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Nest Ecology of a Threatened Woodland Avifauna

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Willie Wagtail *Rhipidura leucophrys* nestlings just prior to fledging

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ABSTRACT

The vast clearing of temperate eucalypt woodland and forest for agriculture in Australia has led to the concomitant decline of its biota. This thesis investigated the nest ecology of this disappearing landscape's threatened avifauna to obtain baseline/life-history data to support the avifauna's conservation and inform evolutionary theory. The nesting ecology of this avifauna was reviewed both qualitatively and quantitatively. Field data were collected from a large 27,000 ha woodland with ecologically functional numbers of birds and where invasive species were controlled. This woodland, Dryandra, is located within a region (in south-western Australia) where up to 97% of the native woodland vegetation has been removed. Despite this Dryandra's avifauna has increased in abundance since the 1950s. An Australia-wide review and a meta-analyses established the identity of 94 nests predators in temperate forest and woodland and identified important metrics and trends, such as: mesopredators being found to iteratively replace one another as larger species were removed; artificial nests were concluded, at best, to be generators of hypotheses to be tested at natural nests; edge-effects were equivocal and thus fragment size, structure and faunal assemblage set in a more complex paradigm were considered more appropriate in explaining differences in nest predation; and, the various types of evidence used to identify nest predators were considered with cameras deemed the most functional and direct observations the most informative. A highly significant and positive correlation was detected between predator and prey masses, showing the mass of nest predators varies between a quarter and a fifth of their prey's mass (based on adult sizes). Exposed cup and dome nests were reported to be depredated more frequently than hollow, ground and burrow nests. In field trials at Dryandra: rare marsupials depredated eggs at artificial ground nests. Since artificial nests only generate hypotheses these results were validated by literature searches, which confirmed that the marsupials had carnivorous components to their diets. The effect 18 storms on the assemblage of birds was assessed: wind was found to be significantly important in nest failure, while nest position (within trees), storm duration and the amount of precipitation were not significant. Tree-nesting birds were recorded nesting more frequently in the northern hemispheres of trees that provided them with significantly greater foliage cover, which led to significantly greater nesting success. These results supported the hypothesis of a group response of nest concealment. Additionally, the threatened assemblage of woodland birds were detected preferentially nesting in the low-lying contours of the landscape, on the most productive soils in *Eucalyptus wandoo* woodland. Overall, the results obtained from this threatened assemblage of birds are proposed as *authentic natural results* derived from within the context of an intact natural community—such results are representative of natural populations prior to European disturbances. Thus, these results are deemed useful for informing strategies for rehabilitation, revegetation, reintroductions and other conservation efforts in temperate Australian forest and woodland landscapes.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications included in this thesis

Fulton, G. R. 2019. Meta-analyses of nest predation in temperate Australian forests and woodlands. *Austral Ecology* **44**: 389-396.

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Fulton, G. R. 2018. Pied Currawong *Strepera graculina* nesting in an underground carpark. *Australian Field Ornithology* **35**: 91-92.

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Submitted manuscripts included in this thesis

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Other publications during candidature

The following publications do not form a part of the thesis, though they were completed during the candidature and carried the address of The University of Queensland.

Peer-reviewed Papers

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Fulton, G. R. 2019. Additions to prey taken by Wedge-tailed Eagles *Aquila audax* after release of Rabbit *Oryctolagus cuniculus* haemorrhagic disease (Rabbit Calicivirus) in 1996. *Australian Field Ornithology* **36**: 11-12

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Fulton, G. R. 2017. The View from Lazy Point: a natural year in an unnatural world. Picador, New York. *In Pacific Conservation Biology* **23** (1): 110-111.

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Contributions by others to the thesis

There were no significant contribution by others. General comments from reviewers of the published peer-reviewed papers (Chapters 1, 2 and 3 in this thesis) have been incorporated, although none were considered significant contributions. Prof. Mike Calver, of Murdoch University, gave general advice on statistics and is mentioned appropriately in the acknowledgement sections of the pertinent chapters. Prof. Hugh Possingham reviewed and gave general advice on the writing of Chapters 5 and 6. Dr Craig Macfarlane, of CSIRO Perth, gave guidance on on the materials and methods associated with digital cover photography and supplied software for the analysis of photographic data. Dr Alison Specht explained the details of crown and canopy growth in *Eucalyptus* spp. Jutta Beher drew the location maps used in this thesis and associated publications. Cheung Yee Wan adapted the wind rose diagram used in Chapter 7.

Statement of parts of the thesis submitted to qualify for the award of another degree

None.

Research Involving Human or Animal Subjects

No animal or human subjects were involved in research during my candidacy at The University of Queensland. Research that involved the monitoring of nesting birds was carried out prior to my candidacy. This research was given ethical approval from Edith Cowan University (Appendices X_1 and X_2).

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Keywords

Dryandra, *Eucalyptus* woodland, temperate woodland, Australian woodland birds, nest ecology, nest predation, landscape ecology, nest concealment, wind, intact natural community

Australian and New Zealand Standard Research Classifications (ANZSRC)

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FoR code: 0602 Ecology 33%
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FoR code: 0608 Zoology 33%

Dedication

This thesis is dedicated to those that invigorated it and my *girls* who supported it.

To my wife Cheung Yee Wan (張議尹) and my daughter Grace Rose Fulton / Cheung Hiu Tin (張曉天) —I give this dedication because you deserve more than an acknowledgement, without you there would be no thesis.

To Henry David Thoreau who went before me.

"'An abode without birds is like a meat without seasoning.' Such was not my abode, for I found myself neighbour to the birds; not by having imprisoned one, but having caged myself near them. ...nearer to those wilder and more thrilling songsters of the forest which never, or rarely, serenade a villager..." Henry David Thoreau (1817-1862)

Thoreau, H. D. 1854. *Walden; or, Life in the Woods*. Ticknor and Fields, Boston.

CONTENTS

CHAPTERS

GENERAL INTRODUCTION

GENERAL BACKGROUND

Opening Statement

The vast clearing and subsequent degradation of Australian forests and woodlands have resulted in extensive bird declines—declines that continue. In such an altered environment it is important to understand the life history strategies employed by birds to halt their declines and facilitate their recoveries. This thesis investigates aspects of avian nest ecology in temperate eucalypt woodlands. It aims to add to the life history data on the nest ecology of woodland birds: Firstly, by reviewing the literature both qualitatively and quantitatively (Chapters 1 and 2). Secondly, through the collection of extensive field data, collected by spending three unbroken field seasons living in the woodland and daily observing the nesting birds. Thirdly, interpreting and analysing the data into a thesis to build an ecological picture of an ecologically functional and intact assemblage of threatened woodland birds.

The reviews explore the main themes in nest predation and develop hypotheses for further quantitative analysis. The identity of nest predators were obtained and their roles quantified both collectively and singularly. Vulnerable prey were determined by species and groupings. A predator to prey mass ratio was identified—the first time this has been done with nesting birds. The field data were collected over three complete breeding seasons from a single and intact assemblage of woodland birds. Thus, enabling the quantification of aspects of nesting success that have not been previously studied. The impacts of 18 consecutive storms were recorded against nearly 500 nests. Nest placement was recorded for the assemblage within trees and in the landscape. An artificial nest experiment was run to determine predators of artificial ground nests with rare marsupials detected as nest predators. The thesis is closed with a chapter designed to promote debate, which synthesises some of the thetic findings with other published work I have undertaken at Dryandra. This is intended to be published as an opinion piece with hypotheses that draw a long bow and will undoubtedly attract criticism.

Overall, the intact assemblage of woodland birds studied was in ecologically functional numbers and present in high quality old-growth woodland, where foxes and other invasive animals have been controlled for forty years. It is Dryandra Nation Park, in south-western Australia, a 27,000 ha reserve.

Vast Landscape Change and Bird Decline

In Australia, temperate eucalypt woodlands were once widespread in what are now vast agricultural expanses (Prober *et al.* 2002). For the last forty years, numbers of woodland birds have been consistently reported in serious decline, throughout Australia, all associated with the clearing and ongoing degradation of their habitat (Ford and Howe 1980; Garnett 1993; Catterall *et al*. 1997; Reid 1999; Ford *et al.* 2001; Fulton and Majer 2006; Watson 2011; Lindenmayer *et al.* 2018; Ward *et al*. 2019). The vast removal of the woodland landscape accelerated following World War II, yet despite a deceleration of broadscale clearing, birds and other biota have continued to decline (Ford *et al.* 2001). Since 2000 woodland birds have decreased on average by 53% (TSX 2018). (The TSX 2018 tracks changes in global vertebrate biodiversity through time and shows the average change in populations compared to a base year, in this case 2000.) Even in large reserves bird declines have been forecast to continue through a diminution of food resources under climate change (Mac Nally *et al.* 2009).

This vast removal and degradation of the landscape, resulting in the widespread losses of birds (and other biota), has not occurred uniformly—spatially or temporally. The woodlands on the most productive soils, in the low-lying areas of the landscape, were cleared first and most thoroughly (Prober *et al.* 2002), despite harbouring the greatest abundance and species richness of birds (Bentley and Catterall 1997; Catterall *et al.* 1997). The surviving forested fragments are generally on poorer soils considered unsuitable for agriculture, particularly on rocky slopes and ridge-tops that are limited in size (Ford et al. 2001; Watson 2011). They continue to be degraded by: the grazing from livestock; changed fire regimes; the removal of woody debris; and invasion by exotic weeds and mesopredators such as cats *Felis catus* and foxes *Vulpes vulpes* (Mac Nally *et al.* 2001; Watson 2011; Taylor *et al.* 2012; Taylor *et al.* 2013; Fulton 2018 [Chpt. 1]). In such an inhospitable environment it is important to understand the life history strategies employed by birds in order to halt their declines and facilitate their recoveries (Watson 2011; Remeš *et al.* 2012a; Fulton 2018 [Chpt. 1]; Fulton 2019 [Chpt. 2]).

In Australian woodlands, some birds have declined more than others—one species, the Paradise Parrot *Psephotus pulcherrimus*, became extinct due to the habitat loss described above (Fulton 1998; Jerrard 2008). Many other species and sub-species have become locally extinct throughout the cleared woodlands, across the Australian continent (Garnett *et al.* 2011). Overall the entire assemblage of woodland birds is listed as a “Threatened Ecological Community” under the Environment Protection and Biodiversity Conservation (EPBC) Act 1999. (Fraser *et al*. 2017; Appendix 2). However, many of the bird losses have been identified as small insectivorous ground nesting and dwelling species (Reid 1999; Barrett *et al.* 2007; Watson 2011). Within the paradigm of woodland bird decline a recurring pattern has emerged with the same birds and bird groups being iteratively reported across the continent as threatened or extirpated. For example, Catterall *et al.* (1998) identified a strong correspondence between woodland bird declines in the lowlands of south-eastern Queensland to other studies of regional decline; they highlighted whistlers, pardalotes, thornbills, gerygones (acanthizids), robins, and small honeyeaters in greatest decline. Reid (1999) reported a predominance of insectivores and ground feeders and emphasised whistlers, acanthizids, robins and babblers having most declined, citing the selective clearance of vegetation types on fertile soils in the sheep and wheatbelt of NSW as the ultimate cause of decline. Across the continent in the wheatbelt of south-western Australia whistlers, robins, acanthizids, flycatchers, quail-thrush, tree-creepers and honeyeaters were reported most affected (Saunders and Curry 1990; Saunders and Ingram 1995). The same groups of birds appear in other temperate Australian woodlands, for example, the Fleurieu Peninsula/Mount Lofty Ranges, in South Australia (Szabo et al. 2011) and the northern plains of Victoria (Bennett and Ford 1997). Despite the continental story of decline one small 27,000 ha patch of woodland, Dryandra, has survived clearing—yet ironically it sits in a vast area of wheat that has been cleared of 97% of its highest quality woodland. Dryandra has been further protected with invasive animals culled since the since the 1980s and retains a full assemblage of woodland birds in an intact community of other biota (Fulton 2013). It sits in direct contrast to other woodlands and provides the opportunity to study woodland birds in ecologically functional numbers—as such is the focus of fieldwork in this thesis.

Low Recruitment and Decline

The loss of birds, in itself, is not a singular explanation for the ongoing decline of woodland birds. It is perhaps the lack of recruitment of new adults into avian populations that might best explain woodland bird declines and extinctions. Adult recruitment must equal or exceed the death rate for a species to avoid declining to extinction (Darwin 1859; Lack 1954). The loss of suitable habitat required by birds to recruit enough adults may be more pertinent to understanding declines than simply quantifying the loss of birds by hectares. Moreover, the processes involved in avian species decline do not exist in isolation—they interact in the decline of birds having a cumulative effect (Fulton 2018 [Chpt. 1]). In order to test hypotheses related woodland bird declines and to reverse them, more detailed knowledge is required on their life histories (Remeš *et al.* 2012a; Fulton 2018 [Chpt. 1]; Fulton 2019 [Chpt. 2]). The nest, or more specifically, its contents is the first and perhaps most complex step in the recruitment of new adults. The second is the survival of fledglings to adulthood—yet without a successful nest there can be no fledglings.

Nest Ecology

The aspects, themes or components of the reproduction by birds using nests may be studied and reported under the umbrella term of nest ecology. The two main themes that dominate the life history studies of nest ecology in birds are food availability (Lack 1954; Martin 1992a; 1992b Luck 2003; Zanette *et al.* 2003) and nest predation (Lack 1954; Martin 1995; Remeš *et al.* 2012a; Fulton 2018

[Chpt. 1]; Fulton 2019 [Chpt. 2]). Additional factors such as weather and disease may also be implicated, but most often to a lesser extent (Fulton 2018 [Chpt. 1]). The opportunity to gather data on the impact variables including climatic variables must be followed if available. Overall, studies of nesting birds are generally interested in comparing nest success against ecological factors in order to quantify their effect on the nesting success (Fulton 2019 [Chpt. 2]). Understanding the processes operating within nest ecology can inform: evolutionary theory, and applied and pure ecology. Understanding nest ecology also informs conservation efforts—particularly in knowing what to measure and manage (Remeš *et al.* 2012a).

The Need to Synthesise the Current Literature and the Call for Nest Predator Identities

Overall, globally and in Australia, nest predation is unquestionably the major cause of nest failure in birds (Ricklefs 1969; Martin 1992a). Yet, reviews and meta-analyses of nest predation, in Australia, are largely missing from the literature, despite the ubiquity of the event and despite the profusion of reports and its prevalence in single species studies (Remeš *et al.* 2012a; Fulton 2018 [Chpt. 1]; Fulton 2019 [Chpt. 2]). Most studies of nest predation have been conducted on birds from North America (e.g., Ricklefs 1969). Yet, much less is known for Australian birds with few empirical studies of natural nests, particularly at the assemblage level (Remeš *et al.* 2012a). One review found that nest predation rates were variable by region and had increased significantly over the 40 years prior to its publication, although the reasons remain speculative. In general, nest predation studies have called for greater knowledge on the identity of nest predators and processes, particularly using a broad array of species and a variety of nest types (Major and Gowing 1994; Fulton and Ford 2001; Remeš *et al.* 2012a; 2012b; Fulton 2018 [Chpt. 1]; Fulton 2019 [Chpt. 2]).

Beyond learning nest predator identities and understanding the roles that they play, more knowledge is required on prey responses (Fulton 2018 [Chpt. 1]). For example, the heterogeneity of nest types and their varied placement highlights a widely recognised response to nest predation (Collias and Collias 1984). However, nest placement also interacts with food availability and landscape productivity (Fulton and Possingham [Chpt. 5]). One specific yet widely hypothesised anti-predator responses involves concealing the nest (Martin and Roper 1988; Filliater *et al.* 1994; Fulton [Chpt. 6]). A subjective measure of estimating the degree of concealment at nests involves estimating how much of a nest is visible to the observer’s eye (Lambert and Kleindorfer 2006; Colombelli-Négrel and Kleindorfer 2009). Yet, such visual assessment remains a subjective approach, dependent on the observer. Digital photography is a novel approach that objectively quantifies foliage density by photographing different parts of the tree and subsequently analysing the pixels (Macfarlane *et al.*

2007; Macfarlane 2011). Future studies using this technique, which can be done with a home SLR camera, may prove to be a more accurate and consistent approach (Fulton and Possingham [Chpt. 6). Another approach to understand how birds place or position their nests involves how they are placed in the landscape. Two studies in south east Queensland identified birds of lowland forests in greatest decline due to their position in the landscape, which is more likely to be cleared for agriculture (Bentley and Catterall 1997; Catterall et al. 1998). Future studies continued to highlight the same suit of insectivorous woodland birds in decline across agricultural areas of Australia (Reid 1999; Ford *et al.* 2001; Watson 2011; Lindenmayer *et al.* 2018; Ward *et al.* 2019; Fulton and Possingham [Chpt 6]). These reports identified the low-lying sections of the landscapes with the most productive soils were preferentially used for agriculture as opposed to the less fertile ridge-tops. Martin (1987) linked food and landscape productivity to reproductive success. He highlighted that food was limited spatially with birds having larger clutch sizes and greater reproductive success in more productive habitats. Therefore, habitats that provide more abundant and reliable food for birds, during their breeding season, would likely be reflected as the choice of breeding habitat (Martin 1992b). Dryandra encompasses a mosaic of habitats including large areas of the more productive valley soils (McArthur *et al.* 1977; DEC 2011) and it shelters an almost intact avifauna (Fulton 2013). As such it provides an opportunity to examine how birds locate their nests in a woodland landscape when many different habitats were available, including the more productive low-lying areas with their higher quality soils.

