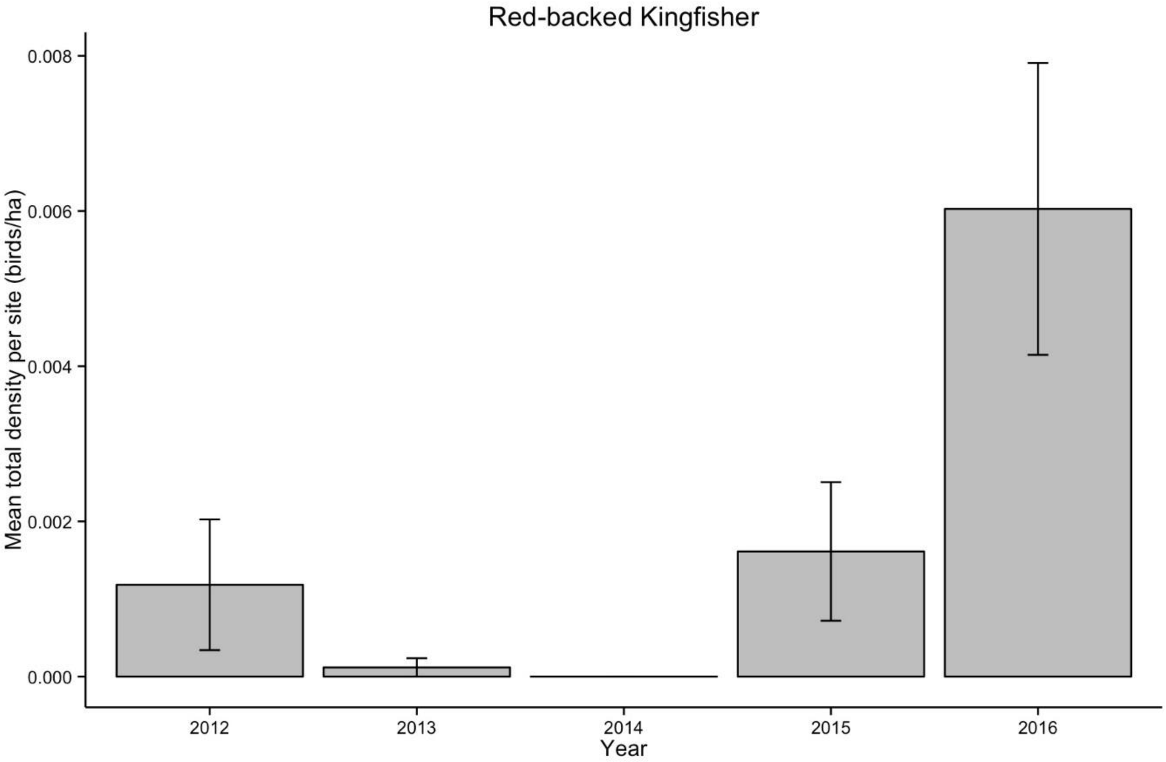
Nankeen Kestrel

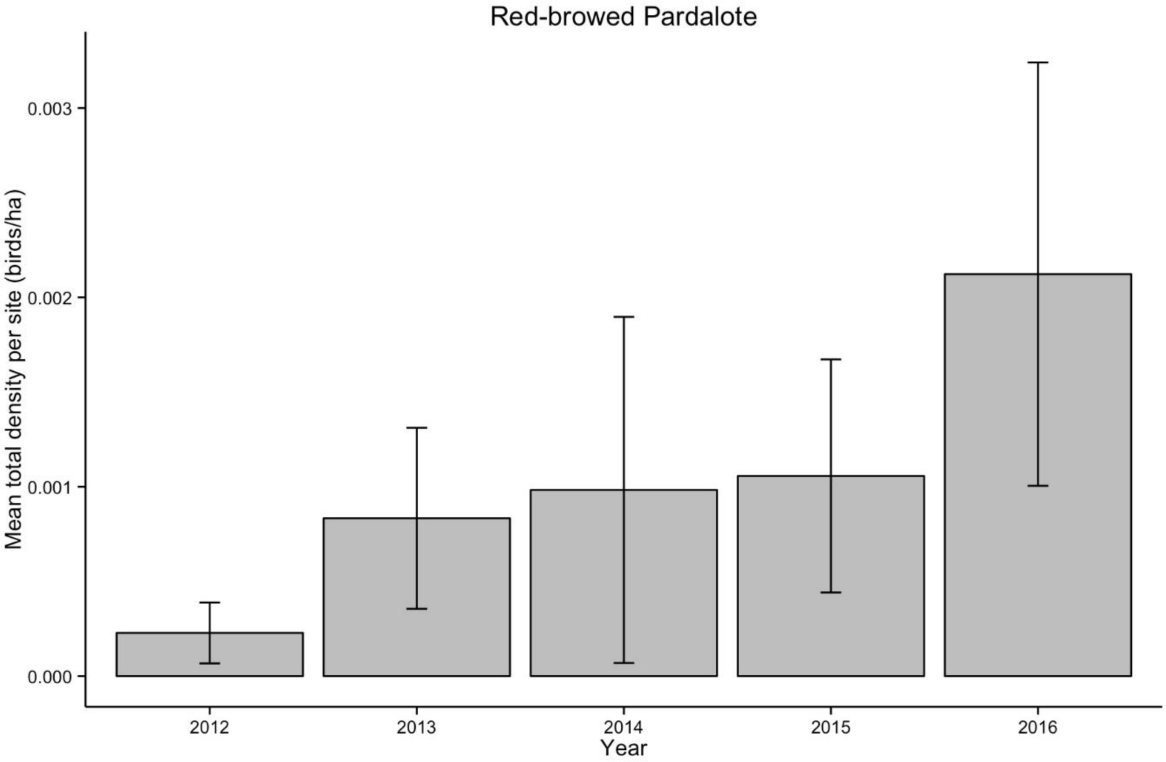


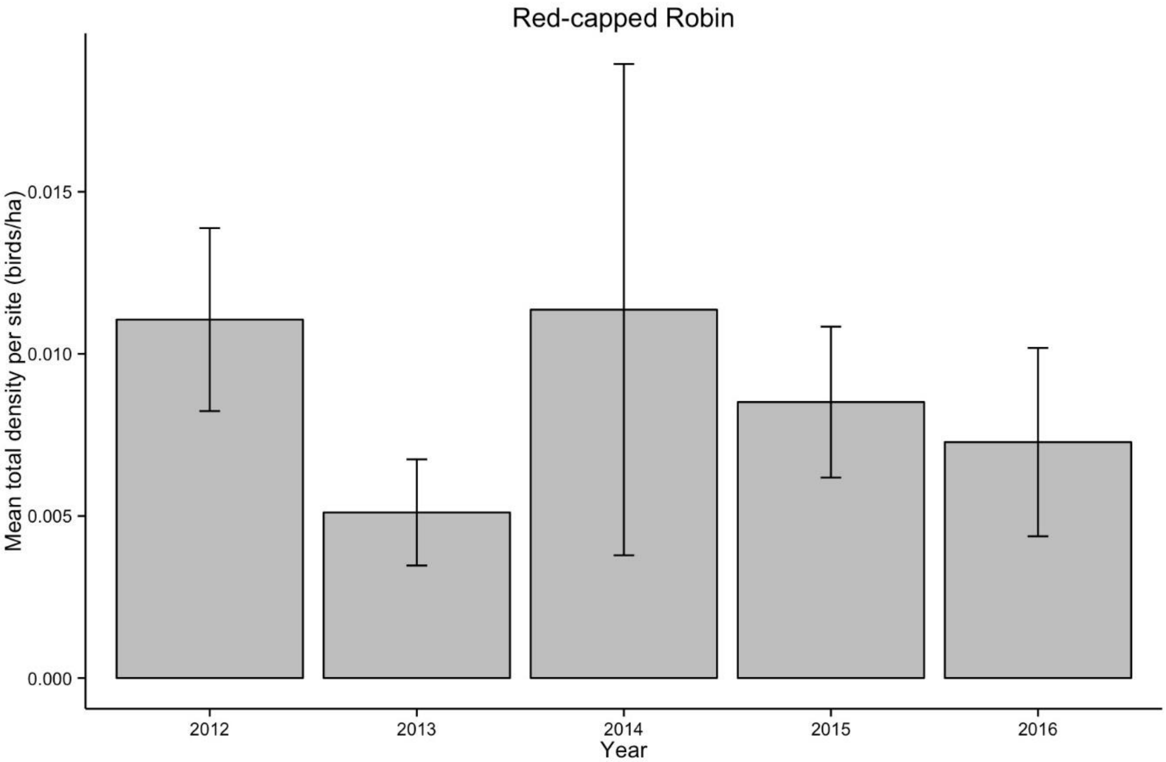
Orange Chat

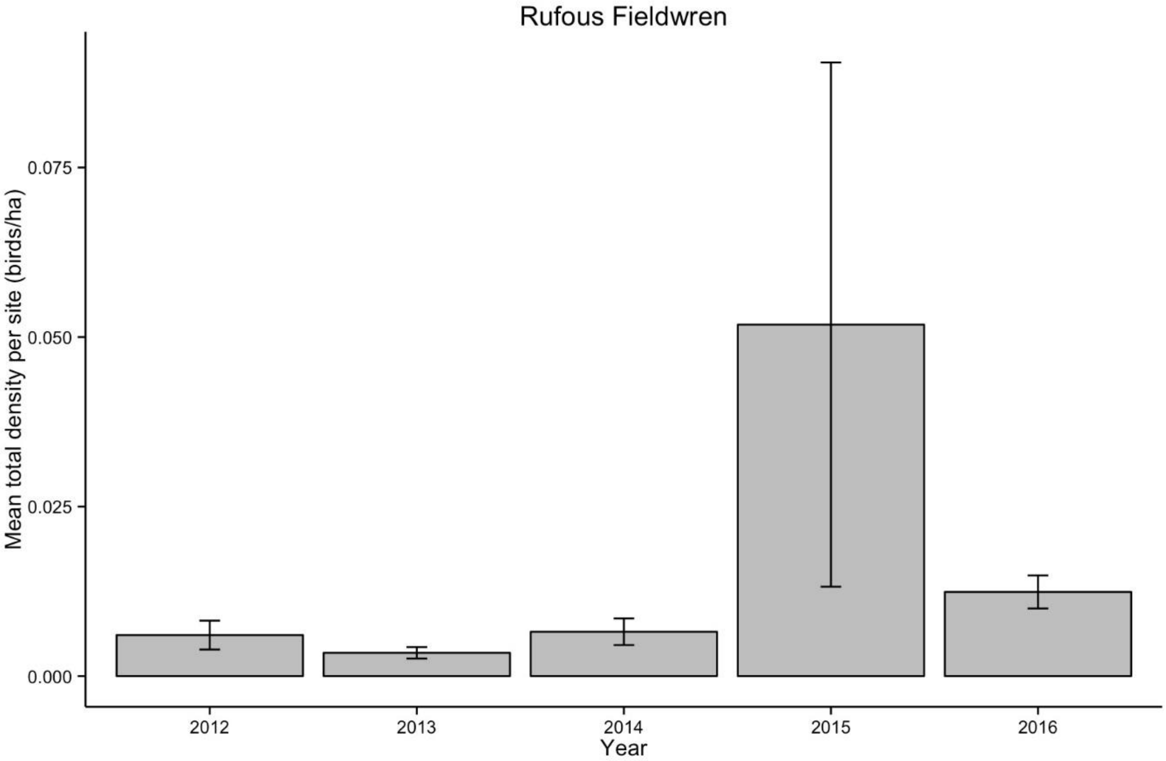

Pallid Cuckoo
Mean total density per site (birds/ha)