Overall Aims

The two reviews (Chapters 1 and 2) aimed to synthesise the current knowledge and identify new ideas that might be broadly conferred to nesting birds. Field studies at Dryandra were targeted at monitoring nests to identify predators and prey responses, particularly with regard to nest placement in the landscape and in the tree. The overall intent of the fieldwork component was to quantify ecological factors in a pristine and old-growth landscape context. Moreover, to do this where the species in the avian assemblage remain in ecologically functional numbers. Note: specific aims are presented in each chapter.

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1. REVIEW OF NEST PREDATION I: OVERVIEW

AVIAN NEST PREDATION IN AUSTRALIAN TEMPERATE FOREST AND WOODLAND: A REVIEW

ABSTRACT

Many forest and woodland birds are threatened by landscape modifications and predation, particularly nest predation. Nest predation affects a critical stage in avian life histories, which impacts the recruitment of new generations of adult birds. This review discusses the main issues in nest predation research in Australia: mesopredators, the use of artificial nests, ‘edge-effects’, the identification and role of nest predators and the responses of their prey. One conservation strategy is to selectively remove introduced mesopredators, but mesopredators iteratively replace one another, so the net benefit may be negligible. Authors have questioned the utility of artificial nests: they often provide results that vary from natural nests, thus I propose they are best seen as generators of hypotheses to be tested at natural nests. Many studies investigated nest success based on the distance to the edge of the forest or woodland with equivocal results. Yet, fragment size, structure and faunal assemblage set in a more complex paradigm, may better explain the presence of absence of effects at edges. There are various types of evidence used to identify nest predators. I argue that cameras are the most functional and direct observations are the most informative. A large number and variety of nest predators are reported yet reviews of nest predation call for more information on the identity and roles of nest predators, particularly on those that add predation pressure beyond what the prey might be able to sustain. The impact of nest characteristics: type, height, vegetation layer, concealment and re-nesting were found to be equivocal in relation to nest predation and in need of focused research on phylogenetic groups and guilds present within assemblages and within the context of assemblages. A handful of research studies have looked at the possible conservation actions of culling nest-predators and placing cages around threatened birds. More such studies are needed because they provide direct information about practical interventions. Research within assemblages are required to identify and elucidate the roles of nest predators and prey responses and to generate broad and useful theories, which may better inform conservation models.

INTRODUCTION

Forest and woodland bird decline

Despite a downturn in clearing in Australia, declines in many species of birds continue due to ongoing habitat loss and degradation of the remaining remnants (Kitchener *et al.* 1982; Saunders *et al.* 1991; Ford *et al.* 2001; Cogger *et al.* 2003 Fulton and Majer 2006; Reside *et al*. 2017). Many of these losses have been identified as small insectivorous and ground dwelling species (Reid 1999; Barrett *et al.* 2007; Watson 2011). Various patterns and processes are recognised in the decline of Australia's woodland birds, which are all associated with habitat loss and degradation, including: the disproportionate loss of forests and woodlands on better quality soils, particularly around watercourses in the low lying areas of the landscape (Bentley and Catterall 1997; Ludwig *et al.* 1999; Mac Nally *et al.* 2000; Martin *et al.* 2006); the inability of some species to disperse through a fragmented landscape, which may reflect the loss of suitable habitat connectivity within the agricultural/remnant matrix (Brooker *et al.* 1999; Fischer and Lindenmayer 2007; Ford 2012); the small size of remnants (Mac Nally and Horrocks 2002) or aggressive exclusion by Noisy Miners *Manorina melanocephala* (Dow 1977; Mac Nally *et al.* 2012; Maron *et al.* 2013) or miners (*Manorina* spp.) in association with larger birds such as Grey Butcherbirds *Cracticus torquatus* and *C. nigrogularis* (Fulton 2004, 2008; Maron 2009).

The processes involved in avian species decline do not exist in isolation, they interact in the decline of birds (Ford *et al.* 2001). The remnants that remain in the cleared landscapes are typically found on the poorer and less productive soils (Watson 2011). They are then subject to grazing by livestock, changed fire regimes and further degraded by the removal of woody debris and invasion by exotic weeds and predators, such as cats *Felis catus* and foxes *Vulpes vulpes* (Mac Nally *et al.* 2001; Watson 2011; Taylor *et al.* 2012; Taylor *et al.* 2013). Long life-spans may hide local extinctions, yet over generations the birds will die out without adequate replacement and an extinction debt will be paid (Tilman *et al.* 1994; Ford *et al*. 2009). Without dispersal acting to replace the taxa declining through poor recruitment local extinction events may occur (Ford 2012), which may eventually lead to the extinction of taxa (Fulton 2017).

Nests

Most avian reproduction involves nesting, which is a specific and critical stage in the recruitment of new adults into avian populations. Adult recruitment must equal or exceed the death rate for a species to avoid declining to extinction. A critical factor in low recruitment rates is the predation of birds' eggs and nestlings and the destruction of their nests. Overall, globally and in Australia, nest predation is unquestionably the major cause of nest failure in birds (Ricklefs 1969; Martin 1992a; Ford *et al.* 2001; Remeš *et al.* 2012).

The heterogeneity of nest types and their placement confers ecological advantages and disadvantages in regard to their: susceptibility to predation, access to food and exposure to weather. Birds also compete for nest sites and nest material (Collias and Collias 1984; Collias 1997). The diversity of eggs and young provide a rich source of food for predators (Lack 1954) and the nest itself provides easy access to nest building materials, e.gs, fine grasses and proteinaceous spider silk (Ley *et al.* 1997; Fulton 2006a).

Apart from nest predation, the other major factor leading to the success or failure of a nest is food availability (Lack 1954; Martin 1992a; 1992b Luck 2003; Zanette *et al.* 2003). Additional factors such as storms and disease have also been implicated in the mortality of eggs and nestlings; however, these facets of nesting ecology will not be explicitly reviewed here. This review focuses on avian nest predation in temperate Australian forests and woodlands, because these habitats share an avifauna and predator assemblage, which are both in part different to those reported in tropical forest (Laurance and Grant 1994; Noske et al. 2013). It is organised into large well studied areas of research that hinge around nest predation including: mesopredator release; edge-effect theories, which interact with artificial nest experiments; and the role and identity of predators, focused on the evidence involved in obtaining their identity. In addition, the major findings of the limited yet illuminating reviews of nest predation are presented, followed with a consideration of anti-predator prey responses. Finally comments are given on the way forward with conservation and future research.

METHODS

This review was compiled from searches of the data base Google Scholar for key words including: nest success, nest predation and rates (re nests), nest predators, reproductive success, breeding biology, nest (site, concealment, height, experiments, success, mortality), life history, nest abandonment/desertion, diet, re-nesting. Only peer-reviewed papers, in English, were included with the cut-off date being when the manuscript was accepted for publication in 2018. Careful reference harvesting was used to complement these searches when reading each paper by following citations in those papers (including footnotes) and the papers they led to and so on until all citation leads had been exhausted. In some rare cases additional information was sourced from authors. When required leading scholars were identified and their papers searched for the required information. For example, Thomas Martin and associates have published extensively on the life history and evolutionary theory around nest ecology. These searches led to 290 papers, from which 161 are used here. Papers that were excluded typically presented data only on (or discussed birds) not found in forest or woodlands.

The sources on mesopredators grew from initial and continued reading, although it stayed predominately based in the theory of mesopredator release and was largely focused on mammalian mesopredators. Continued reading then focused on the next mesopredator released as larger predators were controlled.

Names and taxonomic order follow: for birds, Christidis and Boles (2008); for mammals, Jackson and Groves (2015); for frogs and reptiles Cogger (2014); and for ants Andersen (2002).

MESOPREDATORS, ARTIFICIAL NESTS AND EDGE-EFFECTS

Mesopredators as nest predators and predators of ground dwelling birds

A prominent theory for the general decline of birds globally is the mesopredator release theory. The process is typically characterised as releasing medium-sized predators (mesopredators) from the predation of larger predators. The subsequently increased numbers of mesopredators result in a greater mortality of smaller prey (Soulé *et al.* 1988; Crooks and Soulé 1999). In Australia, the introduction of foxes and cats, along with the reduction in numbers of the Dingo *Canis lupus dingo* is thought to have adversely impacted a range of smaller mammals (Burbidge and McKenzie 1989; Glen *et al.* 2007). However, mesopredator release may also be driven by habitat modification. Notably, currawongs *Strepera* spp., butcherbirds and the Australian Magpie *Cracticus* spp. and corvids *Corvus* spp. are thought to have been released (increased range and abundance) by the clearing of forest and woodlands, and its replacement with roads, pasture and urban areas with berry-bearing plants (Rowley 1973a; Bass 1995; Fulton *et al*. 2008).

The greatest impact of nest predation associated with mesopredator release is assumed for ground dwelling birds, which have been reported in greater decline than other ecological guilds (Reid 1999; Ford *et al*. 2001; Kennedy 2003; Antos and Bennett 2005). In particular, Reid (1999) identified 20 bird species in greatest decline within the sheep and wheat belt of New South Wales, all of which were characterised as ground and/or low shrub feeders and dwellers; he also pointed out that 18 of the 20 were passerine and 15 of the 20 were insectivores. But, such results may not simply be an artefact of quantifying predation in fragmented and degraded landscapes. Ford *et al.* (2001) compared mean nest-success rates in fragmented and continuous landscapes and found no statistically significant difference. Mesopredators are present in both landscapes and presumably affect birds in both landscapes in similar ways, regardless of the releasing process.

Investigations in areas where mesopredators are controlled using baits targeting foxes (typically sodium fluoroacetate otherwise known as 1080 poison) show increased nesting success, adult recruitment and adult survival (Priddel and Wheeler 1997; Fulton 2013). For example, Priddel and Wheeler (1997) found reduced predation on Malleefowl *Leipoa ocellata* in baited areas compared to non-baited areas they also found that foxes were the most important predator of this species. At Dryandra, in south-western Australia, 1080 poisoning has been used to control foxes since the 1980s (Friend *et al.* 2001; Marlow *et al.* 2015a). Fulton (2013) in a study dating from 1953 found that many bird species known to be declining in Australian forests and woodland had increased at Dryandra, including ground nesters. Luck (2003) found that Rufous Treecreeper *Climacteris rufa*, a species that spends considerable time on the ground, although it nests in hollows, showed significantly higher nesting success and annual productivity at Dryandra compared to other woodlands in south-western Australia.

Cascading effects of mesopredation

However, the control of foxes using 1080 poison can lead to an increase in numbers of cats and thus increased predation by cats on adult and nestling birds (Algar and Smith 1998; Molsher *et al.* 1999; Risbey *et al.* 1999). This is thought to be the case at Dryandra. At Dryandra, Marlow and colleagues monitored a marsupial, the Woylie *Bettongia penicillata*, which increased 20 fold with fox control but later its population crashed due to increased predation by cats (Marlow *et al.* 2015a; 2015b). Cats are known to take adult and juvenile birds (Paton 1991; Dickman 1996; Dickman 2009). Risbey *et al.* (1999) found cats to be more important predators of adult birds than foxes, at Heirisson Prong, in Western Australia. But are cats predators of eggs and nestlings? The diet of cats on islands is generally considered restricted or limited, particularly if mice and rats are absent. In such cases, cats may take unusual prey such as burrowing and ground nesting seabirds (Dickman 1996). In general, hollow nesting birds appear to be less affected by cats, because cats are excluded by small hollow openings. However, one study conducted over 11 years on a species nesting in a larger hollow, Red-tailed Black Cockatoos *Calyptorhynchus banksii*, reported 6.5% of nesting attempts failed when cats climbed trees and preyed on the nest contents and/or brooding females; in one year killing 17% of the nestlings (Saunders 1991).

Contrastingly, Dickman (2009) argued that cats may ameliorate the impact of another mesopredator the Black Rat *Rattus rattus*. In urban forests around Sydney, he identified an inverse correlation between the numbers of nests attacked and the number of cats present. Further to this work Black Rats were removed from habitat patches in Sydney with lower predation rates recorded on artificial nests in the removal areas (Smith *et al.* 2016). Smith *et al.* (2016) also found that Black Rats posed an additive predation threat on nesting birds due to their ability to climb more efficiently than their native counterparts Bush Rat *R. fuscipes*. There is considerable evidence that the Black Rat preys on the nest contents of birds (Major 1991a; Major and Gowing 1994; Matthews *et al.* 1999; Piper and Catterall 2004; Rose and Banks 2007; McDonald *et al.* 2009; Banks and Hughes 2012); however, all of these studies used artificial nests (reviewed below) that lay olfactory cues for the Black Rat to follow. Studies using removal/exclusion experiments, such as the one conducted by Smith *et al.* (2016), are required to understand or confirm the impact of this mesopredator. Such studies must also consider using natural nests. The same applies to the House Mouse *Mus musculus* in that it is recognised as a nest predator predominately through the use of artificial nests (e.g., Zanette 2002; McDonald *et al.* 2009). Only one study reported House Mouse depredating eggs at a natural nest (Colombelli-Négrel *et al.* 2009). Yet, this small rodent may pose a greater threat than has been generally acknowledged. In island environments where mice are the only introduced mammal remaining they have been implicated in the demise of large and previously healthy seabird chicks (Angel *et al.* 2009). This hierarchy of mesopredators with one becoming dominant after a larger one is removed prompts me to visualise the process, symbolically, like Russian dolls (a series of wooden dolls that fit inside each other). I give it here as a mnemonic to encourage greater research into the cascading of mesopredators.

Artificial nests

Artificial nests became a popular method of identifying predators and assaying various hypotheses relating to nest ecology (Major and Kendal 1996). However, their results do not match well with natural nests, thus undermining their usefulness. The main criticisms include: they frequently attract different predators (Willebrand and Marcström 1988; Zanette 2002; Berry and Lill 2003; Thompson and Burhans 2004); they provide a scent-line, which allows a single predator to consume eggs at many nests leading to overstating that predator's importance (Major 1990; Burke *et al.* 2004); their greater density and synchrony did not match real populations (Reitsma 1992; Burke *et al.* 2004); they lack adult birds to defend them, or conversely, to attract predators (Skutch 1949, 1985; Major and Kendal 1996); and they often use easily obtainable Common Quail *Coturnix coturnix* eggs, which might be inappropriate surrogates because their size and thick shell excludes some small mammalian predators (Roper 1992; Fulton and Ford 2003). Moore and Robinson (2004) argued that external validity (the degree to which results of an experiment can be generalized outside experiment) between artificial and natural nests is poor and that artificial set-ups cannot be generalized to natural nests outside the experiment. Faaborg (2004, p 370) dismissed artificial nests on the bases given above; he proposed a resurgence in the monitoring of natural nests stating, “Put on some insect repellent and find real nests.”

But, what can be said in the defence of artificial nests? Villard and Pärt (2004) argued not to throw the baby out with the bathwater reiterating the need for artificial nests to be good mimics of and calibrated against the results from natural nests; they also highlight that monitoring of natural nests still retains biases. The most persuasive argument for artificial nests remains that which was forwarded at their peak of usage, they allow large sample sizes from fewer field hours and they support field manipulation and experimentation. The former argument of extracting large data sets from limited time budgets is, alas, negated by the above caveats with the results being unreliable. Such data must be validated by comparison to natural nests. Thus, why bother with the artificial nests at all? I suggest that they may be used to provide data that can generate hypotheses to be tested and validated at natural nests.

A tightening of the use of artificial nests procedures came after the publication of several influential critiques (e.gs Zanette 2002; Burke *et al.* 2004; Villard and Pärt 2004). Faaborg (2004) argued manuscripts using artificial nests must have compelling reasons for publication. Such procedures can be justified where a particular variable is manipulated and impact of the altered condition measured provided that researchers remain cognisant of the caveats and limitations of artificial nests. Some such compelling studies have involved the culling or exclusion of nest predators or have investigated their learning behaviour. Debus (2006a) combined artificial nests and culling to highlight Pied Currawongs *Strepera graculina* were important nest predators and validated this work with natural nests and exclusion cages. His work extended to monitoring fledglings and identifying emigration by Eastern Yellow Robin *Eopsaltria australis* into patches where it had become extinct. Cages and artificial nests were also used effectively to exclude avian predators and enhance nesting success at natural nests of an endangered population of White-fronted Chats *Epthianura albifrons* (Major *et al.* 2015). Price and Banks (2012) tested if the Black Rat might learn and respond to olfactory and density cues. The focus of this experiment was on what the predator could learn, prompting thought about how these rodents might search for natural nests.

Other novel experiments have been used in recent studies using artificial nests. In one, flowers were (or were not) added to artificial nests to copy their use in some natural nests by the Diamond Firetail *Stagonopleura guttata*. No positive or negative effect was detected and the attempted validation at natural nests was problematic due to extremely high predation (McGuire and Kleindorfer 2007). Noske *et al.* (2008) identified effects between habitat types with mangroves experiencing four times higher nest predation than paperbark and eucalypt forests. This study was partly validated by a prior study showing that mangrove-dwelling Gerygones experience a high rate of nest predation (Noske 2001). Without validation artificial nests results remain to be verified by natural nests, the result remains a hypothesis requiring testing. However, generating useful hypotheses for further testing is surely an important function in any branch of science.

'Edge-effect' or complex interactions

Many studies have used artificial nests to ask if an 'edge-effect' exists (Gardner 1988; Taylor and Ford 1998; Lindenmayer *et al.* 1999; Luck *et al.* 1999; Major *et al.* 1999; Matthews *et al.* 1999; Zanette and Jenkins 2000; Berry 2002a; Piper *et al.* 2002; Boulton and Clarke 2003; Fraser and Whitehead 2005; Piper and Catterall 2006a). The 'edge-effect' hypothesis questions if nest predation is greater at forest edges, particularly in smaller and linear fragments that have a greater edge to interior ratio. Such an effect has been detected in North America (Paton 1994), but has not been similarly found in Australia. Only three of the above mentioned studies detected significantly greater nest predation at edges or in smaller forest fragments (Luck *et al.* 1999; Major *et al.* 1999; Berry 2002a), while Gardner (1988) gave differing results based on nest type. Overall, despite some equivocal results, most studies (8 out of 12) failed to detect an 'edge-effect'. However, these results were for artificial nests. The results cannot be simply inferred to more complex natural nests, which provide different cues and parental defence.

Two of the abovementioned studies attempted confirmation or validation with natural nests; Zanette and Jenkins (2000) found no significant 'edge-effect' with either natural or artificial nests while Boulton and Clarke (2003) found that natural nests were significantly more successful closer to the edge. Yet (from above) Ford *et al.* (2001) reviewing mean rates of nest success, found no significant difference in nest predation between fragmented and continuous landscapes. Taking both artificial and natural nests results together it appears that it may not be possible to infer with great certainty any overall result. It may be that site specific factors are more important in understanding nest predation in forest fragments of varying shapes and sizes (Fulton 2006a). For example, Brooker and Brooker (2001) monitored 536 natural nests of the Blue-breasted Fairy-wren *Malurus pulcherrimus* in fragmented habitat in the Western Australian wheatbelt; they found greater nest success in smaller forest fragments and suggested that small or degraded fragments may be unsuitable for predators that require a large territory. Similarly, Noske (1998) found "exceptionally high" nesting success for Rufous-banded Honeyeater *Conopophila albogularis* in urban Darwin, due to a scarcity of nest predators. Rose and Banks (2007), on Sydney's North Head, had greater nest predation in bushland than an adjoining urban area from avian predators, while rat predation was even across both habitats.

In a parallel example, site specific factors influence the distribution of the Noisy Miner, in particular it has benefitted from habitat fragmentation and simplification. The Miner's presence changes the occupancy and therefore influences nest predation at some forest edges and roadside remnants within its range (Maron 2009; Maron *et al.* 2013; Robertson *et al.* 2014). Thus, factors relating to life history attributes of species and the type of habitat play important roles in nesting outcomes complicating the notion of a simple and widespread 'edge-effect'.

NEST PREDATOR IDENTITY AND IMPORTANCE

Nest predators vary from the well recognised specialists e.g., Pied Currawong (Major *et al.* 1996; Prawiradilaga 1996; Fulton and Ford 2001a) and Square-tailed Kite *Lophoictinia isura* (Barnes *et al.* 2001; Griffiths *et al.* 2002) to those recorded at single events e.g., Koala *Phascolarctos cinereus* (Fulton and Ford 2003) and Bilby *Macrotis lagotis* (Fulton 2006b). Across the middle of this range lay those that have been reported occasionally or infrequently and include Grey Shrike-thrush *Colluricincla harmonica* (Major *et al.* 1999; Fulton 2006a), Laughing Kookaburra *Dacelo novaeguineae* (Guppy *et al.* 2014) and Red Wattlebird *Anthochaera carunculata* (Fulton 2006a). However, the identity and precise role of most nest predators is poorly understood (Major and Gowing 1994; Remeš *et al.* 2012). For example, the Brushtail Possum *Trichosurus vulpecula*, in New Zealand, is regarded as an important predator of young birds and eggs (Brown *et al.* 1993; 1996; Moorhouse *et al.* 2003). Yet the role played by the Brushtail Possum in Australia is not clear. Because Australian birds have evolved alongside it, does this mean it cannot be an important nest predator in Australia?

This lack of knowledge pervades Australian ornithology with the identities of many nest predators remaining unknown (Fulton and Ford 2001a; Debus 2006a), as does their relative or absolute role in nesting ecology. Major and Gowing (1994) highlighted that our knowledge on relative roles was based on relative suspicion, which leads to doctrine without a heuristic base. A catch-cry of generalised 'large birds' particularly butcherbirds, ravens and kookaburras is given without evidence (e.gs Dorfman and Read 1996; Zanette 1997). In contrast, Eastern Spinebills *Acanthorhynchus tenuirostris*, with a mass of 11 g, have been photographed flicking eggs from the nests of other birds (Guppy *et al.* 2016). Clearly, further study is required to better understand the role and importance of nest predators, particularly to highlight predictors of nest predation and to identify populations, guilds and species that are vulnerable and that may benefit from conservation actions (Remeš *et al.* 2012). Despite the limited data on the identity of nest predators a burgeoning understanding of their identity and the role they play is emerging. Data on predator identity has been primarily derived from four lines of evidence: direct observations, which take large investments of time; experimentation with artificial nests (discussed above); analyses of stomach contents; and the deployment of cameras at natural nests.

Direct observations

The first direct observation is perhaps the most reliable and informative, yet it is the hardest to come by. In one observational study of Australian Magpie *Cracticus tibicen* the predation of nestlings was witnessed only once in 2000 hours (Brown and Veltman 1987). Direct observations also have the advantage of being able to capture peripheral information that is outside the field of view of cameras. Observers can monitor the animals as they move through the landscape, placing the 'predatory' event in context (Fulton 2006b; 2006c). For example a Rufous Treecreeper was observed destroying eggs at a Willie Wagtail *Rhipidura leucophrys* nest to take nesting material while showing no interest in the eggs as a source of food. The treecreeper was also the nearest neighbour to the wagtail with their nests positioned merely 20 m apart (Fulton 2006b). Researchers must acknowledge that to gain such valuable data they must place themselves in the field for long periods during the breeding season. More importantly such anecdotes must be published to advance our knowledge.

Artificial nests

The advent of artificial nests procedures led to a sharp increase in our knowledge of the identity of predators (e.gs Major *et al.* 1996; Major *et al.* 1999). Predators and patterns were identified. For example, avian predators were most frequently detected at arboreal nests of passerines while mammals and reptiles using olfactory cues were frequently detected closer to the ground (Paton 1994; Major and Kendal 1996). Prior to the use of cameras (see below) the identity of nest predators was ascertained by collecting teeth and beak imprints in clay eggs, a practice which failed to identify some predators including snakes (Thompson and Burhans 2004). However, one large trial involving 2000 members of the public, who returned 1803 artificial nests with useful data, found Pied Currawong was an important predator of arboreal nests in urban areas (Major *et al.* 1996). The same study included 69 direct observations of the currawong depredation (Major *et al.* 1996). This work, in identifying Pied Currawong as a significant nest predator is supported by external validation: such as exclusion experiments involving culling currawongs and the subsequent observations of artificial nests (Fulton and Ford 2001a; Debus 2006) and with culling of currawongs and placing cages around prey species (Debus 2006). Yet, while artificial nests have added to our knowledge they must be considered estimates or trials that generate hypotheses to be tested at natural nests (see above). However, one study eradicated Pied Currawongs from an island, an action which led to enhanced nesting success for Gould's Petrel *Pterodroma leucoptera* (Priddel and Carlile 1995).

Analyses of gut contents from nest predators

Confirmation of a nest predator may come from careful examination of its gut particularly the stomach contents. Fulton and Ford (2001b) identified avian bones from a nestling and a portion of intestine, which contained a moth proboscis in stomach analyses of Pied Currawongs; the latter highlighting that the currawong had ingested, at least, parts of an insectivore. In studies of snakes, Vestjens (1977a) identified nestlings of 18 different bird species consumed at one site by the Tiger Snake *Notechis scutatus* and Shine (1991) analysed colubrid snakes finding 11 eggs and 6 nestlings in a sample of more than 1400 museum specimens. Analyses of gut contents has advantages over pellet analyses, which can be biased by the overrepresentation of indigestible hard parts of some food types while lacking the unswallowed hard parts of others (e.g., vertebrate bones), and the absence of easily digestible items (e.g., caterpillars and vertebrate flesh) (Fulton and Ford 2001b). Conversely, gut analyses suffer from a general inability to accurately identify the prey species from parcels of flesh or fragments of eggshell (Fulton and Ford 2001b). Predator status may be confounded by the presence of eggshell, because many birds consume the eggshell from their own hatchlings (Guigueno and Sealy 2012).

Cameras

Camera monitoring is becoming more accessible as smaller, wireless and cheaper digital cameras are developed. Its biases are less pronounced than in artificial nest procedures, although nests with cameras may experience lower predation rates with some predators wary of novel stimuli at nests (Richardson *et al.* 2009). Less conspicuous cameras in terms of visual and olfactory cues may minimise aberrant behaviour (Richardson *et al.* 2009). In Australia, cameras have evolved from those using film at artificial nests (Berry 2002b; Fulton 2006a) and at natural nests (Major and Gowing 1994; Garnett *et al.* 1999) to more sophisticated digital cameras and video at natural nests (Guppy *et al.* 2014; Stojanovic *et al.* 2014; Guppy *et al.* 2017). Overall camera procedures have confirmed suspected nest predators and identified unsuspected predators (Fulton 2006a; Guppy *et al.* 2017). Colombelli-Négrel *et al.* (2009) extended the procedure by using visual and audio data, collected simultaneously, to identify predators and monitor prey responses. The audio component allowed some interpretation of events outside the camera's field of view.

PREVIOUS REVIEWS OF NEST PREDATION

One Australian review of the literature undertook long term and large scale analyses for trends in nest predation (Remeš *et al.* 2012). They found nest predation was lower in temperate regions than the tropics with the lowest rates in south-western Australia. Likewise, in an assemblage wide study of nest success (and failure) at Dryandra in south-western Australia, I found that nest predation was also comparatively low (unpublished data). Also, Debus (2006) found nest success lower and predation rates higher in eastern Australia when comparing his study on robins to that of Russell *et al.* (2004), which was done in south-western Australia. Possible reasons for this lower predation in the southwest may be the absence of the Pied Currawong, or that greater levels of clearing and fragmentation may have resulted in insufficient prey to support nest predators or other mesopredators. For example Grey Currawong *Strepera versicolor*, which is a nest predator (Fulton 2006a; Colombelli-Négrel and Kleindorfer 2009), has declined and is threatened in the region particularly disappearing from smaller forest fragments (Storr l99l).

Remeš *et al.* (2012), also found nest predation had increased over the four decades of their study (1970-2010). They forwarded two hypotheses for the latter: 1 – there may be more recent studies in fragmented landscapes that are impacted by anthropogenic disturbances or 2 – there have been population increases in important nest predators. Their first hypothesis is somewhat negated by the analysis in Ford *et al.* (2001), finding no difference between degraded and continuous habitats and that of Fahrig who found predominately positive responses to fragmentation, irrespective of habitat amount (Fahrig 2017a; Fahrig 2017b). Remeš' second hypothesis corresponds better, at least for the temperate regions, for the presence (and absence) of Pied Currawong. Remeš *et al.* (2012) also found that nest predation was greater in smaller birds suggesting that larger species may be able to defend their nests. Yet, this generalisation is unlikely to fit all species with some employing strategies to ameliorate nest predation including: group mobbing, agonistic behaviour and territorial exclusion in birds such as the Noisy Miner (e.g., Maron 2009) and group mobbing by unrelated species (Fulton 2007).

In 1994, Major and Gowing, asserted that what was "critically lacking" from studies of nest predation was the identity of predators that bring about increased or additive predation pressure. Since then they identified significant nest predation by the Pied Currawong. The Pied Currawong has expanded its range and population largely through the availability of exotic berry bearing trees and shrubs in urban areas (Bass 1989; 1990; 1995). With an expanded range and greater survival it has increased its predatory impact on other species (Fulton and Ford 2001a; Debus 2006a). Since then the Grey Shrike-thrush has been implicated as an important predator in degraded and linear habitats with Major *et al.* (1999) photographing it at more nests than other predatory species; and Fulton (2006a) finding it shares the same core territory with and depredates an assemblage of threatened woodland birds. However, in both cases, it is only presumed that its predation is a threat, because its prey species are in decline. A more compelling example is the introduced Sugar Glider in Tasmania. This species was recorded depredating eggs of Swift Parrot *Lathamus discolor* and in 83% of cases killed and consumed the adult female on the nest. Yet, on Bruny Island (an off-shore island to Tasmania), where the Sugar Glider is absent, no predation occurred (Stojanovic *et al.* 2014). Given the Sugar Glider is introduced to Tasmania then surely it must be applying additive nest predation pressure to Tasmanian birds.

One focus of nest predation strives to investigate principal predators such as the Pied Currawong (e.g. Fulton and Ford 2001a), yet the totality of *other* species may represent the largest proportion of all nest predation. Two studies that have focused on identifying nest predators of a forest or woodland avifaunal assemblage have both found a large proportion of novel predators were acting on the assemblage (Fulton 2006a; 2006b; 2006c; Guppy *et al.* 2014; 2016; 2017). Future research might quantify the comparative and collective importance of the principal and other nest predators to construct a more holistic understand of nest predation.

ANTI-PREDATOR PREY RESPONSES

Nest characteristics and nest predation

Many nest predation studies have been conducted on north temperate birds and various hypotheses have been tested (many from artificial nests) regarding the characteristics of bird nests (e.g., Ricklefs 1969). Comparisons of predation rates at different nest types have been made (e.gs Lack 1954; Nice 1957; Collias and Collias 1984; Skutch 1985; Martin *et al.* 2017), for which most agree that cavity nesters suffer lower predation. In Australia, Remeš *et al.* (2012) found no evidence that daily predation rates differed between nest types, a result supported globally (with exceptions) for enclosed and open nests. However, Remeš *et al.* (2012) combined cavity and enclosed nests (e.g., malurids) stating they sampled only three species sheltered by hard material. Future heuristic studies comparing nest types in Australia may find that cavity nesters experience lower predation rates than enclosed and cup nests as per northern temperate birds.

Other characteristics such as nest height, vegetation layer and nest concealment reportedly experience varying predation rates, which are often attributed to the predator type, typically mammal and reptile predation on low nests with avian predation on high nests (e.gs, Best and Stauffer 1980; Martin 1993a; Remeš 2005). Much less is known for Australian temperate birds with few focused empirical studies at natural nests. Three studies on these characteristics found concealment had either no effect (Ford 1999) or was significantly important (Lambert and Kleindorfer 2006; Colombelli-Négrel and Kleindorfer 2009). Ford (1999) found no relationship between nest height and success in an eight year study of two honeyeaters while two shorter studies found contrasting results regarding success and height: Boulton and Clarke (2003) had greater predation at low nests and Colombelli-Négrel and

Kleindorfer (2009) had greater predation at high nests. However, Boulton and Clarke (2003) did not find this for natural nests, only for artificial nests. In another artificial nest study less nest predation was detected in Mistletoe *Amyema* spp., compared to the surrounding eucalypt trees (Cooney and Watson 2008). Cooney *et al.* (2006) reviewed nesting in Mistletoes in Australia and postulated that they provide structural support and greater concealment for nests. Colombelli-Négrel and Kleindorfer (2009) focused on the interaction of concealment, nest height and the type of predator. Using artificial and natural nests they found well concealed nests experienced lower predation from visual predators than exposed nests; however, nest predation by animals using olfactory cues were not influenced by height or concealment. This study focused on a single prey species, yet further research is needed across assemblages and guilds to establish if height might be a consistent predictor of nest predation over a variety of different species with differing ecological responses.

One area of research has investigated the incubation and nestling stages to determine which, if any, suffer greater (or lesser) predation. In 1949 p 435, Alexander Skutch stated, “A possible advantage of small broods and infrequent parental visits to the nest is the smaller likelihood of betraying its position to enemies… The fewer their visits, the less likely are the parent birds to betray the position of a well concealed or inconspicuous nest”. His thoughts are typically referred to as the Skutch hypothesis, which is usually interpreted as greater clutch sizes will attract greater predation, as will the nestling stage due to more frequent visits by the adults compared to the incubation stage. His thoughts are based on accepting that predators use a visual search image, which detects the adults making repeated trips to the nest. In contrast, other studies have found equal nest predation at the egg and nestling stages (Roper and Goldstein 1997) or lower nest predation at the nestling stage (Best and Stauffer 1980; Lambert and Kleindorfer 2006). Martin *et al.* (2000) found another solution by eliminating poorly concealed nests that incurred rapid predation (all at the incubation stage) from their analysis resulting in finding increased predation at the nestling stage and supporting Skutch’s hypothesis (see also Ruxton and Humphries 2001). Clearly there is not a simple one-size-fits-all answer and studies focused in Australia are required. In addition, building stages are too infrequently reported despite the significant investment of energy placed into building nests by passerines (Collias and Collias 1984). This stage might also be considered in future studies, particularly given the emerging data on nest losses from the theft of nest material and the poorly understood reasons for nest abandonment during this stage (Ley *et al*. 1997; Fulton 2006a).