0.020
0.015
0.010
0.005
0.000
2012
2013
2014
2015
2016
Year

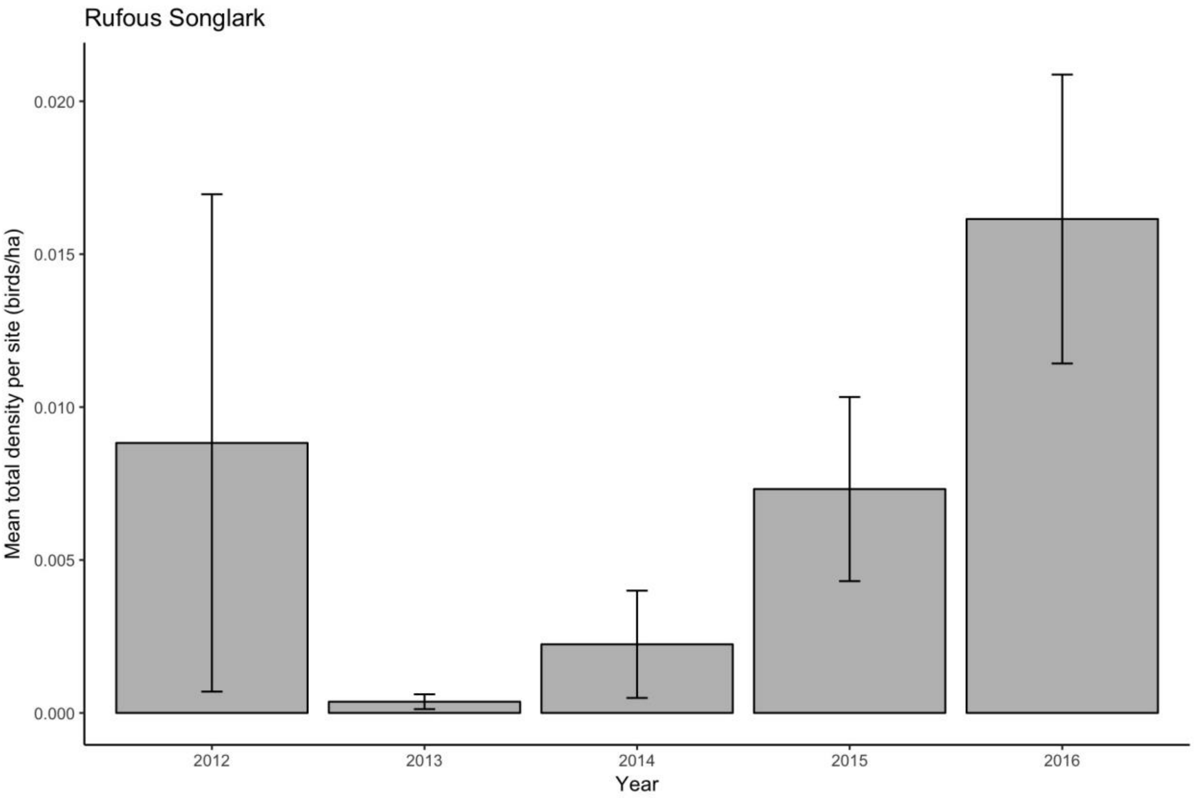

Pied Honeyeater
Mean total density per site (birds/ha)
0.04
0.03
0.02
0.01
0.00
2012
2013
2014
2015
2016
Year

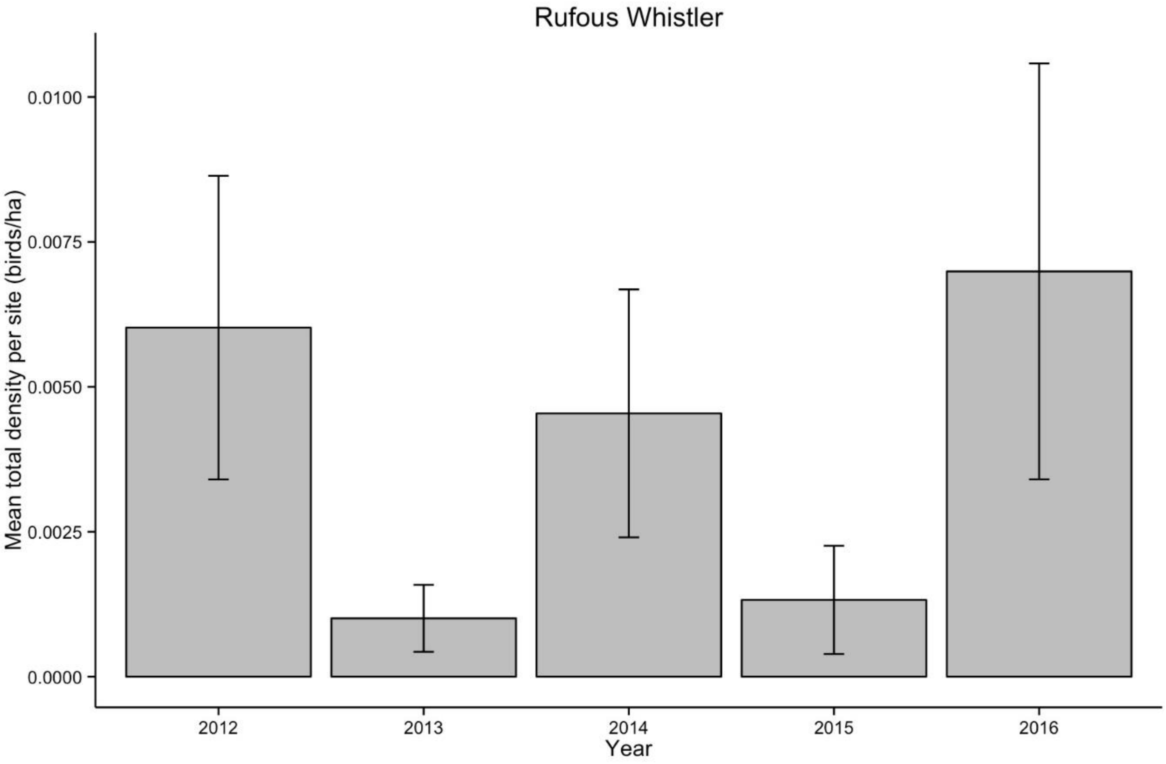

Red-backed Kingfisher

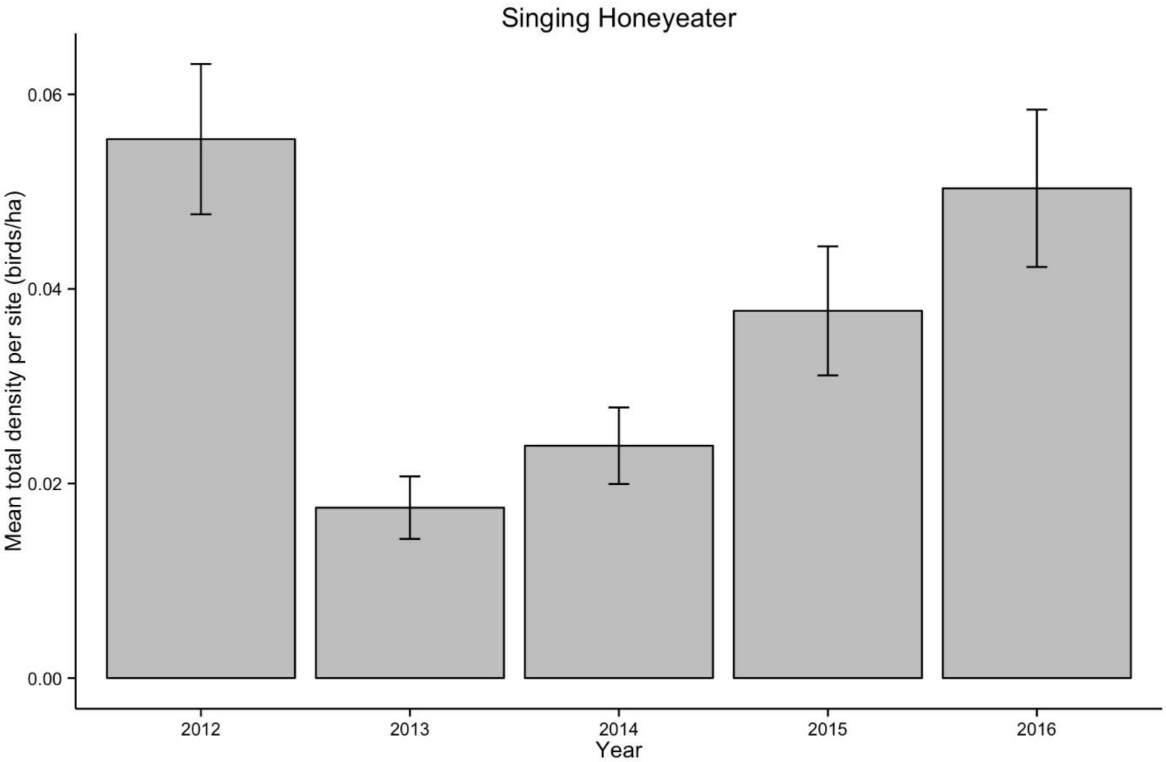

Red-browed Pardalote

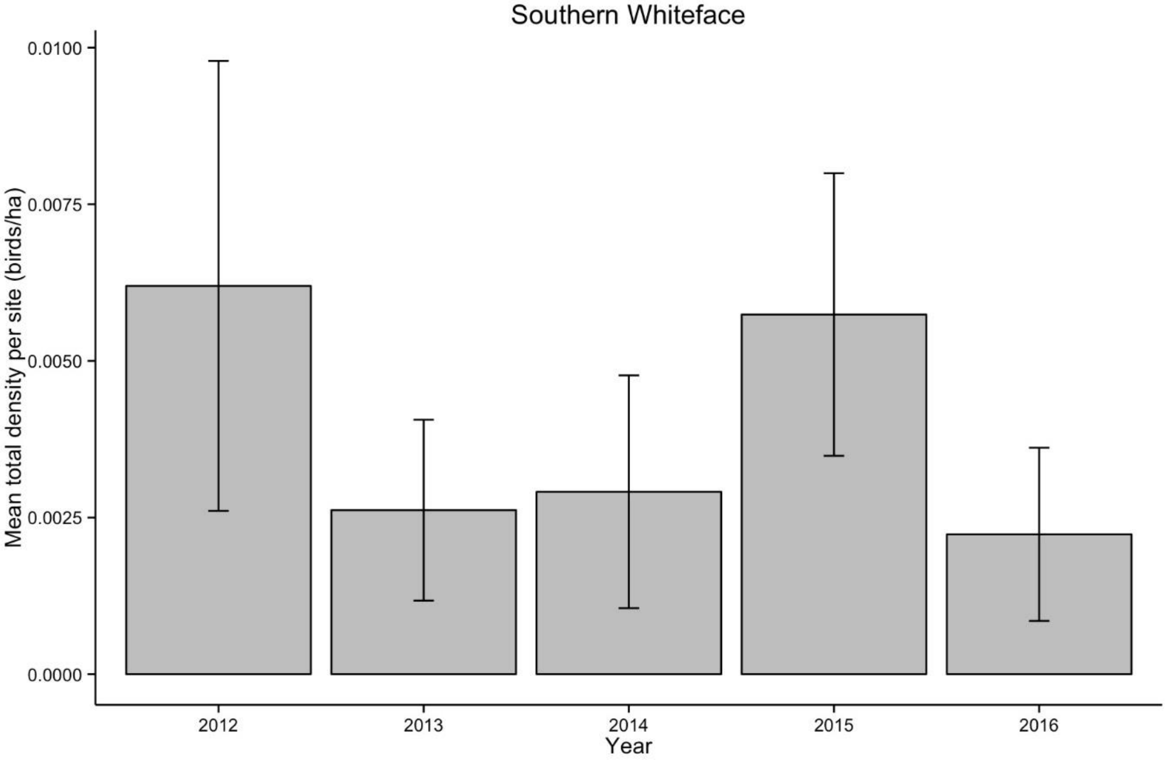

Red-capped Robin
Mean total density per site (birds/ha)
0.000
0.005
0.010
0.015
2012
2013
2014
2015
2016
Year

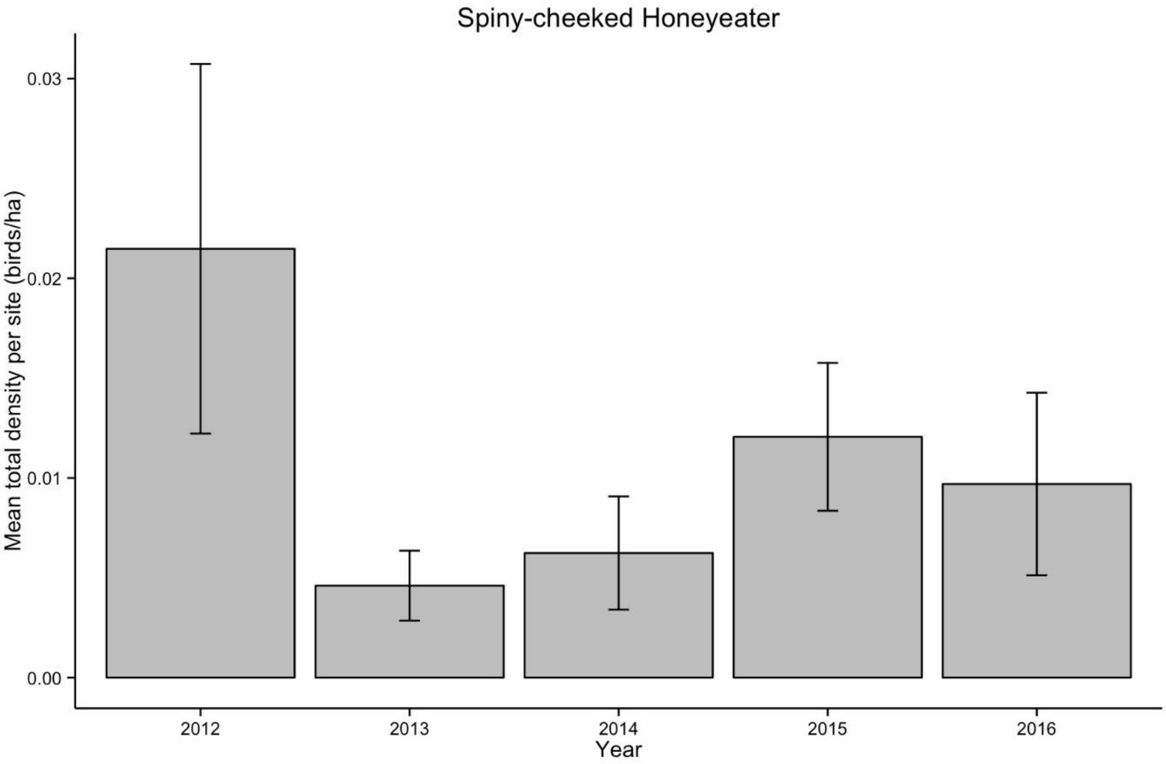

Rufous Fieldwren
Mean total density per site (birds/ha)
0.000
0.025
0.050
0.075
2012
2013
2014
2015
2016
Year