Changing the nest’s location in response to nest predation

Re-nesting response to nest predation is less well studied than nest characteristics or predator identity, particularly in Australia. Forest and woodland birds experience high levels of nest predation and commonly nest several times in a season (Woinarski 1985). In response birds may relocate successive failed nests differently to successive successful nests. The Grey Fantail *Rhipidura albiscapa* was proposed as a study species to analyse nest relocation because they commonly abandon up to 71% of their nests before egg-laying, re-nesting up to seven times in a season (Berger-Tai *et al.* 2010; Beckmann and Martin 2016). One study attempting to explain this high level of abandonment found nest concealment was 9% less at abandoned compared to successful nests, suggesting that nests were abandoned if they had "deficient security" (Beckmann and Martin 2016). Beckmann *et al.* (2015) found Grey Fantails would re-nest further from their previous nests following failed and depredated nests compared to successful nests, although this response was highly varied within each individual. Additionally, a study using stuffed models found Grey Fantails would abandon building when presented with a stuffed Pied Currawong, but not when presented with a stuffed King Parrot *Alisterus scapularis*, suggesting abandonment was related to a perceived threat of nest predation (Berger-Tai *et al.* 2010). Yet another species, the Bell Miner *M. melanophrys* either re-nested with greater concealment or by lowering its nests' height, it did not move further from previous nests. The authors suggest that because Bell Miners are an aggressive colonial bird, which excludes other birds from their territories, moving further away when re-nesting would have been disadvantageous (Beckmann and McDonald 2016).

CONSERVATION AND FUTURE RESEARCH

Robust evaluations of predation rates and predator identities are required (Remeš *et al.* 2102). Without this information, effective conservation action may not be possible (Vladimír Remeš *in litt.*). The role and identity of nest predators remains poorly understood, particularly where predation pressure is additive to natural predation rates or at least enough to drive recruitment below adult mortality. Excluding off-shore islands, the Pied Currawong and Sugar Glider are the only nest predators shown to have added nest-predation pressure that directly threatened another species (Priddel and Carlile 1995; Heinsohn *et al.* 2015).

Control or exclusion measures are justified in defending and researching species under threat (Fulton and Ford 2001c; Ford *et al.* 2001; Debus 2006a). Debus (2006a) recorded the successful breeding, recruitment and then emigration of the two robin species after using cages and culling to exclude Pied Currawongs. Exclusion cages also provided an improvement of 63% in nest success (n = 7) for threatened White-fronted Chat *Epthianura albifrons* (Major *et al.* 2015). More research on exclusion cages and exclusion methods are required, and more conservation actions using both methodologies are warranted (Debus 2006a: Smith *et al.* 2011).

Studies that have garnered large sample sizes have typically investigated single species (e.g. Rowley *et al.* 1991; Brooker and Brooker 2001). Few observations have come from heuristic Australian studies from phylogenetic groups and guilds present within the assemblage and within the context of the assemblage. Greater life history knowledge is required, particularly when drawn from within avian assemblages looking at shared predator or prey responses. For example, nest predation may act to organize assemblages as predators have been found to specialise on certain nest types (Martin 1988; 1993a). Indeed the spatial partitioning of nest sites is thought to be influenced by predation (e.g. horizontally: Kendeigh 1942; Martin 1993b; and vertically: Colombelli-Négrel and Kleindorfer 2009). Studies of assemblages are needed to identify phylogenetic groups and guilds that are vulnerable to nest predation (Remeš *et al.* 2012) or are impacted in a collective way. Further study within the assemblage is required to test if nest characteristics (e.gs type, stage, height, location and prey size) predict nest predation.

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2. REVIEW OF NEST PREDATION II: META-ANALYSIS

META-ANALYSES OF NEST PREDATION IN TEMPERATE AUSTRALIAN FORESTS AND WOODLANDS

ABSTRACT

Nest predation is the leading cause of nesting failure. Thus it is a crucial area of research needed to inform conservation management and to understand the life history of birds. I surveyed the literature to review the identity of nest predators and the factors affecting nest predation, in Australia using 177 studies. Overall, 94 nest predators were identified when incorporating artificial nests, 69 without. Using only natural nests, the Pied Currawong *Strepera graculina* was the most frequently reported nest predator. Five nest predators, including Pied Currawong, depredated 40% of the prey measured by the number of prey species taken. Yet, 60% of predation was carried out by the other 64 species, which included by order of importance birds, mammals, reptiles, frogs and ants. Predation at cup and dome nests was more frequently reported than at burrow, ground and hollow nests. Only 28% of predators were observed at both artificial and natural nests suggesting artificial nests have limited, but not negligible, ability as tools for identifying predators. There was a highly significant and positive correlation between predator and prey masses. The predator prey mass ratio (PPMR) was calculated with a mean 0.25 and a median 0.22, a result closely matching with the proportional size of prey taken by raptors. The finding that predator size is proportional to prey opens a pathway for more life history and conservation research.

KEYWORDS: Pied Currawong, predator prey mass ratio (PPMR), Nest stage, Nest type, Natural and artificial nests

INTRODUCTION

Avian reproduction and juvenile recruitment are fundamental areas in which to study life history traits and evolution (Martin 1992; Martin 1995). In particular, nest predation as a subset of nest ecology provides an area to investigate life history and behavioural traits that are expressed in evolutionary outcomes (Martin 1995; Remeš and Martin 2002; Remeš *et al*. 2012a). For example, birds that experience high rates of nest predation re-nest more frequently, have shorter nesting cycles and smaller clutches (Martin 1995). Understanding the processes operating in nest predation informs conservation efforts, particularly in knowing what to measure and manage (Remeš *et al*. 2012a).

Many studies of nest predation have been conducted on birds from North America (e.g., Ricklefs 1969). Comparisons of predation rates at different nest types have been made (Collias and Collias 1984; Skutch 1985; Remeš *et al*. 2012). Characteristics of the nest such as nest type, height, vegetation layer and nest concealment can affect predation rates and predator type: typically predation by mammals and reptiles is highest on low nests with avian predation more frequent on high nests (e.g., Best and Stauffer 1980; Martin 1993; Remeš 2005). Yet, much less is known for Australian birds with few empirical studies of natural nests, particularly at the assemblage level (Remeš *et al.* 2012a; Fulton 2018 [Chpt. 1]). One review of nest predation patterns in Australian songbirds reported a latitudinal gradient with less nest predation in temperate compared to tropical regions and with the lowest predation in the south-west (Remeš *et al*. 2102). This review also found that nest predation rates had increased over the 40 years prior to its publication, although the reasons remain speculative. In general, nest predation studies have called for greater knowledge on the identity of nest predators and processes, using a broad array of species and for a variety of nest types (Major and Gowing 1994; Fulton and Ford 2001; Remeš *et al.* 2012a; 2102b; Fulton 2018 [Chpt. 1]).

Artificial nests have been criticised for not matching predator identity and predation rates of natural nests (Willebrand and Marcström 1988; Reitsma 1992; Zanette 2002; Burke *et al.* 2004; Thompson and Burhans 2004). Despite the many valid criticisms against artificial nests they are thought to have added to our understanding of nest predation processes and predator identities (Paton 1994; Major and Kendal 1996; Villard and Pärt 2004). Yet a broad assessment of their success in matching predators identified at natural nests may help understand the veracity of their past findings and future uses with regard to identifying nest predators.

Interactions between nest predators and their prey form part of a complex food web. One way to understand these relationships is through a focus on size relationships using a predator prey mass ratio (PPMR) (Nakazawa *et al*. 2011; Tsai *et al*. 2016). In many animal communities larger predators tend to consume larger prey (Vézina 1985; Shine 1991a). The PPMR is a ratio derived from the mass of the predator and the mass of their prey, and used to describe size-structured dynamics of food webs (Brose *et al*. 2006; Nakazawa *et al*. 2011; Tsai *et al*. 2016). Early studies tested hypotheses searching for general drivers of the ratio. For example, are predators optimising their intake or is the ratio restricted by foraging opportunities (Fisher and Dickman 1993)? More recently, Tsai *et al*. (2016) questioned why the ratio is not constant across different taxa and suggested a preferred prey size, which takes into account the size of prey available from within the predator's foraging range. To my knowledge no-one has considered that the PPMR be applied to the predation of birds' eggs and nestlings. Perhaps this is due to the disparity in size between eggs, juveniles and adults of the same species (Nakazawa *et al*. 2011). Yet, this caveat need not apply to bird nests if only the adults mass is considered, because the size and mass of adults who defend nests is comparatively constant and predictable.

The aims of this study were to analyse data from the literature: (1) to survey the identity of nest predators, to quantify their roles and to find any phylogenetic signals that might inform conservation efforts; (2) to detect if different nest types (cup, dome, hollow, ground, burrow and platform) experience greater or lesser levels of nest predation; (3) determine the relationship between the mass of adults defending eggs and nestlings (prey) and nest predators by deriving the PPMR; and (4) to assess how frequently artificial nests shared the same species of predator as natural nests.

METHODS

This review was compiled from searches of Google Scholar for key words including: nest success, nest predation and rates, nest predators, reproductive success, breeding biology, nest (site, concealment, height, experiments, success, and mortality), life history, nest abandonment/desertion, diet and re-nesting. These keywords were followed when they coincided with avian taxa of Australian temperate forest and woodland. Google Scholar was used because it is fast and comprehensive, and freely available compared to other substantially expensive Internet tools. Careful reference harvesting was used to complement these searches by following citations in those papers (including footnotes); I located 290 papers, from which 177 are used here. Papers were excluded when they failed to identify a nest predator or where the predator's identity was speculated. In rare cases, additional information was sourced from authors to help confirm a nest predator's identity. The sample of nest predators and prey obtained was extensive, although it is not intended to be complete (Appendix 1).

Taxa were limited to those considered to be birds of southern temperate woodlands and forests of Australia, an area of about 82 million hectares (adapted from Australia's State of the Forests Report 2013). To test if the review data was representative of the natural population, the number of species for passerines and non-passerines, and nest-type evaluations were compared for equality with the independently obtained community of woodland birds, hereafter: 'independent natural community', which was adapted from Hannah Fraser's unpublished Ph.D. Thesis *Overcoming inconsistency in woodland bird classification* (Appendix 2: 198 spp.).

Nest type, and adult avian masses were taken from the Birds in Backyards (2017) website otherwise the Handbook of Australian, New Zealand and Antarctic Birds volumes 1-7 (HANZAB) (first authors

Marchant and Higgins, 1990-2006) or the CRC handbook of avian body masses (Dunning 2008). Nest types (natural only) were assessed against the number of reported predations from the five taxonomic classes (birds, mammals, reptiles, ants and frogs). Cup nests included corvids and large artamids. Platform nests were large nests of raptors. Names and taxonomic order follow: for birds, Christidis and Boles (2008); for mammals, Jackson and Groves (2015); for frogs and reptiles, Cogger (2014); and for ants, Andersen (2002).

The identity of nest predators for the natural and artificial nests comparison was investigated using all five classes of predators. Nest predators were scored as either being identified at both nest types (natural and artificial) or only at one nest type. A lack of concordance between artificial and natural nests would suggest that they do not attract the same nest predators.

The PPMR was calculated for the arithmetic mean and weighted median, because they are mathematically different measures that together provide stronger support for the existence of a broad PPMR when their results match. They were derived from the masses of prey species for each avian nest predator (natural nests only). The mass of a single species was used when only one species of prey was attributed to a nest predator. The average mass of adult birds were used and not the mass of eggs and nestlings, since adults are assumed to defend eggs and nestlings. While honeyeaters were included in the overall analysis they were also dealt with separately because their results suggested they depredate larger prey. The Black-breasted Buzzard *Hamirostra melanosternon* was omitted from the PPMR analyses, because of its different approach to nest predation. It drops rocks onto the nests and eggs of much larger birds (North 1912, citing Gould 1840; Campbell and Barnard 1917).

Statistical analyses

Artificial nests, farm birds and aviaries were excluded from all analyses, except for the artificial and natural nest comparison. The average refers to the arithmetic mean unless otherwise specified. A significance of the difference between two independent proportions was used for the proportional comparisons of review data with the overall proportional abundance of woodland bird species. This test looked for equality between the two data sets to justify further analyses of the review data. If the proportions in review data matched overall proportional abundance of woodland birds (no bias) then analyses proceeded. A computational calculator on the VassarStats computational website was used for these tests where the numerator k_a (number of nest of predators, prey or parameter in question) was divided by n_a (total of that phylogenetic group, taken from the independent natural community where necessary) (Lowry 1998-2017). Pearson's correlation was used to test for a relationship between predator and prey masses. The coefficient of determination (r^2) and P values were derived from Excel’s regression function. A two sample t-test for equal means, using Past 3 software, was used to assess if honeyeaters took larger prey than all other avian nest predators (re PPMR). This test did not include non-avian predators. A one-tailed exact binomial calculation was run on the VassarStats statistical website (Lowry 1998-2017) to test if predators at natural and artificial nests matched.

Chi-square tests were performed with Graphpad online software to compare observed and expected frequencies between the six nest types, then to test for associations using paired tests for all nest types (Graphpad 2017). These comparisons were excluded from a Bonferroni adjustment following Moran (2003); thus, where results are not highly significant they may be taken as indicative and not conclusive. Moran (2003) argued against the Bonferroni test on mathematical, logical and practical grounds finding that it can lead to falsely accepting null hypotheses in multiple tests by inflating Type II errors. Moran proposed reporting the P values and making reasonable and logical interpretations of the data.

RESULTS

Nest predators

Overall 94 nest predators and 95 prey species were identified when artificial nests aviary and farm birds were considered (Appendix 1). However, 69 nest predators were recorded taking, in total, 91 avian prey species when only natural nests were considered. Nest predators were identified from five classes of animals, which in order of importance were birds, snakes and lizards, mammals, ants and frogs (Figure 1). The five most commonly reported nest predators, measured by the number of prey species, accounted for 40.2 percent of the identified prey (Figure 2). Conversely, 59.8 percent of all nest predation was by the other 64 species. The most frequently reported class of nest predators were birds followed by mammals, reptiles, ants and a frog in that order (Figure 1).

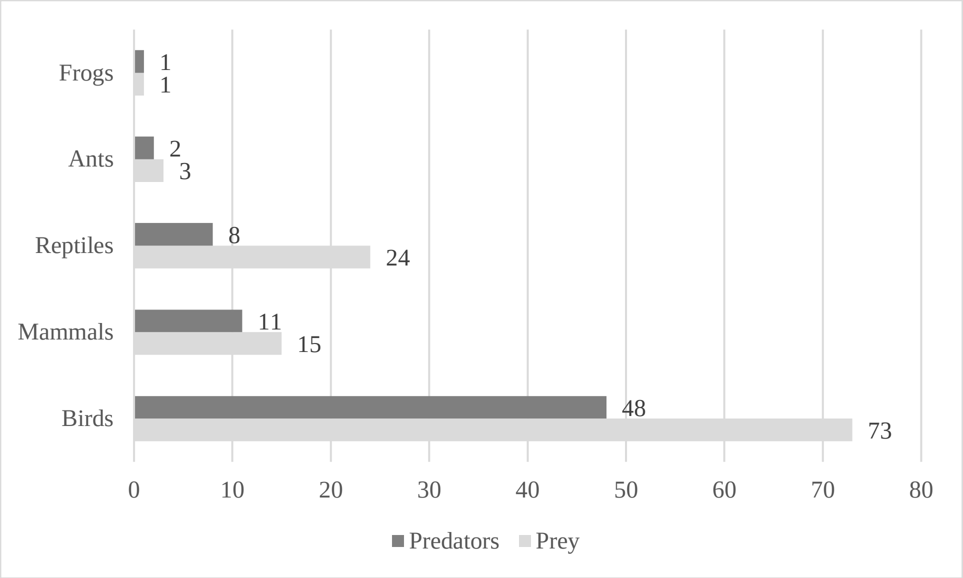

Figure 1: Number of species of nest predators by class and the number of avian prey species taken by each predator class.

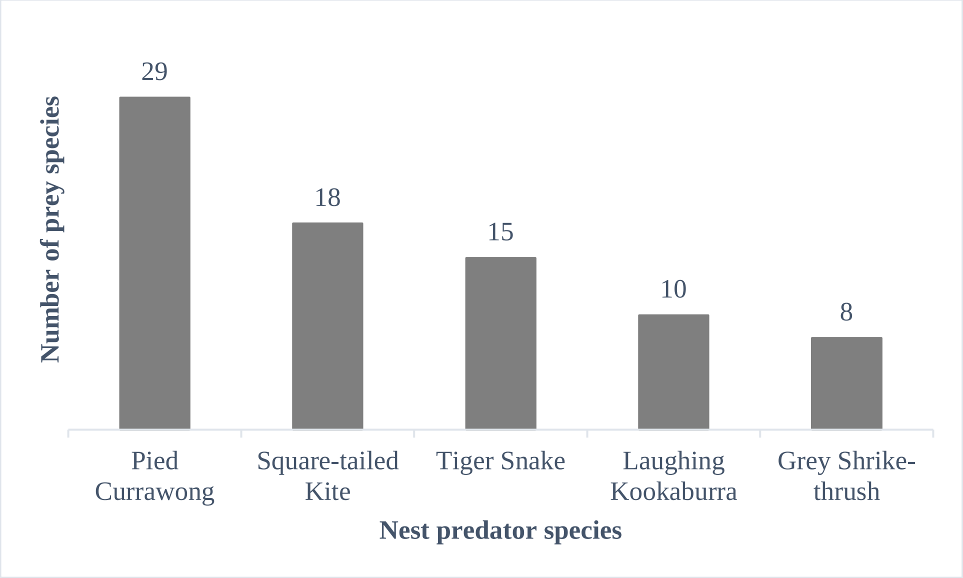

Figure 2: Five main nest predators by number of prey species

Phylogenetic signal

The proportions of birds in the passerine and non-passerine review data corresponded proportionally with the same groups from the independent natural community (Appendix 2) in that they were not significantly different using two-tailed tests (for passerines: P = 0.4231, Z = 0.801 and non-passerine: P = 0.4231, Z = -0.801) (Table 1). Thus, the quantities under review paralleled those from the independent natural community. Furthermore, the proportion of passerines and non-passerines species detected as nest predators and prey in this review also paralleled their proportional abundance in the independent natural community, suggesting that they are equally represented and thus without bias (two-tailed tests: for nest predators: P = 0.2666, Z = 1.111 and prey: P = 0.4342, Z = 0.782) (Table 1). However, a preponderance of honeyeaters (Meliphagidae) as both nest predators and prey was detected (Table 2). The five avian families recorded with the most avian nest predator species were, in order of importance, Meliphagidae, Accipitridae, Corvidae, Artamidae and Cuculidae while Meliphagidae and Petroicidae had the most prey species (Table 2).

Table 1: Numbers of passerine and non-passerine predators and prey species with percentages given in parentheses. The total population is taken from the independently derived community of woodland birds (Appendix 2).

	Predators	**Prey**	**Population**
Passerine	34 (71)	61 (67)	127 (64)
Non-Passerine	14 (29)	30 (33)	71 (36)
Total	48	91	198

Table 2: The number of bird species within each family that have been recorded as predator or prey.

Prey	**Family**	**Predators**
	NON-PASSERINES	
1	Casuariidae	
1	Megapodiidae	
1	Phasianidae	
1	Anseranatidae	
2	Anatidae	
1	Podicipedidae	
4	Columbidae	
1	Ardeidae	
2	Threskiornithidae	
1	Accipitridae	7
1	Falconidae	1
1	Gruidae	

1	Rallidae	1
1	Otididae	
1	Charadriidae	
4	Cacatuidae	
2	Psittacidae	
1	Cuculidae	3
	Strigidae	1
2	Halcyonidae	1
1	Meropidae	
	Pittidae	
	PASSERINES	
1	Climacteridae	1
1	Ptilonorhynchidae	
3	Maluridae	
4	Acanthizidae	
1	Pardalotidae	1
17	Meliphagidae	12
1	Pomatostomidae	3
	Eupetidae	1
1	Neosittidae	
2	Campephagidae	1
2	Pachycephalidae	1
	Oriolidae	1
3	Artamidae	5
2	Rhipiduridae	
1	Corvidae	5
2	Monarchidae	
1	Corcoracidae	1
6	Petroicidae	
1	Acrocephalidae	
1	Megaluridae	
1	Timaliidae	
2	Hirundinidae	
1	Turdidae	
1	Pycnonotidae	
2	Sturnidae	1
2	Estrildidae	
1	Passeridae	1
1	Motacillidae	
91	**Totals**	**48**

Table 3a: The proportional abundance of review species (by nest type) versus the total abundance of woodland bird species is given as the number of species reviewed compared to the overall numbers of the independently derived community of woodland birds (Appendix 2: 198 spp. Note five of these are cuckoos thus 193 species are used here). Numbers (expected values) must be greater than 5 to test between proportions. Percentages are given in parentheses.

Nest type	Review spp.	Overall spp.	P value
Cup	49 (54)	88 (44)	0.14
Dome	12 (13)	28 (14)	0.83
Hollow	14 (15)	46 (23)	0.13
Ground	12 (13)	16 (8)	0.17
Burrow	2 (2)	4 (2)	N/A
Platform	2 (2)	11 (6)	N/A

Table 3b: Predation incidence at each nest type excluding: artificial, aviary and farm nests. Percentages are given in parentheses.

Cup	Dome	Hollow	Ground	Burrow	Platform
137 (56)	57 (23)	23 (9)	17 (7)	10 (4)	2 (1)

Table 3c: Chi-square results comparing the differences of reported nest predation per nest type: P < 0.0001***, P < 0.001**, P < 0.05*, and ns not significant.

	Cup	Dome	Hollow	Ground	Burrow
Dome	***				
Hollow	***	***			
Ground	***	***	ns		
Burrow	***	***	*	ns	
Platform	***	***	***	**	*

Predator and prey masses

A PPMR was detected with adult prey masses averaging between a quarter and a fifth of the predator mass (overall including honeyeaters: mean 25% and median 22%) (Figure 3). Honeyeaters took larger prey than the other avian nest predators compared to their body size (t = 3.36, df = 34, P < 0.001). They depredated nests of birds as large as or larger than themselves with their PPMRs at: mean 100% and median 125%. The mean and weighted median prey masses for all taxa were positively correlated with predator masses. These were highly significant and positive relationships: for means (r = .80, df = 34, p < 0.001) and for weighted medians (r = .81, df = 34, p < 0.001). The coefficient of determination r^2 explained 64% of this relationship for the means and 66% with the medians. A stronger positive correlation was detected when honeyeaters were removed for means (r = .82, df = 23, p < 0.001) and for weighted medians (r = .84, df = 23, p < 0.001).

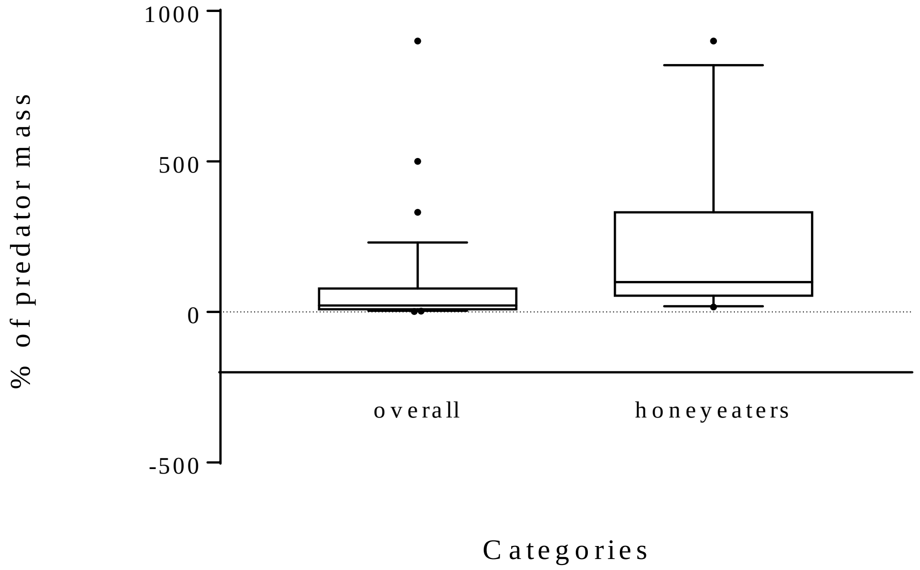

Figure 3: Predator prey mass ratio (PPMR): Overall including honeyeaters: mean 25% and median 22%. Honeyeaters took larger prey than the other avian nest predators: mean 100% and median 125%. 10 to 90 percentiles—the whiskers are drawn down to the 10th percentile and up to the 90th. Outliers below and above the whiskers are drawn as individual dots.

Artificial and natural nests

The relationship between artificial and natural nests was assessed by determining if predators identified at artificial nests matched those observed at natural nests. Overall 90 nest predators were evaluated. A one-tailed, exact binomial test indicated that detection at only one nest type was significantly greater than detection at both (P < 0.0001). In total, 65 (72%) nest predators were recorded only at one nest type, either natural or artificial nests, while 25 (28%) were recorded at both nest types. Precisely, 44 species were recorded at natural nests and 21 species were recorded at artificial nests.

Nest type

No significant bias was detected in the proportion of prey per nest type, compared to the natural proportional abundance of species in the independent natural community (Table 3a). Incidences of predation were more commonly recorded at cup nests than expected given the prevalence of these nests types in the woodland avifauna. Cup nests were followed by dome, hollow, ground, burrow and platform in that order (Table 3b). The difference in the incidences of predation recorded between the six nest types was highly significant ($\chi^2 = 316.0$, df = 5, $P < 0.0001$). The depredation of cup and dome nest were more frequently reported (χ^2 varying from 14.45 to 131.12, df = 1, $P < 0.0001$) than ground, burrow and platform nests (χ^2 varying from 17.64, df = 1, $P < 0.0001$) to not significant (Table 3c).

DISCUSSION

Nest predators

Nest predator identity was broken down into five dominant and 64 other nest predators when excluding artificial nests aviary and farm birds. The Pied Currawong *Strepera graculina* was overwhelmingly the most important nest predator, responsible for depredating the nests and eggs of nearly 40% more species than the next most frequently reported nest predator the Square-tailed Kite *Lophoictinia isura*. Remeš *et al*. (2012) suggested a large scale ecological phenomenon may be responsible for an increase in the rate of nest predation over the four decades prior to their study. They speculated that the Pied Currawong’s range expansion and population increases may parallel this increased predation. The Pied Currawong has long been considered an important nest predator (Fulton and Ford 2001; Debus 2006a). Major *et al*. (1996) reported 134 direct observations in confirming it as an important nest-predator. Fulton and Ford (2001) found significant less nest predation on artificial nests when Pied Currawongs were culled. The other two recognised avian nest predators (from the five most dominant in this review) the Laughing Kookaburra *Dacelo novaeguineae* and Grey Shrike-thrush *Colluricincla harmonica* took surprisingly fewer prey species than the Tiger Snake *Notechis scutatus*. Yet, the Tiger Snake appears to be over-represented in these data with 13 out of its 15 prey species taken from a single study (Vestjens 1977a).

Birds were the most frequently reported nest predators compared to mammals and reptiles. This may be an artefact of reporting diurnal events with most mammals active at night. This is supported by the comparative absence of owls reported as nest predators and the predominance of mammal detection by artificial nests (Appendix 1). Among the birds passerines and non-passerines were not more likely to be either nest predators or prey. Yet, Meliphagidae (honeyeaters) were recorded with many more avian nest predators and avian prey species than any other family a result that may stem from the large number of species (74) in that family (counted from Christidis and Boles 2008). Otherwise, Cuculidae (cuckoos), Accipitridae (raptors), Artamidae (butcherbirds, currawongs and the magpie), and Corvidae (crows and ravens) stand out as the families with the most species of nest predator. These families tend to have larger species with carnivorous components to their diets. Remeš *et al.* (2012) found nest predation was higher in smaller birds somewhat in agreement with the four standout families identified in this study. Notably, Cuculidae were under-represented in these results with five species known to be brood parasites (Brooker and Brooker 1989), but only three were incorporated in this study.

The identity of nest predators ranged from the large Wedge-tailed Eagle *Aquila audax* to the small Eastern Spinebill and the prey varied even more from the largest Australian bird the Emu to the smallest the Weebill *Smicrornis brevirostris* (Appendix 1). Notably, 60 percent of all nest predation was by the other 64 nest predators and not the five most dominant nest predators. This varied group of animals accounted the largest proportion of nest predation. The only two broad studies to date focused on identifying nest predators of forest or woodland assemblages have also reported a diverse array of nest predators (Fulton 2006a; 2006b; 2006c; Guppy *et al.* 2014; 2016; 2017). While dominant nest predators like the Pied Currawong must be considered in conservation actions the large variety of generalist predators are ecologically important too and must also be considered.

Nest type

Cup and dome nests were recorded with the highest frequency of nest predation. Together they accounted for over three quarters of the recorded events. The incidence of nest depredation of cup nests was twice that of dome nests. Cup nests outnumber dome nests by 4:1 in this review and may have been reported with greater frequency due to their greater abundance. Other Australian studies have rendered differing results with artificial nests showing no difference in predation rates between artificial cup and artificial dome nests (Hausmann *et al*. 2005). While an Australian study of natural nests showed greater survival for natural domed nests in woodland remnants on farmland, but not within woodland remnants situated in pine forests (Okada *et al*. 2017). A larger study of natural nests within a natural community may elucidate if one nest type is depredated more frequently. In this review, results for hollow, burrow and ground nests showed no statistical differences to each other. Yet, they had significantly fewer incidences of nest predation than cup and dome nests. Tree hollows and burrow nests reported similarly low levels of nest predation probably because they both have substantial protective barriers—wood from branches and tree trunks or earth from solid ground. Lower predation rates are thought to be typical for hollow nests compared to open nests (Nice 1957; Skutch 1985; Martin and Li 1992). However, this result has not been confirmed in Australia (Remeš *et al*. 2012a; Fulton 2018 [Chpt. 1]). Conversely, fewer incidences of observed nest predation may be related to difficulties in observing cavity nests in general.

Fewer observations of nest predation were recorded for ground nests compared to cup and dome nests, which was unexpected. Greater rates of nest predation are assumed for ground dwelling birds, which have been reported in greater decline than other ecological guilds (Reid 1999; Barrett *et al.* 2007; Watson 2011). In support, Remeš *et al*. (2012a) found no relationship between predation and nest height including when ground, shrub and canopy were compared as categories. Finally, platform nests recorded the lowest incidence of nest predation presumably because these were nests of large raptors.

Artificial nests

Predators were compared on the general assumption that if they were detected at natural nests in addition to artificial nests then this to some degree validates the use of artificial nests to study predation. One of the major criticisms levelled at artificial nests is that they lack external and internal validation (Moore and Robinson 2004). For example, a predator identified at artificial nests may be validated by also being recorded at a natural nest: internally within a study or externally from another study. A little under one third (28%) of nest predators in this review gained a general degree of validation by being identified at both nest types. Clearly this is not a strong result, because two thirds of predators were not validated and particularly because the validation carries little veracity when presented without detail. Overall this result shows that artificial nests may identify some nest predators correctly, but they are of limited value in terms of identifying nest predators of natural nests. Their predictive value may best lie in establishing hypotheses to be tested at natural nests (Fulton 2017 [Chpt. 3]; Fulton 2018 [Chpt. 1]).

Predator and prey masses (PPMR)

The overall ratio (PPMR) obtained in this study (mean 0.25, median 0.22) closely matched what has been found for Australian raptors. Olsen *et al*. (2010) reported 16 studies, of which I averaged the overall proportion of prey size and obtained a mean 0.24 and median of 0.26. The close match between that study and this one points to the existence of an optimal prey size (all other things being equal) shared by avian predators. However, honeyeaters depredated the nests of much larger birds (mean 1.25, median 1.0). Honeyeaters are known to exclude other birds from their territories (Dow 1977; Mac Nally *et al*. 2012; Maron *et al*. 2013). Thus, their PPMR might be more related to group mobbing and territorial exclusion than nest predation. Future research might assess foraging opportunities within a predators feeding range to further develop an understanding of PPMR in a nest predatory context.

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3. ARTIFICIAL GROUND NESTS & NATIVE MARSUPIALS AS NEST PREDATORS

NATIVE MARSUPIALS AS EGG PREDATORS OF ARTIFICIAL GROUND-NESTS IN AUSTRALIAN WOODLAND

ABSTRACT

Reviews of nest predation call for the identification of nest predators. The identity of nest predators is perhaps most poorly known for ground nesting birds. Marsupials are not generally regarded as potential nest-predators of these birds, partly because the biology of rare Australian marsupials is not fully understood due to their rarity. This study identified three marsupials boodie (*Bettongia lesueur)*, woylie (*B. penicillata)* and brushtail possum (*Trichosurus vulpecula*) taking eggs from artificial nests modelled on the threatened painted button-quail (*Turnix varius*). Approximately one third of the eggs were taken by the two bettongs (woylie and boodie) and another third by the brushtail possum. I present dietary evidence of bettongs consuming vertebrate items including taking live prey to provide external validation for the notion that they may depredate natural nests. I suggest more research is required on the impacts of reintroductions to avoid deleterious effects on resident species.

INTRODUCTION

Ground nesting and dwelling birds have generally declined more than other groups of Australian birds (Garnett *et al*. 2011). Predation, including nest predation, has been suggested as an important factor in this decline (Ford *et al*. 2001; Ford 2011). To date, the only long-term and large-scale analysis of nest predation in Australia stated that investigations were required to better understand the role and importance of nest predators (Remeš *et al.* 2012). To date, red fox (*Vulpes vulpes*) and cat (*Felis catus*) have commonly been regarded as the most important predators of ground nesting birds (Burbidge and McKenzie 1989). Yet, at Dryandra, where these predators are controlled, the greatest number of declining bird species and a disproportionate number of bird extinctions have come from ground-nesting and dwelling birds (Fulton 2013). Thus, I chose to investigate what animals, including re-introduced marsupials, might take eggs from artificial ground nests at Dryandra. I modelled these artificial nests on the painted button-quail (*Turnix varius*), because this species is in decline (Storr 1991; Johnstone and Storr 1998) yet was common at my field site. The aims of this study were to: 1) identify nest-predators of artificial ground nests, and 2) discover if rare and threatened marsupials might take common quail (*Coturnix coturnix)* eggs from artificial ground nests.