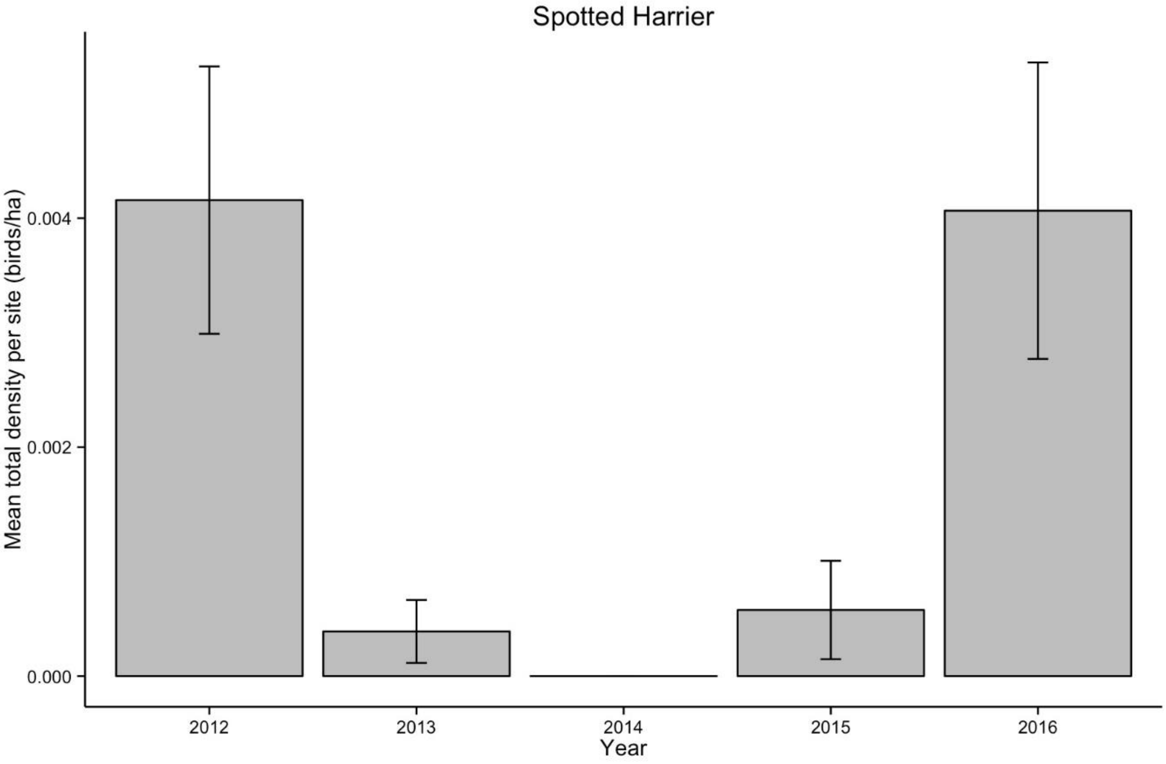

Rufous Songlark

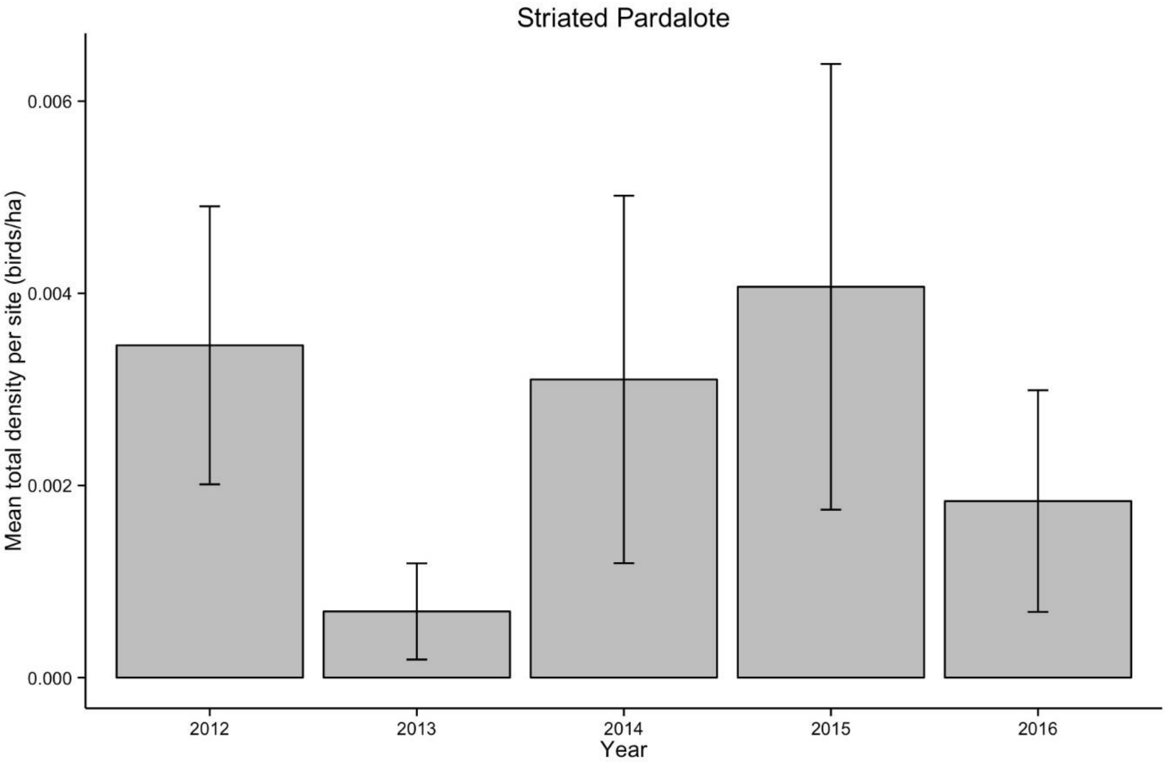

Rufous Whistler

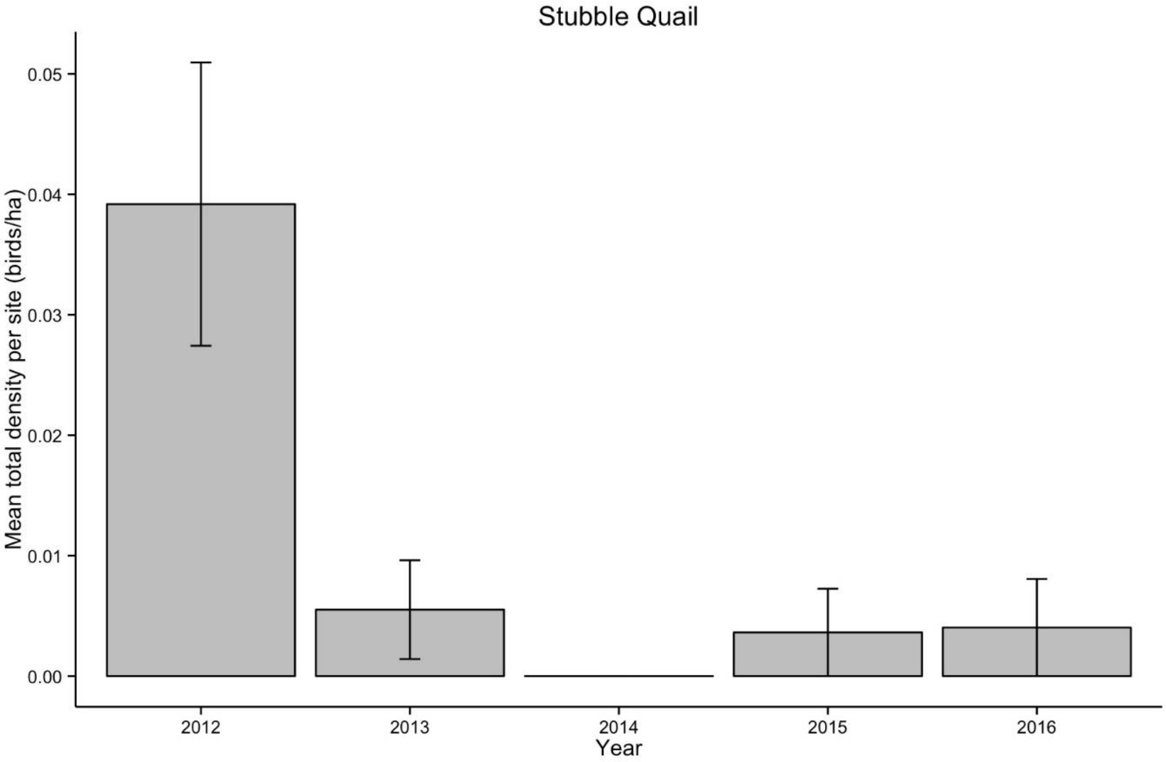

Singing Honeyeater
Mean total density per site (birds/ha)
0.06
0.04
0.02
0.00
2012
2013
2014
2015
2016
Year

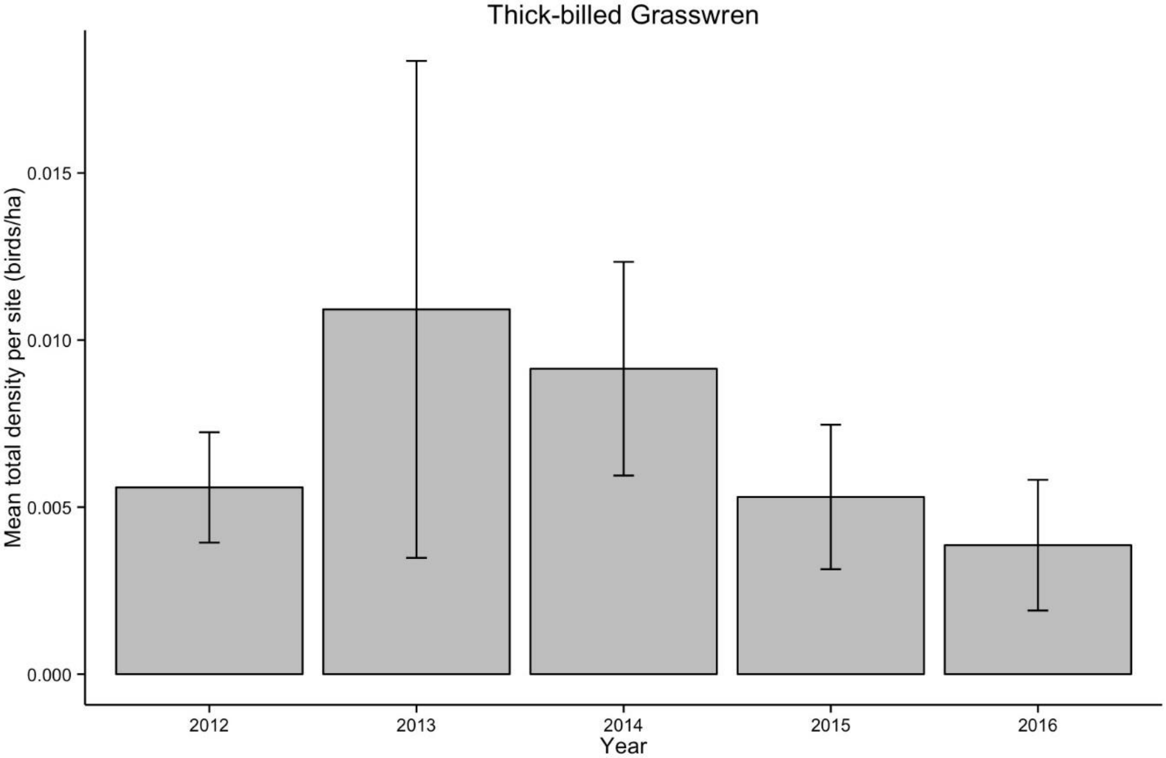

Southern Whiteface
Mean total density per site (birds/ha)
0.0100
0.0075
0.0050
0.0025
0.0000
2012
2013
2014
2015
2016
Year

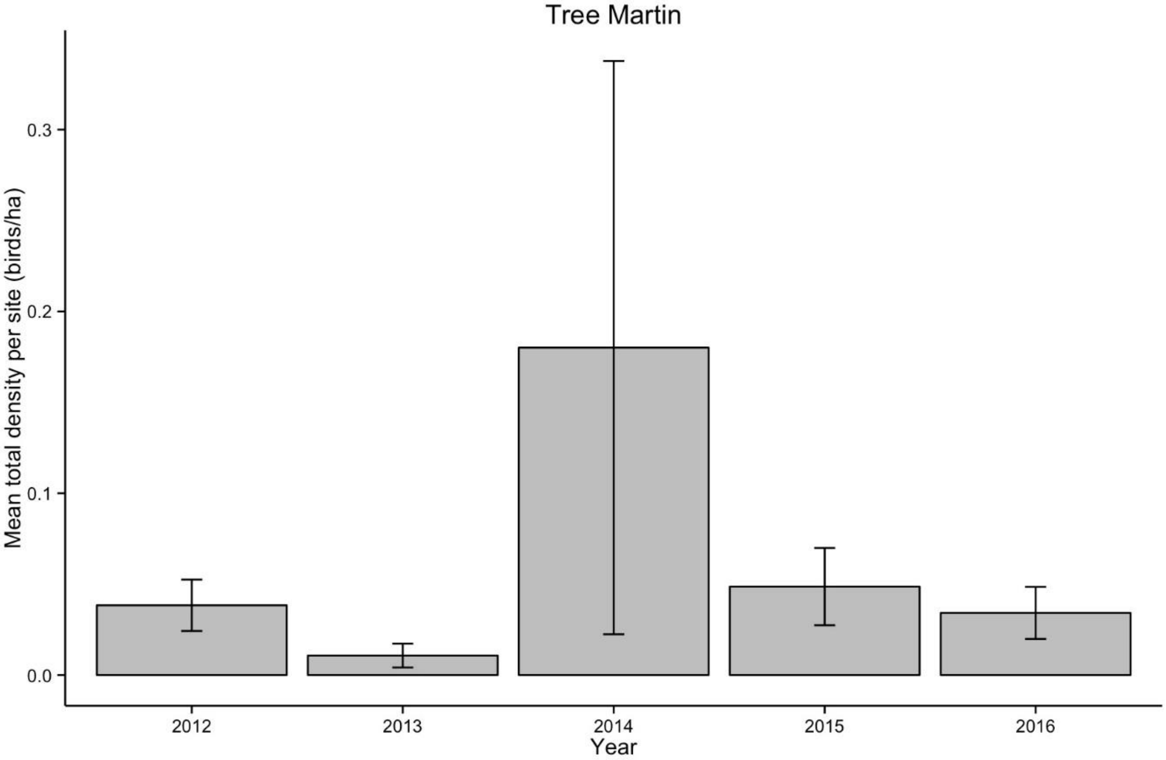

Spiny-cheeked Honeyeater
Mean total density per site (birds/ha)
0.03
0.02
0.01
0.00
2012
2013
2014
2015
2016
Year

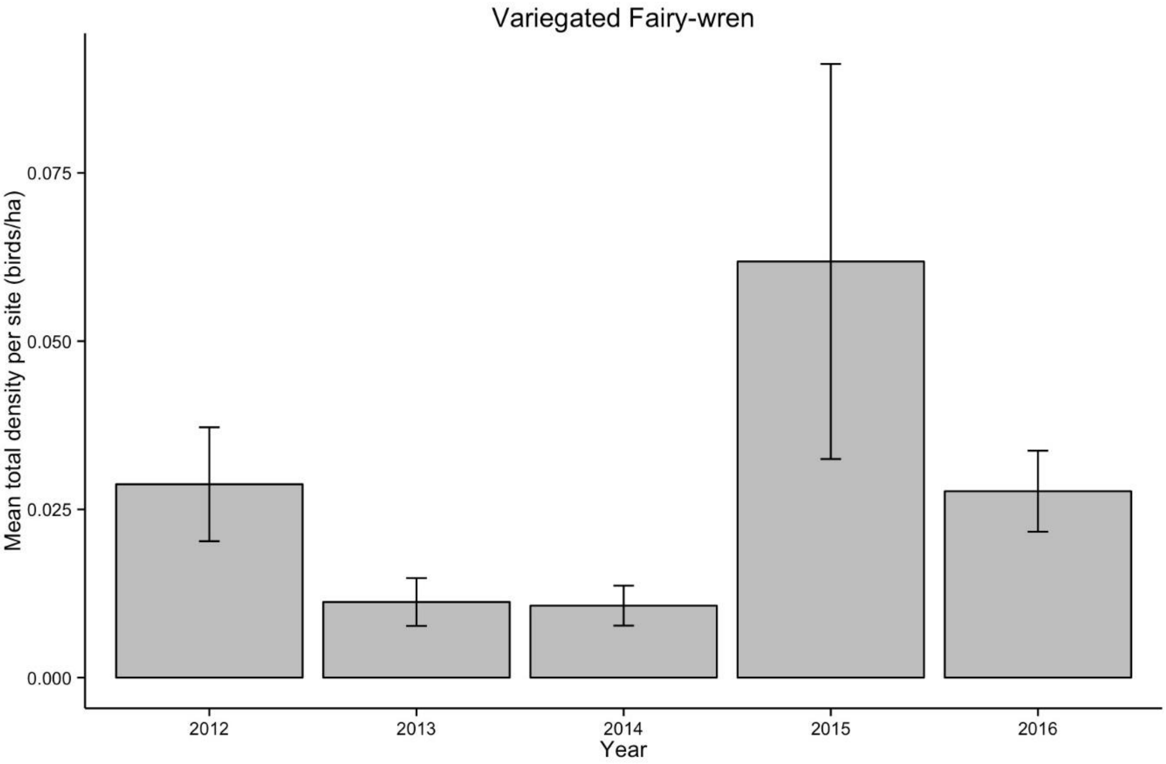

Spotted Harrier
Mean total density per site (birds/ha)
0.004
0.002
0.000
2012
2013
2014
2015
2016
Year

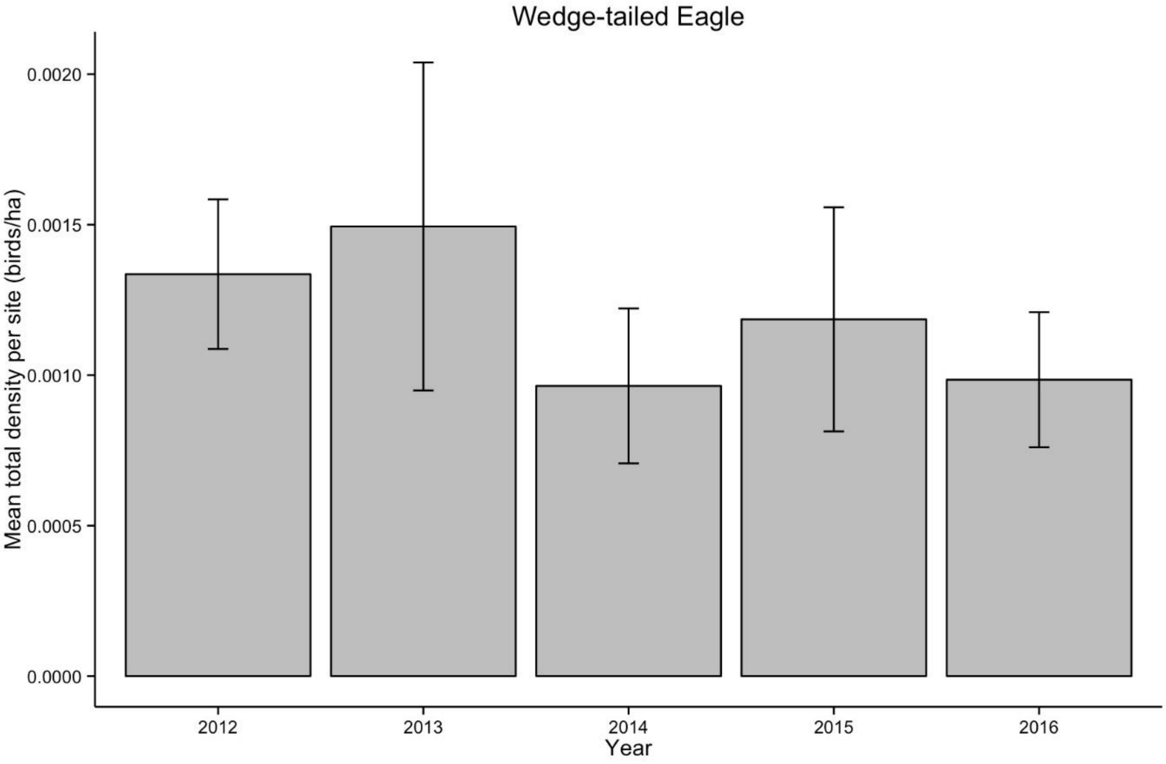

Striated Pardalote
Mean total density per site (birds/ha)
0.006
0.004
0.002
0.000
2012
2013
2014
2015
2016
Year

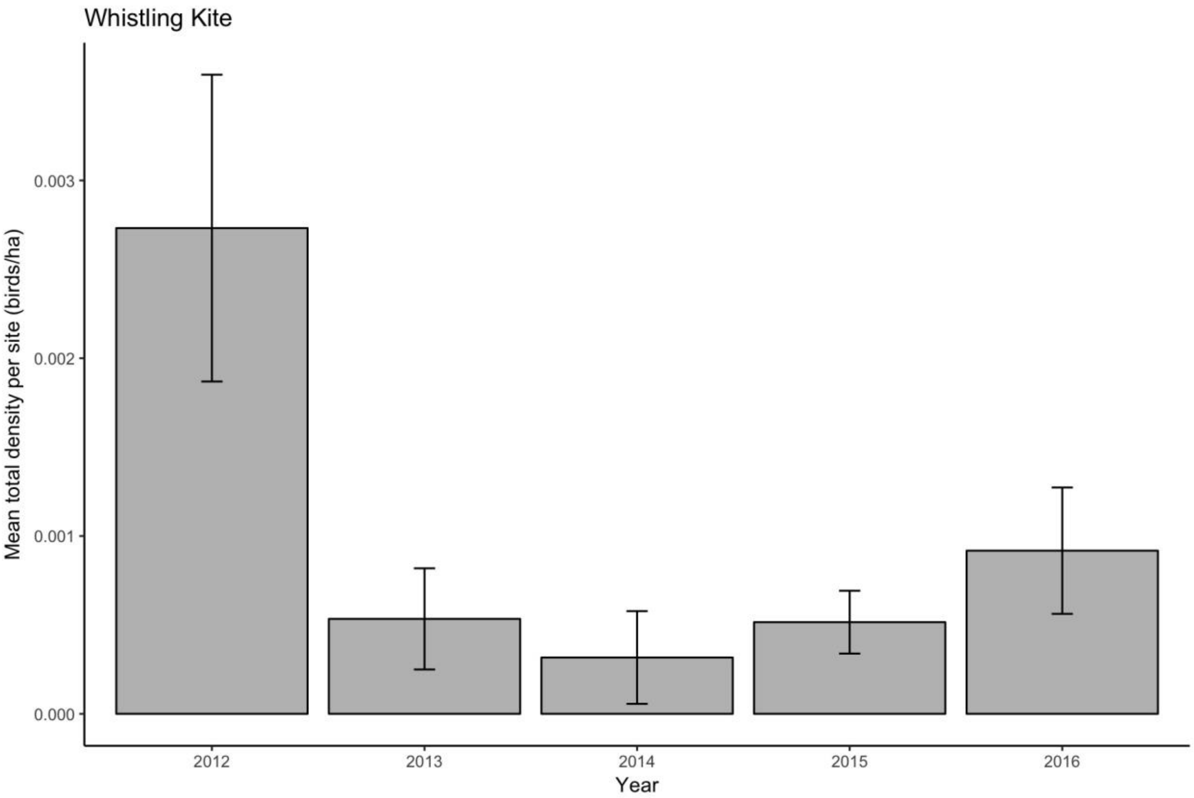

Stubble Quail
Mean total density per site (birds/ha)
0.05
0.04
0.03
0.02
0.01
0.00
2012
2013
2014
2015
2016
Year