METHODS

Study site

Dryandra Woodland (Dryandra) is located about 160 km southeast of Perth (Lat. 32 48' S, Long. 117 0' E) on the western side of the Western Australian wheatbelt. The wheatbelt has had up to 97% of the original native vegetation removed resulting in the decline and extirpation of many animals (Kitchener *et al*. 1982; Saunders and Curry 1990). Dryandra, is unlike other woodland remnants in Australia due to a number of factors including: its overall size at 27 000 ha and being positioned in the wheatbelt. Long-term control of foxes through 1080 poisoning has kept their numbers low, which has allowed remnant populations of native animals to persist (Friend *et al*. 1995; Marlow *et al*. 2015a; b). In addition, some marsupials extinct on the Australian mainland have been re-introduced (Friend and Thomas 1994; Friend *et al.* 2001). Dryandra also retains most woodland bird species in ecologically functional numbers (Fulton 2013).

Artificial nests

The artificial nest study was undertaken over two years, both years during the button-quail's breeding season at Dryandra. It was carried out centrally within Dryandra, in the area with the greatest painted button-quail abundance. Boodie (*Bettongia lesueur*) were re-introduced at this location in the second year. The artificial nests were deployed during the breeding seasons of 2002 and 2003, from 8/12/02 to 19/12/02 (14 days) and from 21/12/03 to 1/1/04 (12 days). The synchrony and spacing of the artificial nests were similar to natural nests of the painted button-quail. Each year, 50 nests were placed in a grid, with nest-site flags spaced 50 m apart east-west and 100 m apart north-south. The grid had five transects, which traversed a management track for 250 m east-west on either side – the overall grid area was 20.2 ha.

Numerous scent trails were used to stop animals from finding nests by following my scent. My scent trails were re-walked on an almost daily basis. They were present in the grid area from late winter, well before the artificial nest trial in late spring. Therefore, my scent was not novel to resident animals. The site was also used for walking transects and completing point counts through both years, in unrelated surveys. Natural bird nests dispersed within the site were surveyed and monitored most days during the breeding seasons. Walking through the site searching for nests included stopping when birds perched and stopping to observe nests. All this combined to create a series of scent trails that occurred throughout both years, which did not provide to a food reward for animals. The artificial nests were not approached closely when being monitored; they were checked using field binoculars from ≥10 m away.

Nest and eggs

The artificial eggs matched those of the painted button-quail in their size, shape and clutch size. The artificial nests consisted of a piece of duct tape matching the size of the four egg clutch – two quail and two clay eggs. The tape was difficult to see due to the eggs on it and the loose sand/gravel that became stuck to the tape. The tape was chosen because of its strength, being non-toxic and not having a strong scent. The nest was fastened to the base of shrubs, typically *Gastrolobium* and *Astroloma* spp., with fine bell wire. These shrubs provided cover from above and had low branches from about 20 cm above the ground or lower. Rainbow Modelling Clay was used for the clay eggs, which is a non-toxic microcrystalline wax that contains food dye meeting Australian standards for having no taste or scent (Fulton and Ford 2001). The clay eggs were left unpainted to avoid a paint odour.

Imprint identification

Clay eggs with imprints from predators were collected and packaged into individual containers to avoid the imprint being distorted. After collection from the field, the clay eggs were frozen to preserve the imprints. The stickiness of the duct tape inhibited removal of the eggs; however, the tape lost its stickiness when the temperature exceeded 43°C on 12/12/02 and some eggs melted in the field, before collection. After this date, in the first year, predators were ascribed as unknown at 13 nests because the clay eggs were absent and could not be found. Nests that appeared to have more shade from greater canopy cover were not affected and retained their stickiness. No attempt was made to identify beak imprints from birds below class, because the size of impressions from beaks are related to the softness of the clay and the vigour of attack (Major *et al*. 1994; Fulton and Ford 2003). Mammalian imprints in clay eggs were identified by comparison to reference impressions made from museum skulls. The boodie and woylie (*Bettongia penicillata*) had very similar dentition and their imprints were difficult to distinguish from each other. Thus, the following characters were used to resolve their identity. The woylie's maxillary (upper) incisors created a narrower and more triangular shaped archform-impression than those of the boodie, which were rounder; the boodie had distinctly smaller second maxillary incisors; the boodie's first maxillary incisors had wider labial (next to the lips) surfaces, and the impressions of its incisors were more oval-shaped than those of the woylie. Despite these differences some imprints were too difficult to interpret and were designated as indeterminate *Bettongia sp*. Brushtail possum (*Trichosurus vulpecula)* imprints are distinctly different from other the marsupials present (Figure 1) and teeth imprints from a skink (*Egernia* sp.) were identified by staff at the Western Australian Museum (see Acknowledgements).

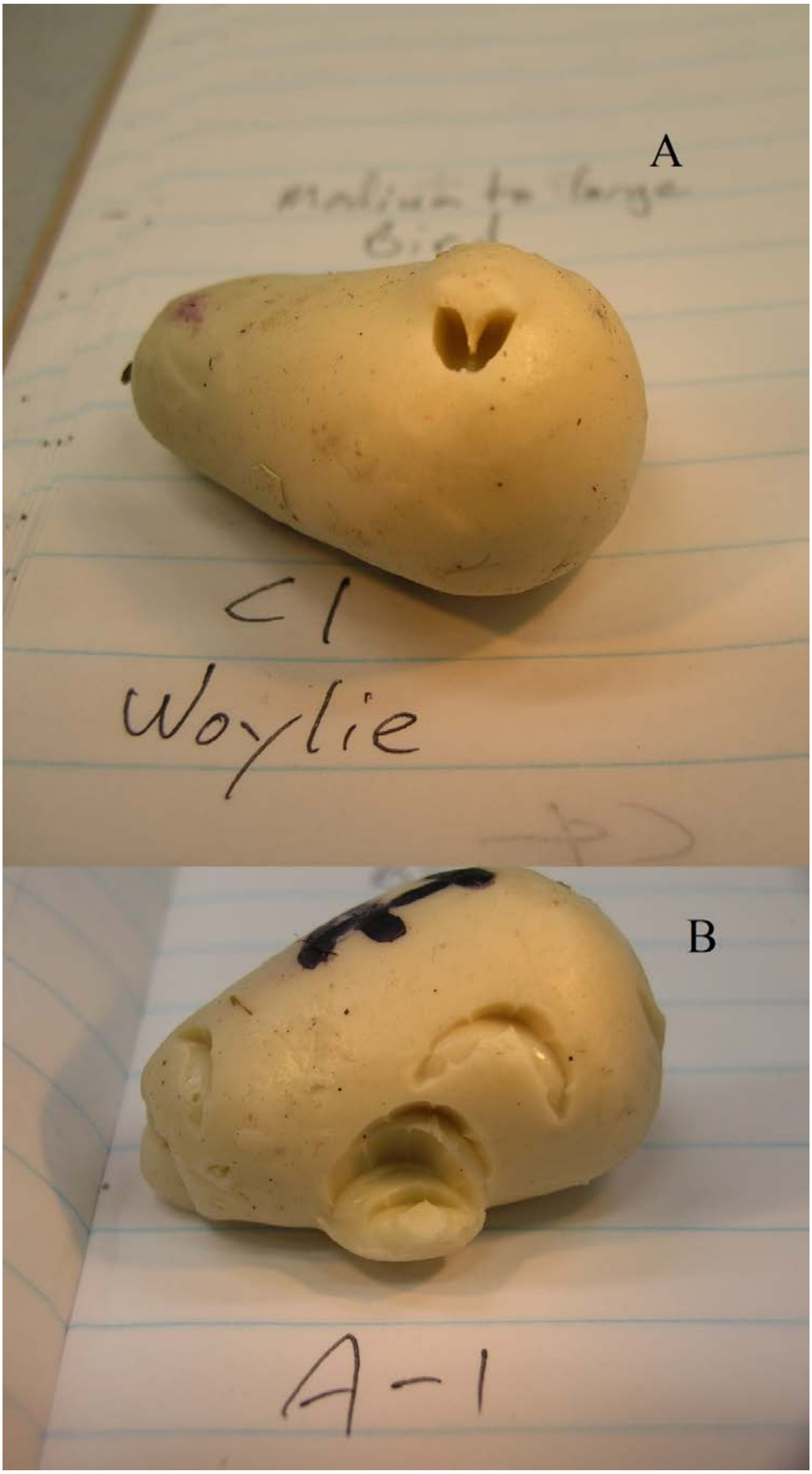

Figure 1. Clay eggs imprinted in the field by woylie (A) and brushtail possum (B). Photographed at the Western Australian Museum during analyses.

RESULTS

Predation averaged 90% (90/100 nests) for both years combined, of which 37% was by bettongs (Table 1). Woylies made up 30%, boodies 5% and indeterminate bettongs 2% of the depredated nests. Brushtail possums were responsible for 35%, unknown predators 15%, unknown birds 3% and 10% were not depredated (Table 1). In the first year, 13 sets of clay eggs were removed and were not recovered and are thus included in the unknown predator category. Boodies did not depredate nests in the first year, because they were only present in the second year of the study when seven were released on 17/9/03 (Neil Thomas pers comm.). The pattern of predation was similar in both years: brushtail possum and bettongs took approximately equal proportions of eggs from the artificial nests each year and the same proportions of nests went untouched each year (Table 1). Skinks (*Egernia* sp.), with an estimated snout to vent length from 8-10 cm, were recorded as secondary predators twice, once in each year. These skinks only imprinted clay eggs that had already been damaged and reduced in size by primary predators, in both cases these were brushtail possums.

Table 1. Number of artificial nests depredated at Dryandra, in southwestern Australia. Percentage of nests given in parentheses. Since 100 nests were used the total for both years is also the percentage.

	Brushtail Possum	Woylie	Boodie	Unknown Bettong	Unknown predator	Bird	No predation
2002	18 (36)	12 (24)	0	0	14 (28)	2 (4)	4 (8)
2003	17 (34)	18 (36)	5 (10)	2 (4)	1 (2)	1 (2)	6 (12)
Both years	35	30	5	2	15	3	10

Table 2. Carnivorous components in the diets of the boodie and woylie.

Boodie

Sheep *Ovis aries* carcasses and marine refuse (Shortridge 1910)

Fish (Tyndale-Biscoe 1968)

Meat (while in captivity) (Tyndale-Biscoe 1968)

Meat and bones (while in captivity) (Ride 1970)

Rabbit *Oryctolagus cuniculus* (hair recorded in regurgitated pellets) (Brunner and Coman 1974)

Rabbit carcasses (Robley *et al*. 2001)

Loggerhead turtle *Caretta caretta* dug and ate hatchlings (Thomas 2003)

Fresh road kill on Barrow Island (pers. comm. Andrew Burbidge)

Meat sausages from a bar-b-que (pers. obs)

Woylie

Climbed and ate three adult zebra finch *Taeniopygia guttata* in an aviary (pers. comm. Stephen Davies)

Caught in trap baited with australian ringneck *Barnardius zonarius* (Keith Morris pers. comm.)

DISCUSSION

The data show that woylie, boodie and brushtail possum will take quail and clay eggs from artificial ground nests. But, how likely is it that the same marsupials and others might depredate natural nests? The validity of artificial nests has been criticised with predation rates and predator identity on real and artificial nests found to be different (Zannette 2002; Thompson and Burhans 2004). Transferring findings from artificial to natural nests requires external validation (Moore and Robinson 2004), showing that the suspect animals are carnivorous and/or that they do consume eggs from natural bird nests.

Brushtail possums were photographed and confirmed as nest-predators of arboreal nesting altricial birds (Garnett *et al.* 1999), and at artificial nests, at Dryandra (Fulton 2006). They are known nest predators from other studies (Brown *et al*. 1993; 1996; Luck 2003; Moorhouse *et al.* 2003; Piper and Catterall 2004; Smith *et al.* 2016). Thus, there appears to be enough external validation to accept them as predators of natural nests belonging to ground nesting birds.

Bettongs were thought to be primarily mycophagous or omnivorous (Van Dyck and Strahan 2008; Eldridge and Frankham 2015). Woylies are thought to be principally mycophagous on hypogeal (truffle like) fungi and plant material, while boodies take plant material especially roots and tubers with both species taking invertebrates (Eldridge and Frankham 2015). However, there is a growing list of *a posteriori* evidence showing that bettongs do have a carnivorous component in their diets for vertebrates (Table 2). In particular, both woylie and boodie are known to have taken live prey, including small birds (Table 2).

These result suggests a cautious approach is required when introducing animals whose behaviour is not fully understood due to their rarity. Further research is needed to determine if and how frequently bettongs and other marsupials might depredate natural nests. Further scientific studies with re-introductions might investigate what effects the re-introduced species have on resident birds, particularly if the birds are threatened.

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4. STORMS

THE EFFECT OF STORMS ON THE NESTING SUCCESS OF TEMPERATE WOODLAND BIRDS

ABSTRACT

The impact of storms on bird's nests has long been acknowledged but has rarely been quantified, particularly across an avian assemblages. The effect of 18 storms (strong winds and/or rain) on bird nests in eucalypt woodland in south-western Australia is reported. Of 542 nests monitored, 468 experienced storms. Seven percent of nests that experienced storms failed due to the storms; 10% of cup (28/293) and enclosed nest (3/30) failed, but no hole nests (145) failed. Wind speeds were significantly and positively correlated with nest failure; 87% (27/31) of failed nests occurred when mean wind gusts exceeded 40 km/hr and mean speed exceeded 20 km/h. Species with nests made of fine nest material such as grasses were more susceptible to storms than those with stick nests. The amount of rainfall was not correlated with nest failure and the duration of storms did not increase nest failure. More birds nested on the windward (northern and western) hemispheres of tree crowns, though most storm winds came from those directions. Nests placed in the centre of tree crowns experienced significantly lower failure rates. In general, the assemblage was not affected by the degree of either horizontal or vertical nest placement, or between late and early season placement in a Mediterranean climate.

KEYWORDS: Wind; Rain; Australia; Nest type; Nest placement/position

INTRODUCTION

Extreme weather (including storms), food shortages, brood parasites and predation are the most important causes of nest failure (Nice 1957; Collias 1997). Of these, predation is generally regarded as the main cause of nest failure in passerines and consequently has drawn the attention of researchers (e.g. Nice 1922; Lack 1954; Ricklefs 1969; Martin 1992; Fulton 2018a [Chpt. 1]; Fulton 2019 [Chpt. 2]). In contrast, few studies have specifically addressed the effects of different storm elements on nest success presumably due to the unpredictability of storms. Thus, the existing studies tend to be opportunistic examining data retrospectively (e.g. Begg 1977; Seki and Sato 2002; Faccio 2003; Seki 2005; Zhang *et al*. 2016). Most frequently the data that is reported are from the impacts of single storms that were recorded opportunistically (e.g. Fautin 1941; Baldwin 1979; Bridges 1994; Bowman and Woolfenden 2002; Bonter *et al.* 2014; Zhang *et al*. 2016). The few studies designed to investigate the effect of the individual storm elements on bird nests found: wind gusts were a significant factor in nest survival (Brett 1989; Reville *et al.* 1990a; 1990b; Jedraszko-Dahrowska 1991; Thorn *et al.* 2016); prevailing wind direction influenced where some birds positioned their nests in trees (Chapman 1928; Lauro and Nol 1993; Summers *et al.* 2002); and, the duration of long periods of precipitation and cold weather increased daily mortality in alpine birds (Martin *et al*. 2017). These studies were motivated by hypotheses suggesting that a particular storm element was likely to be important. However, empirical data demonstrating how storms affect the nesting ecology of threatened species and assemblages of temperate forest and woodland birds are not known. Yet, such data are required in understanding the part inclement weather plays in the breeding success of these birds. Such baseline data both informs evolutionary theory and has implications for understanding the ongoing effects of climate change, particularly when comparing future data influenced by altered climactic conditions.

I report the on effect of 18 storms on an assemblage of threatened woodland birds, over three consecutive breeding seasons, in south-western Australia. This research forms part of a larger study of nesting ecology investigating causes of nest failure. The aims of this paper are to quantify the number of nests lost to storms; identify the nest types most at risk; and determine the importance of wind, rain and the duration of the storm in nest failure. This study was pointedly interested in the direct impact of storms (as discrete events) and the individual effect of their elements as the proximate causes of nest failure. However, the position of nests in trees is also investigated to test if birds sheltered from storm winds by nesting in the leeward (down-wind) side of tree crowns or if the position of their nests within the tree, either horizontally or vertically, affected their fate in storms. Because this research was undertaken in an area with a Mediterranean climate (dry summers and wet winters: thus periods of high and low storm frequency) the position of the nests within the tree (horizontally and vertically) were compared between early and late season nests, to detect if fewer nests were lost or if nest positions differed later in the season when there were fewer and less intense storms. Finally, species with sufficient sample sizes were compared to detect if any were more susceptible to failure during storms.

MATERIALS AND METHODS

Study site

Dryandra Woodland (Dryandra) is located about 160 km southeast of Perth (Lat. 32 48' S, Long. 117 0' E) on the western side of the Western Australian wheatbelt (Figure 1). Dryandra is comprised of a series of large woodland fragments, which are separated by agricultural land and scattered over an east-west distance of approximately 35 km (Friend *et al.* 1995). In general, the woodlands are characterized by Powderbark Wandoo *Eucalyptus accedens*, Jarrah *E. marginata* and Brown Mallet *E. astringens* on the mid and upper slopes, with Wandoo *E. wandoo*, Jam *Acacia acuminata*, (and less commonly Marri *E. calophylla*) on the lower slopes and valleys — Powderbark Wandoo and Wandoo (*E. wandoo*) woodland make up approximately 50 per cent of the total area (McArthur et al. 1977; Coates 1993).