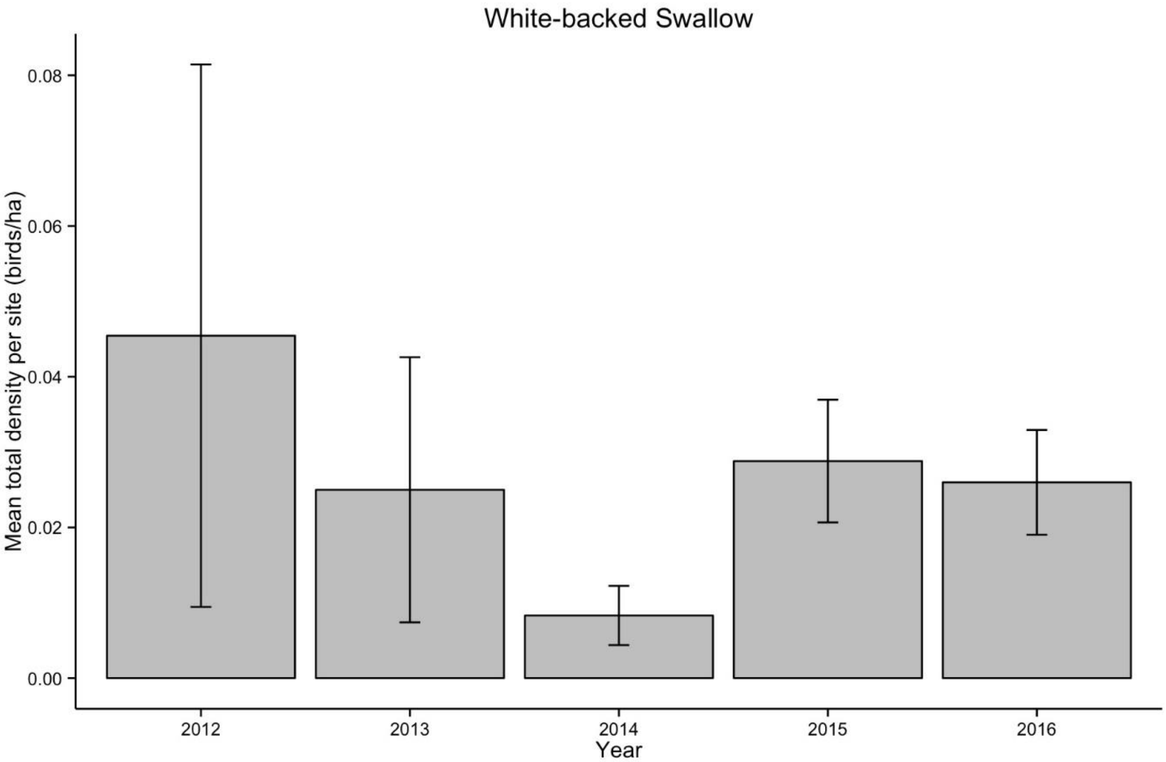

Thick-billed Grasswren
Mean total density per site (birds/ha)
0.000
0.005
0.010
0.015
2012
2013
2014
2015
2016
Year

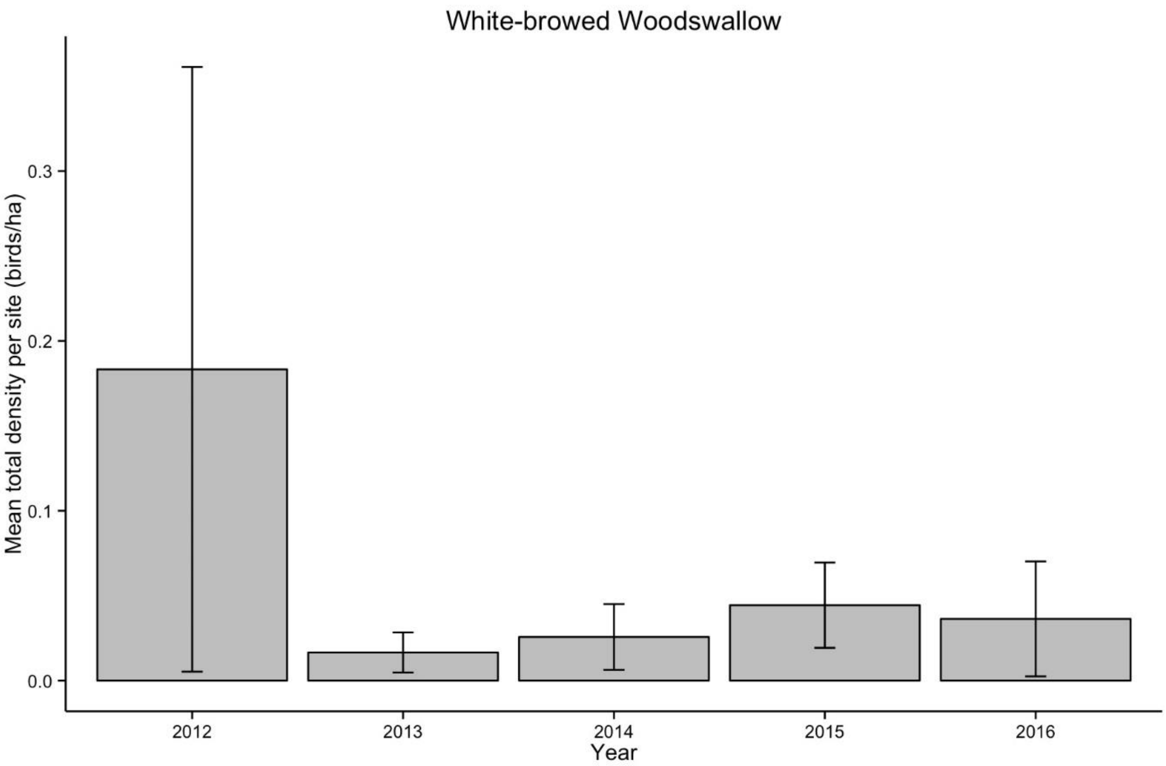

Tree Martin
Mean total density per site (birds/ha)
0.0
0.1
0.2
0.3
2012
2013
2014
2015
2016
Year

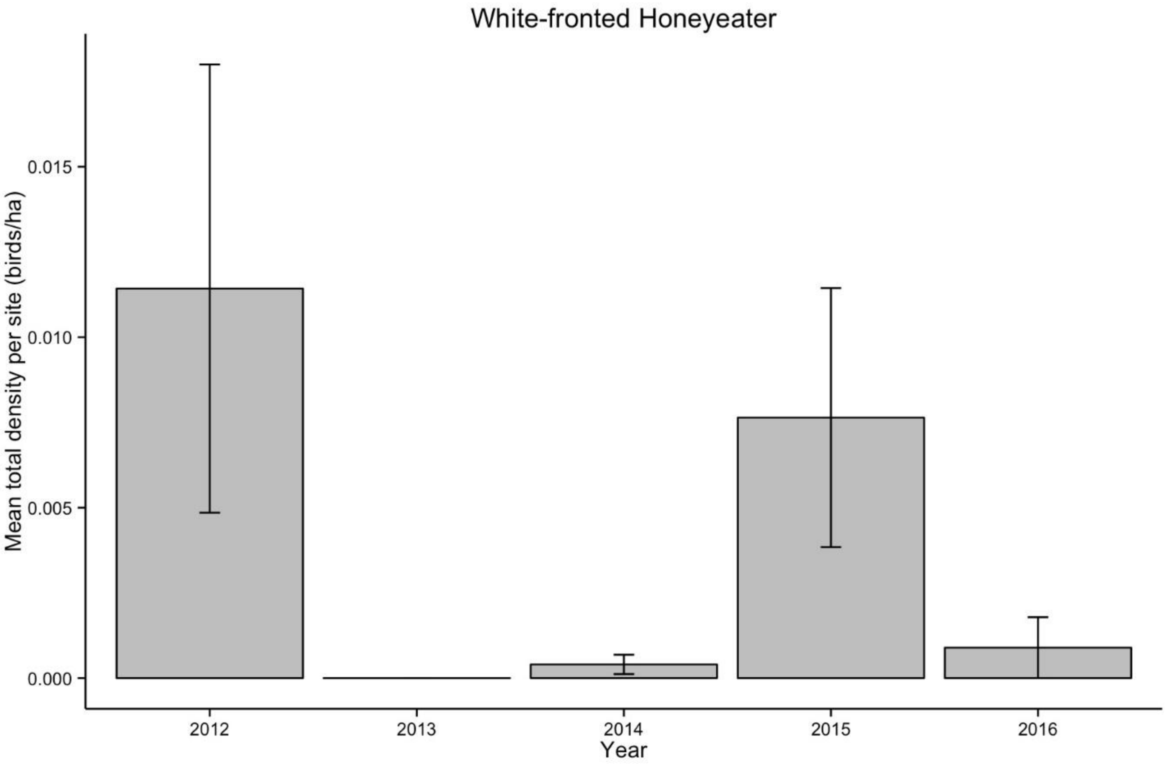

Variegated Fairy-wren
Mean total density per site (birds/ha)
0.075
0.050
0.025
0.000
2012
2013
2014
2015
2016
Year

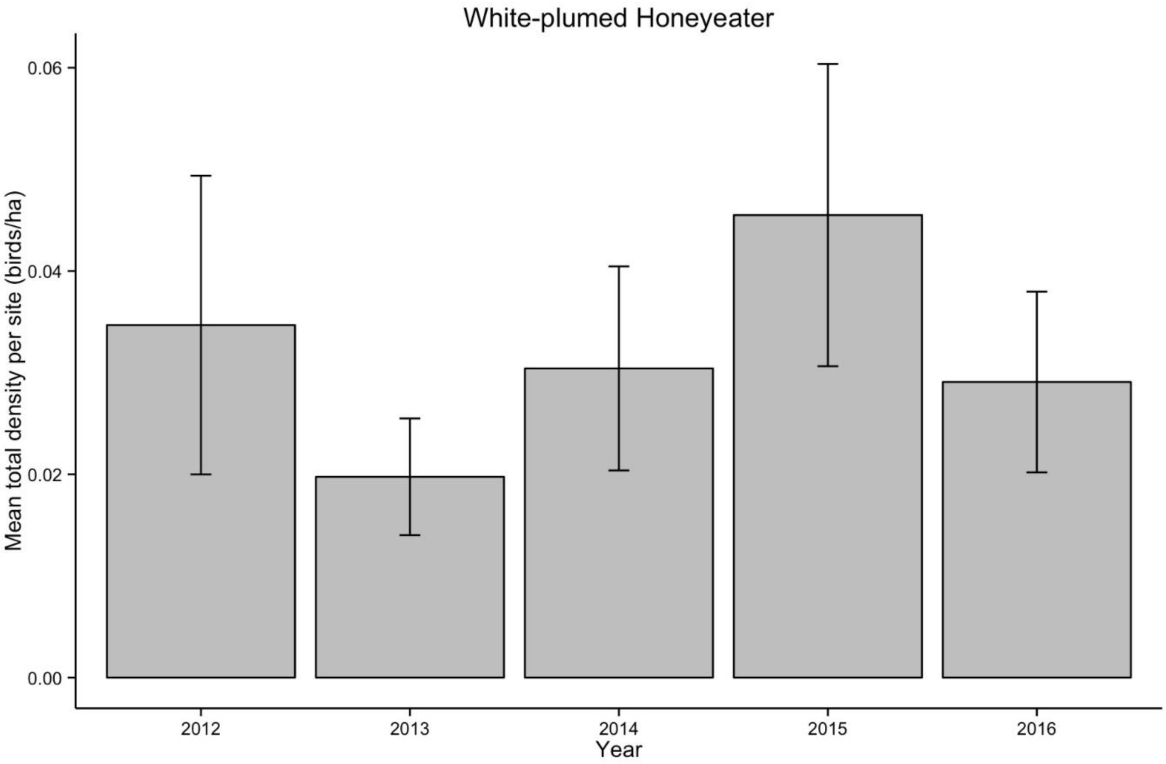

Wedge-tailed Eagle
Mean total density per site (birds/ha)
0.0020
0.0015
0.0010
0.0005
0.0000
2012
2013
2014
2015
2016
Year

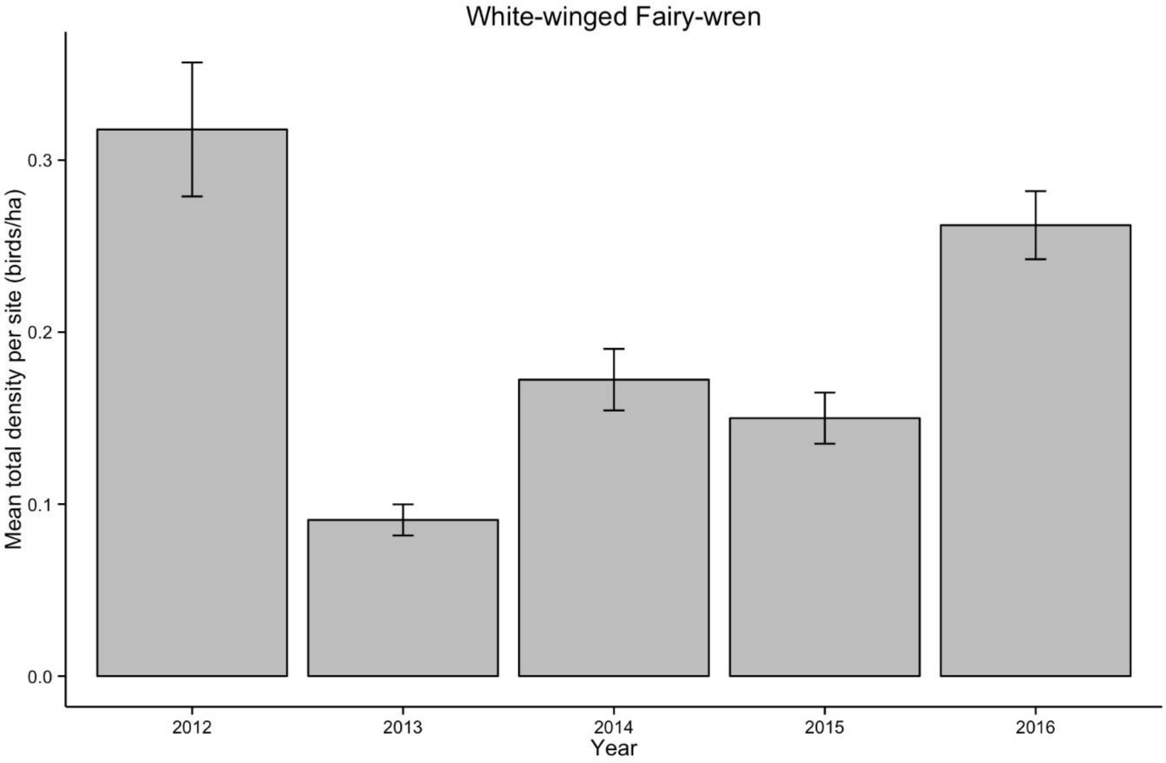

Whistling Kite
Mean total density per site (birds/ha)
0.003
0.002
0.001
0.000
2012
2013
2014
2015
2016
Year

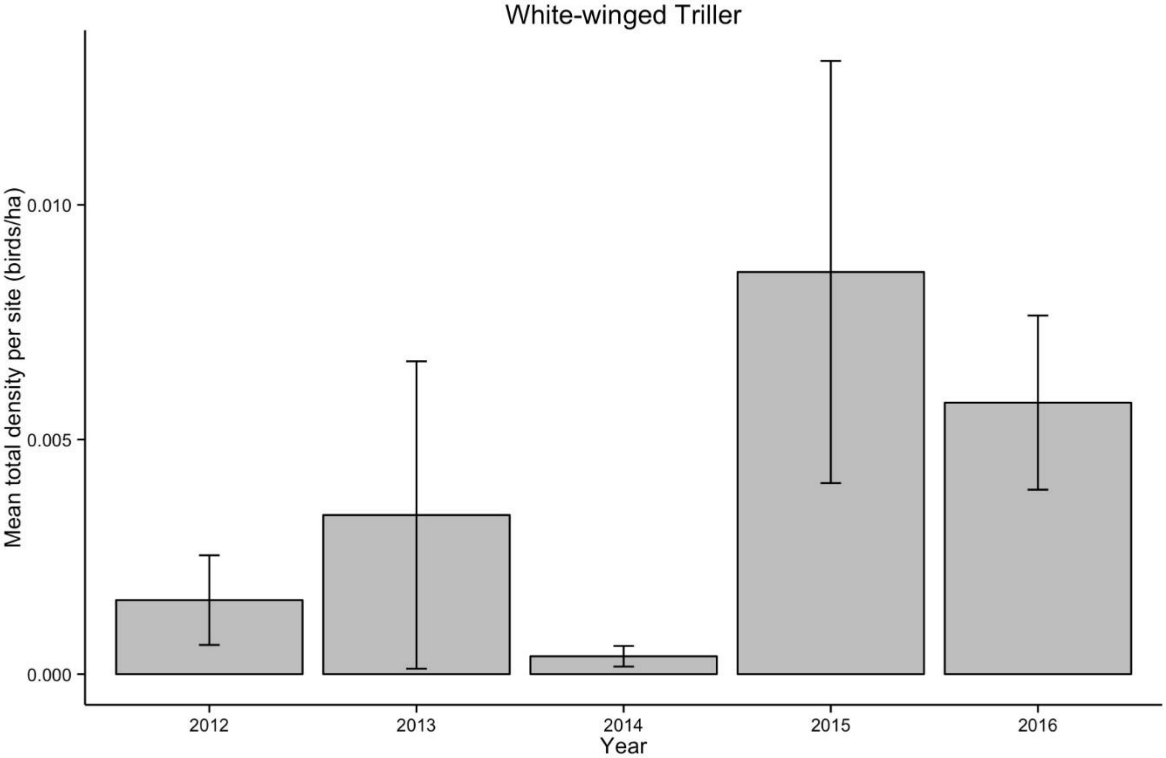

White-backed Swallow
Mean total density per site (birds/ha)
0.08
0.06
0.04
0.02
0.00
2012
2013
2014
2015
2016
Year