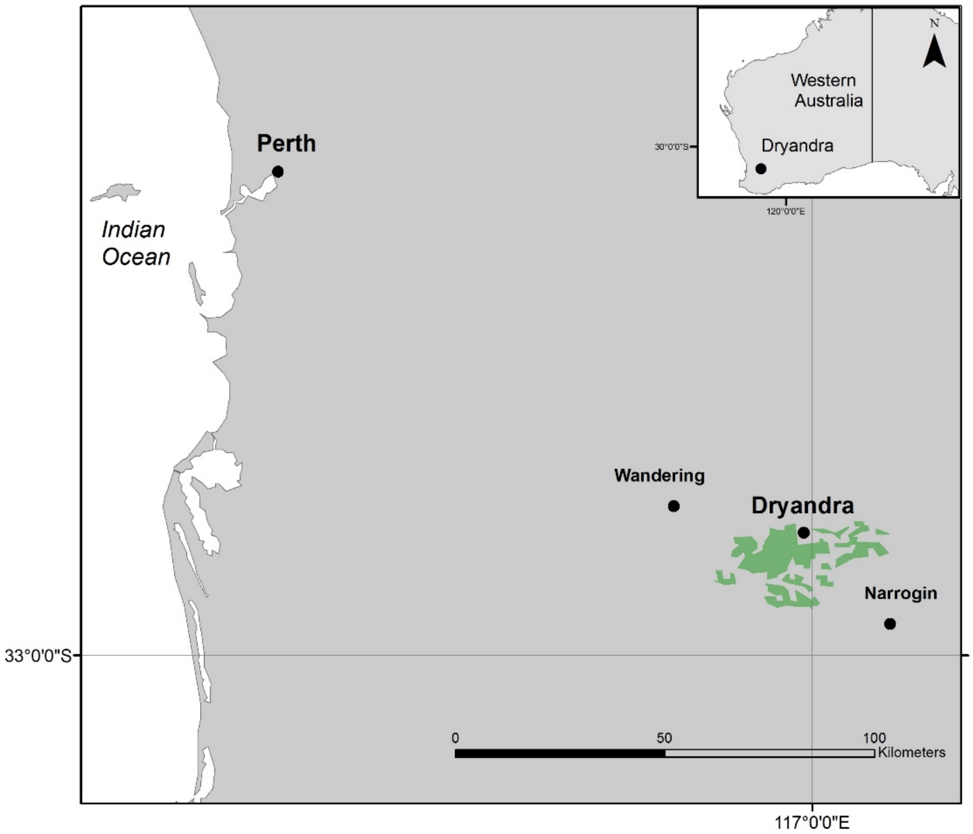

Figure 1

Dryandra in relation to Perth and southwestern Australia

Dryandra is unlike other woodland remnants, in Australia, due to a number of factors including its overall size (27 000 ha), which embraces large areas of undisturbed old-growth woodland (Friend *et al.* 1995) and its location on the central western side of the Western Australian wheatbelt where up to 97% of the original native vegetation has been removed (Saunders and Curry 1990, Saunders and Ingram 1995). Dryandra holds an almost full complement of bird species present in ecologically functional numbers, including many lost from remnants of the central wheatbelt (Fulton 2013). It also contains rare marsupials that have become extinct in the surrounding wheatbelt and others that have been re-introduced (Fulton 2017 [Chpt. 3]).

Climatic conditions

The Western Australian Regional Office of the Bureau of Meteorology supplied the meteorological data used in this study unless otherwise stated. The annual mean minimum and maximum temperatures range from 8.4°C to 23°C (*N* = 98 years; 1901-2003). Dryandra experiences a Mediterranean climate with hot dry summers, punctuated with occasional thunderstorms, and mild wet winters: January is the driest month (mean 13.1 mm) and July the wettest (mean 94.3 mm). The wettest six-month period is May to October, accounting for 80 per cent of the annual precipitation (*N* = 115 years; 1887-2003).

Regional wind patterns

In winter, the prevailing winds over the region are north-westerly. In the summer months, the winds are principally from the east. Cold fronts that circulate around Antarctica and their associated storm winds are a common feature at Dryandra during winter and spring, and are the origin of storms during this time. Storm winds come predominately from the northwest during the wet season. The winds associated with all storms are considered one of the most important natural hazards that affect Dryandra (Main 1987; Sutton *et al.* 1994).

METHODS

The effects of 18 storms on bird nests were surveyed over three breeding seasons from September 2002 through December 2002, August 2003 through January 2004 and July 2004 through December 2004. Storms were defined as having mean wind speeds of approximately 20 km/h, with gusts $\geq$ 30 km/h, or total precipitation of $\geq$ 7 mm, with or without hail. Storms of this magnitude are recorded as moderate using the Beaufort Wind Scale (Beaufort 1832; Bureau of Meteorology 2006). Storms with light rain and without strong winds are given to contrast with stronger storms.

Four basic nest types are referred to in this paper: 1) cup nests (not in cavities nor placed on the ground); 2) enclosed nests (dome) – pensile with a constructed roof (can have one or more attachments); 3) hole nests, which include tree hollows, burrows, cup nests in open cavities (in broken branches or in knot-holes) and non-pensile enclosed nests constructed in the cracks of branches or the main stem (note: cup nests and non-pensile enclosed nests in open cavities have been included with the 'hole' nests because they are all sheltered from the weather, particularly wind, in a similar way); and 4) ground nests, which took the form of a meagre cup on the ground, usually under shrubs or alongside woody debris, or eggs placed directly on the ground. This nest classification follows from the basic nest structures suggested in Collias and Collias (1984) and Collias (1997).

Nest searches and monitoring

I developed a detailed knowledge of the birds from spending most daylight hours in the woodland, throughout the three breeding seasons. This was facilitated by living in a hut within the woodland. Many of the birds were known to me individually, some through the three seasons, by their behaviour and individual characteristics, and by their association with their nests and territories. Such knowledge helped me find and check the nests quickly following each storm. Despite remembering the precise location of all nests they were flagged from a distance far enough away to no disturb them. Instructions on where the nests were positioned with regard to the marker were written on the marker. High nests were monitored with field binoculars. Each nest was given a unique number and notes were taken regarding its development at each visit. This information was databased each night and used to prioritise nest searches the following day.

Nests were searched for at 11 sites within the main block at Dryandra (32°48'S, 117°0'E) and at the most remote and isolated block, 14 Mile Brook (32° 49' 00"S, 117° 05' 45"E). The main block at Dryandra is 12,283 ha of continuous woodland situated centrally within Dryandra (Friend *et al.* 1995); 14 Mile Brook is approximately 40 ha of degraded woodland. All sites were located in the low lying areas of the woodland where the majority of birds breed (Fulton and Rose 2007). These sites were in slightly rolling hills and were not considered to be protected from winds by higher landscape features such as laterite breakaways. The slope or gradient in the study areas ranged from 1:300 to 1:500 (McArthur et al. 1977).

Storms were considered to have caused a nest to fail if branches were lying across the nest, nest-branches were broken, nestlings were blown out of nests and subsequently died or nests showed clear damage attributable to the storm (without signs of predation). To confirm that a nest had failed during a storm, a search of the area around the nest site was made for nest-material, eggs and egg fragments, or adults feeding fledglings. If nestlings were blown from the nest due to the storms, but subsequently fledged, the nest was recorded as successful; if the nestlings were depredated or died, after they had prematurely fledged in a storm, then the nest was regarded as failed due to the storm. These were rare events (unquantified) and were easily monitored by watching if the adults fed premature fledglings. Some nests were obviously water-logged and had lost their shape and strength. Storm damage was differentiated from predation by close examination of the damage to the nest. Some nests were counted more than once because they experienced more than one storm.

Detectability

The repeated, sometimes daily, visits to each site enabled me to know where birds were or should be. I learnt the habits of individual and species. If their behaviour changed it or one of a pair or a pair were missing it would be noticed and a cause searched for. Yet, despite my continued observations some birds remained difficult to detect. For example, I sat beside Tawny Frogmouths *Podargus strigoides* without noticing them causing then to fly away, but never found their nests. Button-quails *Turnix* spp., and the Bush Stone-Curlew *Burhinus grallarius* are not uncommon at Dryandra (Fulton 2013), but their numbers could not be confidently estimated nor their nests frequently found because their detectability was low. In general many nests of ground nesting birds were missed. There was some heterogeneity of habitat density; *Gastrolobium* spp. thickets occurred patchily, especially on less fertile laterite breakaways situated above *Eucalyptus wandoo* woodland. Birds that frequented this vegetation, e.g. fairy-wrens *Malurus* spp. were more difficult to detect. However, knowing this meant that more careful and prolonged observations were undertaken in these areas. In general, the habitat heterogeneity did not obscure the movement of birds to and from denser patches and all observations led to appropriate nest searches. Despite this some species were too cryptic, which resulted in low detection rates for their nests.

Nest maintenance and independence

Australian passerines have evolved nest building and maintenance capabilities with species adapting the structure of their nests to fit the local climatic conditions. The nests of the same species will show clear structural changes relating the local climate (Heenan et al. 2015). Thus, in this study, nests of the same species were considered equal in terms of design and construction. At Dryandra, all nests (within each species) appeared to be constructed identically expect for the cup and enclosed nests that were placed in open cavities, cracks or hollows. All nests were checked visually for obvious construction flaws, although no flaws were detected. All nests were continually repaired by the adult birds, in all conditions, regardless if the nest had or had not experienced a storm (personal observations). Therefore, each nest was regarded as an independent measure of each storm in this study.

Wind speed and nest losses

Wind speed was recorded at the Bureau of Meteorology’s automatic weather station at Wandering, approximately 35 km northwest of Dryandra. These data matched my field notes for periods of time coinciding with the most severe winds and rain observed at the field site. The mean wind gusts associated with storms were calculated by averaging the speeds for wind gusts recorded during a storm. Wind gusts are the greatest speeds of wind measured by instantaneous readings over the 10 minutes preceding an observation time. The wind speed is the average speed of winds over the 10 minutes preceding the observation time. Both measurements are expressed in kilometres per hour (km/h) and were recorded hourly, although more frequently during strong storms. Prevailing wind directions were assessed from monthly wind roses (a wind rose is a diagrammatic representation of wind direction). Storm winds – directions, wind speed and wind gust speed were taken from hourly and half hour data sets.

Wind direction and nest position

The number of nests within each of eight quadrants and two hemispheres of the tree-crown were compared to each other and to nests positioned in the centre of trees and to those on exposed ground wood (stags; snags in North America). Eight quadrants and not four were assessed to increase the sensitivity of this measure. Each quadrant was 90° wide and the two hemispheres were each 180° wide. The quadrants and hemispheres used in the analyses were arbitrarily selected to match wind direction and compass nomenclature. Ground wood is the dead wood on the ground from fallen branches, fallen trees. Stags are small trees that have died but still stand, both do not have surviving foliage.

Nest placement

To detect if birds selected aspects sheltered from storm winds, nest placement was assessed with a hand-held compass from the base of the nest-tree and bearings were recorded to the nearest five degrees. Tree crowns provided opportunities for birds to nest through 360°. Thus, I could test for non-random nest site selection.

The horizontal distance of a nest from the base of the tree was measured by placing a marker under the nest and measuring the distance by pacing; the same method was used to establish the radius of the tree-crown, following the same bearing as the nest. A variation on this procedure was used to measure nest- and tree-height. Field binoculars were focused on the nest and the tree-top, in turns, and then without changing the focus, I identified a point on the ground at the same focal distance. This distance was paced and my height added to the distance to estimate the nest and tree heights. Early and late season nests were divided into two discrete groups, which matched a natural weather boundary: those originating within the storm season and those originating after the storm season. The end of the storm season was defined by the last storm that originated from circulating cold fronts and after a 180° shift in the dominant wind direction (from the north and northwest to the south and southeast) had occurred. The three end-of-storm-season dates were identified: 14 November 2002, 8 November 2003 and 11 October 2004.

Cup and enclosed nests, including shrub nests, were chosen for analyses regardless of whether or not they experienced a storm. Hole (hollow, cup nests in open cavities and (non-pensile) enclosed in cracks or cavities), ground and burrow nests were excluded from the nest position analyses, as they are not subject to the effects of wind and rain to the same extent as cup and pensile nests (Nice 1957; Kendeigh 1961; Ricklefs, 1969; Skutch, 1966, 1985; Martin 1992; Collias 1997).

STATISTICAL ANALYSES

Unless otherwise stated these analyses used computational calculators on the VassarStats: Website for Statistical Computation (Lowry 1998-2017). Pearson's product moment correlation co-efficient was used to compare wind speeds to nest losses (a one-tailed test was used assuming that greater wind speeds will lead to greater nest losses whereas lesser speeds would not). Wind direction and nest position assessed the 90° quadrats and 180° hemispheres of tree crowns using a chi-square tests of association. Subsequently, the position and fate of 352 cup and pensile enclosed nests were evaluated using chi-square goodness of fit tests. A correction for continuity was applied to tests where only two categories were compared (Zar 1999). When the proportion of failed nests from the centre of tree crowns was low *P* values were confirmed via Monte Carlo simulation. Chi-square contingency tables were used to compare failure rates of different nest types (defined above).

Nest placement analyses

Nest placement was calculated from horizontal and vertical ratios. The horizontal ratio was calculated from the radial position of the nest divided by the radius of the tree crown and the vertical ratio was calculated from the nest height divided by tree height. Nests described as at the centre (horizontally) were against the tree trunk. To determine if nests placed further out and up in tree-crowns might be more susceptible to failure in storm winds; nest success or failure (the dependent categorical variable) was compared to the horizontal and vertical nest placement (independent variables) using binary logistic regression in Intellectus Statistics Version 1.01. Three species (Yellow-plumed Honeyeater *Lichenostomus ornatus*, Dusky Woodswallow *Artamus cyanopterus* and Willie Wagtail *Rhipidura leucophrys*) were selected for this horizontal and vertical nest placement analysis, to which a Bonferroni adjustment for the multiple hypotheses testing was applied to determine the appropriate P values. Criteria for the selection of these species included: that enough nests were available to test (arbitrarily here 28 minimum); that the nests were not hole, open cavity or non-pensile enclosed nests placed in cracks; that they were not placed on the ground or on dead ground wood (stags or fallen branches); and that they were not large stick nests (e.g. Australian Raven *Corvus coronoides* and raptors). A final comparison was made to determine if early and late season nests were placed differently, which used a one-way MANOVA with the dependent variables of horizontal and vertical nest placement, in SPSS version 25.

Effect of storms per species

Species with fewer than 20 nests, monitored in storms, were excluded from these analyses leaving six species for individual analysis. These six species were analysed using Spearman's rank order correlation (r_s) to determine if the total number of nests measured, positively correlated with the number of nest lost in storms and thus detect if there was a bias resulting from simply more nests leading to more nest failures. Following this a χ^2 (6x2) contingency table was used to detect if there was a significant difference between the proportions of failed and successful nests between species. Pair-wise comparisons were then made, using non-directional Fisher exact tests, to detect those species that were significantly different from other species. These pair-wise comparisons were excluded from a Bonferroni adjustment following Moran (2003).

Bonferroni adjustments

Moran (2003) argued against the Bonferroni adjustment on mathematical, logical and practical grounds finding that it can lead to falsely accepting null hypotheses in multiple tests by inflating Type II errors. He proposed reporting all *P* values and making reasonable and logical interpretations of the data. In this case, when comparing species, it was logical to conclude that large stick nests are intrinsically different to grass nests. However, Bonferroni adjustments were applied to the binary logistic regression analyses for horizontal and vertical nest placement, because the logical interpretations of these data supported its application where all but one species were not significant and essentially the same thing was being measured. There was thus no logical reason to exclude the Bonferroni adjustment. A study wide alpha level of 0.05 was set with the Bonferroni adjusted alpha level of 0.016 used: (0.05/3). A modified Bonferroni adjustment such as Jaccard and Wan (1996) was not considered, again because there was no clearly logical reason to exclude the full Bonferroni adjustment.

RESULTS

Overall losses and nest type

Nest type

I monitored 542 nests of 45 species at Dryandra, during the study period. Nests active during storms totalled 468, of these 31 (7%) failed during storms (Table 1). The proportion of nests for each of the three nest types (cup, pensile enclosed and hole nests) that failed in storms were significantly different $\chi^2_2 = 9.79, P = 0.008$. There were 293 cup nests, of these 28 (10%) failed during storms. Another 30 were pensile enclosed nests, of these three (10%) failed during storms. The rest consisted of 145 hole nests, of which none failed.

Table 1. *Nest type*

The numbers of nests (#) active in each storm and the numbers of nests that failed are given for: cup nests; enclosed nests (encl), and hole nests. N/A indicates that this nest type was not active during the associated storm.