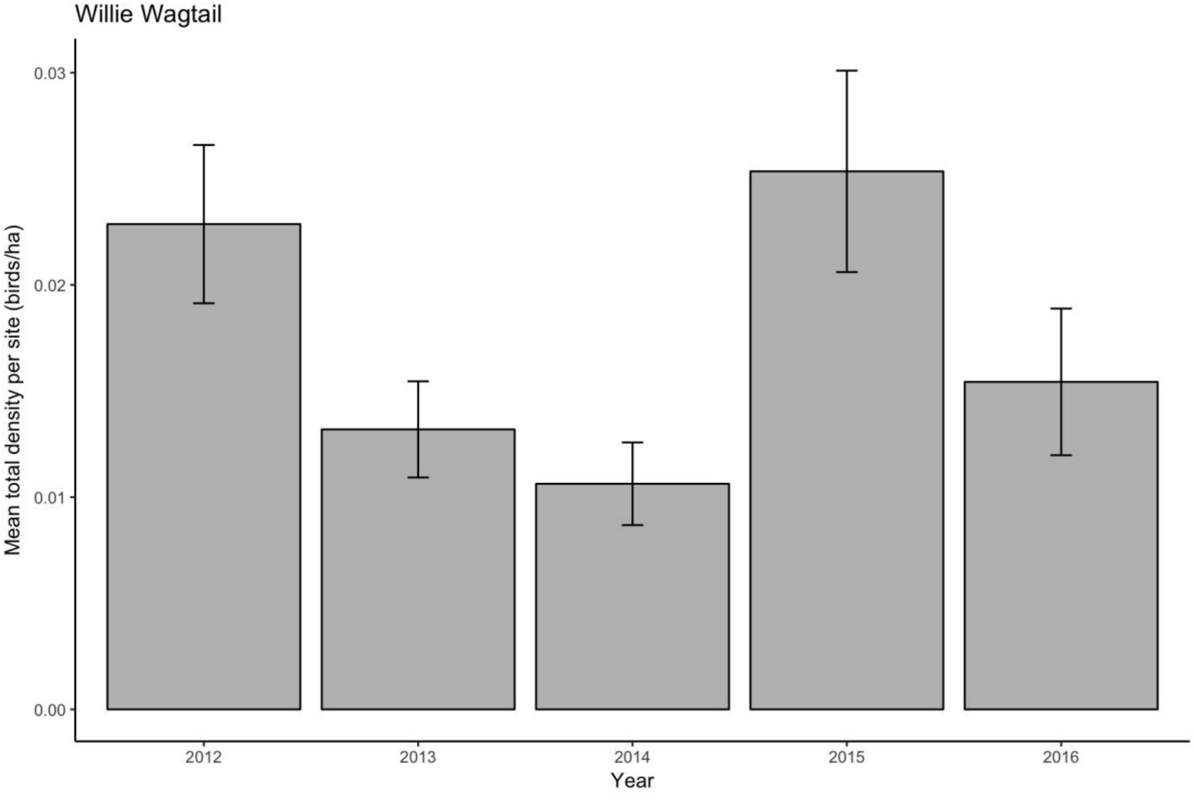

White-browed Woodswallow
Mean total density per site (birds/ha)
0.3
0.2
0.1
0.0
2012
2013
2014
2015
2016
Year


White-fronted Honeyeater
Mean total density per site (birds/ha)
0.015
0.010
0.005
0.000
2012
2013
2014
2015
2016
Year


White-plumed Honeyeater
Mean total density per site (birds/ha)
0.06
0.04
0.02
0.00
2012
2013
2014
2015
2016
Year


White-winged Fairy-wren
Mean total density per site (birds/ha)
0.3
0.2
0.1
0.0
2012
2013
2014
2015
2016
Year


White-winged Triller
Mean total density per site (birds/ha)
0.010
0.005
0.000
2012
2013
2014
2015
2016
Year


Willie Wagtail
Mean total density per site (birds/ha)
0.03
0.02
0.01
0.00
2012
2013
2014
2015
2016
Year

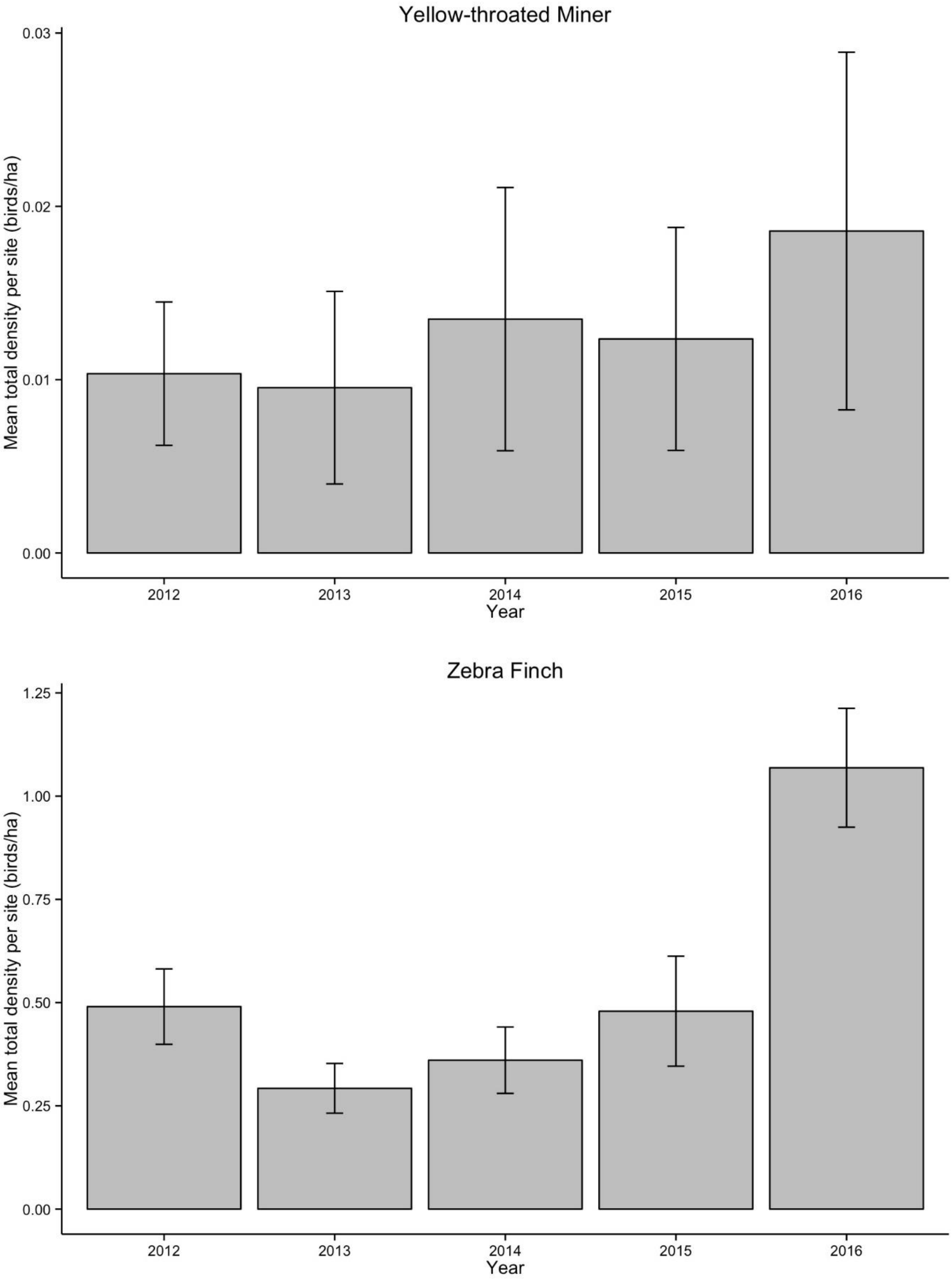


Figure S2. Mean annual densities for 64 arid bird species averaged across sites ± standard error across all survey years.

Table S1. Total operating costs calculated for each survey team and summed for total survey cost. Calculated for a 16-day period. *Costs assume use of own camping equipment (stoves, chairs, pots and cutlery, tents, sleeping bags) and survey equipment (radios, GPS units, compass, laser rangefinders, binoculars).

Item	*Cost per day ($AUD)*	*Total per team ($AUD)*
Consumables		
Food	44	700
Accommodation (hotels, camping fees)	19	300
Petrol (diesel)	38	600
Equipment (e.g. batteries, stove fuel, misc camping gear)	19	300
Survey booklets	9	150
Equipment hire		
4x4 vehicle	115	1840
Satellite phone	14	230
Emergency Position Indicating Radio Beacon (EPIRB)	8	120
Travel		
Airfare per person (domestic return flight (Adelaide) + extra bags)	430 each	1290
Total cost per team		5530
Total cost of survey		16590

Table S2. List of species codes used in Chapter 3.

Species	Species code
Australasian Pipit	AUPI
Australian Magpie	AUMA
Australian Raven	AURA
Banded Lapwing	BALA
Banded Whiteface	BAWH
Black Honeyeater	BLHO
Black Kite	BLKI
Black-faced Cuckoo-shrike	BFCS
Black-faced Woodswallow	BFWO
Black-shouldered Kite	BSKI
Brown Falcon	BRFA
Brown Songlark	BRSO
Budgerigar	BUDG
Chirruping Wedgebill	CHWE

Cinnamon Quail-thrush	CIQT
Cockatiel	COCK
Crested Bellbird	CRBE
Crested Pigeon	CRPI
Crimson Chat	CRCH
Diamond Dove	DIDO
Emu	EMU
Fairy Martin	FAMA
Flock Bronzewing	FLBR
Galah	GALA
Gibberbird	GIBB
Horsfield's Bronze-cuckoo	HOBC
Inland Dotterel	INDO
Little Button-quail	LIBQ
Little Corella	LICO
Little Crow	LICR
Little Eagle	LIEA
Magpie-lark	MALA
Masked Woodswallow	MAWO
Mistletoebird	MIST
Nankeen Kestrel	NANKE
Orange Chat	ORCH
Pallid Cuckoo	PACU
Pied Honeyeater	PIHO
Red-backed Kingfisher	RBKI
Red-browed Pardalote	RBPA
Red-capped Robin	RCRO
Rufous Fieldwren	RUFI
Rufous Songlark	RUSO
Rufous Whistler	RUWH
Singing Honeyeater	SIHO
Southern Whiteface	SOWH
Spiny-cheeked Honeyeater	SCHO
Spotted Harrier	SPHA
Striated Pardalote	STPA

Stubble Quail	STQU
Thick-billed Grasswren	TBGR
Tree Martin	TRMA
Variegated Fairy-wren	VAFW
Wedge-tailed Eagle	WTEA
Whistling Kite	WHKI
White-backed Swallow	WBSW
White-browed Woodswallow	WBWO
White-fronted Honeyeater	WFHO
White-plumed Honeyeater	WPHO
White-winged Fairy-wren	WWFW
White-winged Triller	WWTR
Willie Wagtail	WIWA
Yellow-throated Miner	YTMI
Zebra Finch	ZEFI