Storm	Date	Cup	# failed	%	Encl.	# failed	%	Hole	# failed	%	Total	# failed	%
1	17-Oct-02	18	5	28	1	0	0	6	0	0	25	5	20
2	31-Oct-02	17	3	18	N/A	N/A	N/A	7	0	0	24	3	13
3	14-Nov-02	15	3	20	N/A	N/A	N/A	9	0	0	24	3	13
4	22-Nov-02	14	0	0	N/A	N/A	N/A	6	0	0	20	0	0
5	23-Nov-02	14	0	0	N/A	N/A	N/A	6	0	0	20	0	0
6	6-Sep-03	12	1	8	1	0	0	2	0	0	15	1	7
7	9-Sep-03	12	0	0	2	0	0	2	0	0	16	0	0
8	19-Sep-03	27	6	22	6	2	33	10	0	0	43	8	19
9	21-Sep-03	20	0	0	5	1	20	10	0	0	35	1	3
10	7-Nov-03	28	0	0	6	0	0	26	0	0	60	0	0
11	15-Nov-03	22	0	0	6	0	0	27	0	0	55	0	0
12	31-Jul-04	5	0	0	N/A	N/A	N/A	1	0	0	6	0	0
13	9-Aug-04	8	0	0	N/A	N/A	N/A	1	0	0	9	0	0
14	11-Aug-04	9	0	0	N/A	N/A	N/A	1	0	0	10	0	0
15	22-Aug-04	12	0	0	N/A	N/A	N/A	1	0	0	13	0	0
16	23-Aug-04	13	0	0	N/A	N/A	N/A	2	0	0	15	0	0
17	4-Oct-04	22	2	9	1	0	0	14	0	0	37	2	5
18	10-Oct-04	25	8	32	2	0	0	14	0	0	41	8	20
Totals		293	28	10	30	3	10	145	0	0	468	31	7
Means		16	2		3	0		8	0		26	2	
SE		1.6	0.6		1	0		2	0		4	1	

Storm elements: wind, rain and storm duration

The storms monitored during this study had moderate wind speeds averaging 20 km/h with average wind gusts of 34 km/h. Higher wind speeds were associated with greater nest losses. A positive and significant relationship was detected between nest losses and mean wind speed $r_{16} = 0.41, P < 0.05$ and marginally significant for mean wind gust $r_{16} = 0.40, P = 0.05$ (Table 2). Of the 31 nests that failed in storms, 27 (87% of the failed nests) failed in storms with mean wind gusts exceeding 40 km/h and mean wind speeds greater than 20 km/h (Figure 2). No significant associations were detected between nest losses and the other storm elements precipitation and the duration of storms (Table 2). No nest losses occurred during late season storms after the 180° shift in the dominant wind direction (Table 1). Five sets of two storms were separated by one to three days (Table 1). In each case, there was no increase in the number of nests that failed during the second storm, which emphasizes that the duration of storms was unrelated to nest failure.

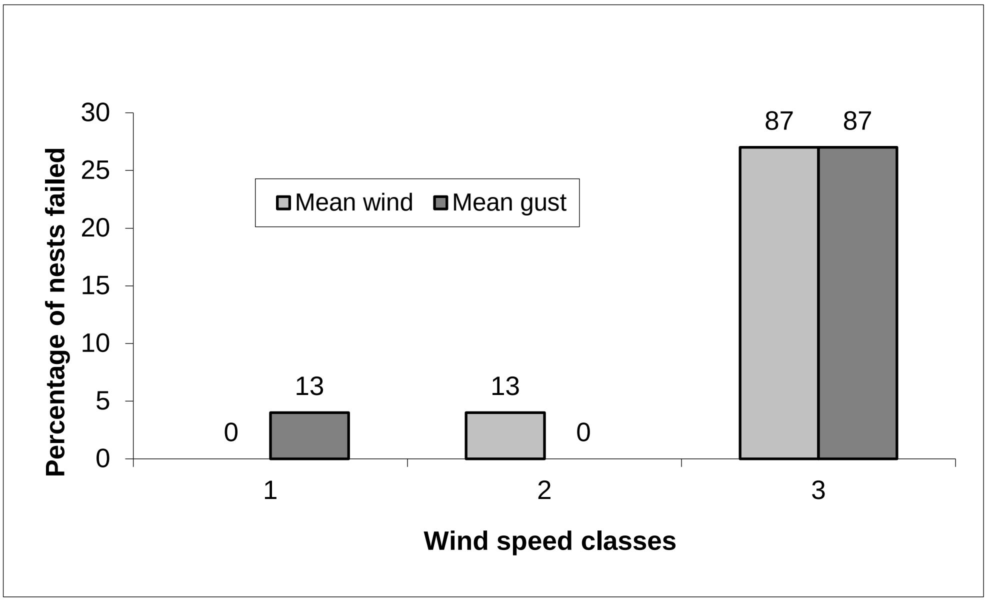

Figure 2. The effect of mean wind and mean wind gust speeds on nest failure. Percentages are only those of the nests that failed. Wind speeds are in units of km/h. Mean wind speeds by classes are: 1(0 to 10 km/h), 2 (10 to 20 km/h) and 3 (greater than 20 km/h). Mean wind gust speeds by classes are: 1 (20 to 30 km/h), 2 (30 to 40 km/h) and 3 (greater than 40 km/h).

Table 2. *Storms elements, wind rain and storm duration*

Storms are ranked in descending order by mean wind speed. Mean wind speed and mean wind gusts showed significant and marginally significant positive correlations with nest losses (Pearson's one-tailed test $r_{16} = 0.41, P < 0.05$ and $r_{16} = 0.40, P = 0.05$ respectively). Mean wind speed is the average wind speed during the storm period. The mean wind gust value has been calculated from the greatest wind gusts measured by instantaneous readings during each storm. Rain is the accumulated precipitation during each storm.

Storm no.	Nest losses	Mean wind speed (km/h)	Mean wind gusts (km/h)	Storm duration (hrs)	Rain (mm)
3	3	32	53	6.3	0
1	5	29	49	7	7.8
15	0	28	50	16	14.8
18	8	25	44	16	15.6
6	1	25	43	6	0
8	8	25	42	13	5.8
17	2	24	48	10	10.6
16	0	24	43	13	16
10	0	23	34	6	0
13	0	22	33	9	34.4
7	0	21	38	6.5	4.6
14	0	19	35	5	0.8
12	0	17	33	9	6.6
2	3	17	28	32	8.8
9	1	12	20	32	22.4
11	0	0	0	2	11
4	0	0	0	1	7
5	0	0	0	1	9.2
Correlation co-efficients		0.41	0.40	0.26	-0.05

Wind direction and nest position

Prevailing winds for the months July-September came from the north and north-west, and for the months October-December from the south and south-east (Bureau of Meteorology: monthly wind roses). Storm winds throughout the survey periods came predominately from the north (43%) (315°-045°) and west (54%) (225°-315°) with few originating from the south (3%) (135°-225°) and no storm winds originated from the east (Bureau of Meteorology: hourly and half hour data sets) (Table 3).

Table 3. *Storm winds*

Wind data were recorded at the automatic recording station, at Wandering, 35 km from Dryandra. The duration in minutes and direction of storm winds, for each 90° quadrant (defined by its bearings), were sourced from the Bureau of Meteorology's hourly and half hour data sets (no storm winds originated from the east). Storms 4, 5 and 11 were isolated storms at the field site and had no noticeable wind.

Storm no.	Range (bearings)	North 315-045° (minutes)	West 225-315° (minutes)	South 135-225° (minutes)
1	340-240°	140	40	0
2	350-220°	60	270	0
3	010-300°	130	50	0
4	-	0	0	0
5	-	0	0	0
6	330-310°	70	20	0
7	320-280°	10	70	0
8	350-270°	70	90	0
9	340-280°	80	140	0
10	170-150°	0	0	70
11	-	0	0	0
12	310-250°	0	100	0
13	360-310°	100	10	0
14	290-240°	0	60	0
15	340-270°	120	110	0
16	330-250°	50	120	0
17	320-270°	20	110	0
18	340-310°	130	60	0
Totals		980	1250	70
Means		70	89	5
Percent		43	54	3

More nests were placed on the windward side of trees with regard to storm-winds than on the leeward side of trees. More nests were placed in the northern hemisphere (360° ± 90°) than in the southern hemisphere (180° ± 90°), of tree crowns $\chi_1^2 = 15.3, P < 0.001$ (Table 4). More nests were placed in the northern and eastern quadrants (315°-045° and 045°-135°) than the southern and western quadrants (135°-225° and 225°-315°) $\chi_1^2 = 6.1, P < 0.02$. More nests were placed in the northern and north-western quadrants (315°-045° and 270°-360°) than in the centre of tree crowns $\chi_2^2 = 9.83 \textit{ and } 9.95, P < 0.01$. While the numbers of nests placed in the southern, south-eastern and south-western quadrants (135°-225°, 90°-180° and 180°-270°) were similar to the numbers of nests placed in the centre of tree crowns $\chi_3^2 = 0.28, P = 96.37$ (Table 4).

Table 4. *Nest position and wind direction*

The eight arbitrarily selected quadrants are each 90° wide. Nests placed in the centre of the trees and those placed on dead ground-wood (stags (snags in North America)) had no bearings since bearings were derived in degrees from the centre; nests on stags are in comparatively highly exposed positions compared to nest placed in the centre of trees. Nests placed in the centre of trees were significantly more successful than those of compass quadrants (chi-square goodness of fit tests) $\chi_4^2 = 11.75, P < 0.02$ and were more successful (marginally significant) than those placed on stags and dead ground wood $\chi_1^2 = 3.28, P = 0.06$.

Position	North 315.1- 045°	East 045.1 -135°	South 135.1 -225°	West 225.1 -315°	NW 270.1 -360°	NE 360.1 -090°	SE 090.1 -180°	SW 180.1 -270°	Centre	Stags
# nests	91	68	54	63	92	79	50	55	54	22
# failed	6	7	8	4	7	8	4	7	1	2
% failed	7	10	15	6	8	10	8	13	2	9

No significant difference was detected between the eight quadrants for the proportions of nests that failed due to storms $\chi_7^2 = 6.48, P = 0.45$, although the proportion of failed nests that had been placed in the centre of trees was significantly less than the proportions of failed nests from the four quadrants north, south, east and west $\chi_4^2 = 11.75, P < 0.02$ this *P* value was confirmed via Monte Carlo simulation of the multinomial distribution using 20 000 random samples each of *N* = 40 with five categorical outcomes following (Lowry 1998-2017). Another 22 nests had been placed on bare ground-wood (coarse woody debris on the ground originating from fallen trees and branches) and on stags (standing dead trees usually < 4 m in height). These nests were situated in the open and appeared to receive little shade or protection from any living vegetation. There was no significant difference between the proportions of nests on ground-wood and stags that failed when compared with the proportions of failed nests from the four quadrants north, south, east and west $\chi_4^2 = 5.23, P = 0.26$. However, the proportion of failed nests from the centre of tree crowns were less than those on ground-wood and stags with the *P* value approaching significance $\chi_1^2 = 3.28, P = 0.06$ this P value was confirmed via a Monte Carlo simulation with 50 000 samples of *N* = 11 with 2 categorical outcomes (Table 4). Fifteen species of cup and pensile enclosed nests had at least one nest placed in the centre of tree crowns. Only Western Yellow Robins *Eopsaltria griseogularis* had high proportions of nests placed in the centre of trees, 17 of 25 nests (68%).

Horizontal and vertical nest placement

The overall logistic regression model was not significant $\chi_2^2 = 4.91, P = 0.086$ suggesting that crown and height ratio did not have a significant effect on the odds of observing a failed nest over the whole assemblage or for cup nests $\chi_2^2 = 3.86, P = 0.145$. Only one failed pensile enclosed nest prohibited the analysis on that group. Of the three species tested only Yellow-plumed Honeyeaters showed a significant effect on the odds of observing a failed nest $\chi_2^2 = 9.79, P = 0.007$. The assemblage of cup and enclosed nesters did not show a significant change in nest positioning between early and late season nests $\lambda_{(2,300)} = 0.99, P = 0.88$ (Table 5).

Table 5. *Horizontal and vertical nest placement*

Horizontal and vertical nest placement was assessed in relation to success and failure for the assemblage of cup and enclosed nests, and three selected cup nesting species with binary logistic regression. Horizontal measurements are ratios of the nest's radial distance from the tree trunk compared to the tree crown radius; vertical measures are ratios of nest height to tree height. The measurements given are species means with standard errors in parentheses. The asterisk (*) indicates a significant P value and the En Dash (–) indicates not applicable.

Species or group	Horizontal	Vertical	Successful nests	Horizontal	Vertical	Failed nests	P value
Cup and enclosed nests	0.42 (.02)	0.58 (.01)	276	0.48 (.02)	0.68 (.01)	27	0.09
Cup nests	0.43 (.02)	0.60 (.01)	239	0.49 (.02)	0.67 (.01)	26	0.14
Yellow-plumed Honeyeater	0.48 (.02)	0.60 (.01)	55	0.35 (.01)	0.81 (.01)	9	0.007*
Willie Wagtail	0.48 (.02)	0.42 (.01)	28	0.51 (.01)	0.45 (.004)	3	0.94
Dusky Woodswallow	0.43 (.02)	0.65 (.01)	33	0.58 (.01)	0.64 (.01)	8	0.27
Early season nests	0.45 (.02)	0.60 (.01)	190	–	–	27	–
Late season nests	0.43 (.02)	0.59 (.01)	86	–	–	0	–

Effect per species

The number and proportions of cup and enclosed nests that failed in storms for each species are presented in Table 6a. Only six species, those with ≥ 20 nests were used in the following analyses. No significant correlation was detected between them, indicating that variation in the number of the nests that failed was unrelated to the total numbers of nests available per species $R_{s(4)} = 0.020, P = 0.97$. A χ^2 6x2 contingency table found the proportion of failed nests were significantly different between the six species analysed $\chi^2_5 = 36.83, P < 0.001$. Further non-directional Fisher exact probability tests were performed as pair-wise comparisons to highlight which species were (or were not) significantly different from each other (Table 6b). Larger stick-nests of the Australian Magpie *Gymnorhina tibicen* and the Red Wattlebird *Anthochaera carunculata* were significantly safer in storms than smaller passerine cup nests, which are typically made from finer material such as grasses. The enclosed nests of Yellow-rumped Thornbills *Acanthiza chrysorrhoa* were equivocal in that they did not significantly differ from either smaller or larger nests (Table 6b). Hole nesting species suffered no losses during storms (Table 6c).

Table 6a. *Effect per species*

Numbers, of each species, of cup and enclosed nests that failed in storms including those that nested in cracks, hollows and open cavities. ‡ enclosed nester; * non-passerine

Species	Total active	Failed	% failed
Yellow-plumed Honeyeater	45	10	22
Willie Wagtail	40	6	15
Red Wattlebird	40	2	5
Dusky Woodswallow	36	8	22
Australian Magpie	34	0	0
Yellow-rumped Thornbill ‡	27	2	7
Grey Fantail *Rhipidura fuliginosa*	19	1	5
Black-faced Cuckoo-shrike *Coracina novaehollandiae*	14	0	0
Western Yellow Robin	13	0	0
Red-capped Robin *Petroica goodenovii*	12	0	0
Scarlet Robin *Petroica multicolor*	12	0	0
Western Gerygone ‡	10	3	30
Restless Flycatcher *Myiagra inquieta*	9	1	11
Australian Raven	9	0	0
Jacky Winter *Microeca fascinans*	6	2	33
White-winged Triller *Lalage tricolor*	3	0	0
Common Bronzewing * *Phaps chalcoptera*	2	1	50
Blue-breasted Fairy-wren ‡ *Malurus pulcherrimus*	2	0	0
Grey Shrike-thrush *Colluricincla harmonica*	2	0	0
Brown Goshawk	2	0	0
Silvereye *Zosterops lateralis*	2	0	0
White-naped Honeyeater *Melithreptus lunatus*	1	1	100
Varied Sittella *Daphoenositta chrysoptera*	1	0	0
Totals	341	37	

Table 6b. *Selected species comparisons*

Pair-wise comparisons of the proportions of failed and successful nests, between six selected species using Fisher's exact probability tests (non-directional): underlined values are significant. The table significance level was set at $P < 0.05$. Note: if a Bonferroni test were applied no comparisons would be significant. *Abbreviation: yphe = Yellow-plumed Honeyeater

	*yphe	dws	ww	yrtb	rwb
Dusky Woodswallow (dws)	1.0000				
Willie Wagtail (ww)	0.4216	0.5556			
Yellow-rumped Thornbill (yrtb)	0.1897	0.1669	0.4590		
Red Wattlebird (rwb)	0.0294	0.0401	0.2633	1.0000	
Australian Magpie (am)	0.0039	0.0051	0.0280	0.1918	0.4965

Table 6c. *Hole nesting species*

Identity and number of hole nests active in storms. (Hole nests include burrows, hollows, nest in cracks and open cavities.) ‡ The Yellow-rumped Thornbill nests given here were enclosed nests that were built in cracks and thus hole nests. Also the Dusky Woodswallows (marked with an asterisk) typically have open cup nests, though the five given here were positioned in cavities and therefore treated as hole nests. No hole nesting species lost any nests to storms.

Species	Nests
Rainbow Bee-eater	41
Tree Martin *Petrochelidon nigricans*	29
Rufous Treecreeper *Climacteris rufa*	25
Striated Pardalote *Pardalotus striatus*	13
Western Thornbill *Acanthiza inornata*	8
Yellow-rumped Thornbill ‡	8
Laughing Kookaburra *Dacelo novaeguineae*	5
Dusky Woodswallow*	5
Southern Boobook *Ninox novaeseelandiae*	4
Scarlet Robin	4
Grey Shrike-Thrush	2
Australian Wood Duck *Chenonetta jubata*	1
Total	145

DISCUSSION

Overall impact and impact on nest type

There is a paucity of data on the proportion of nests lost to storms derived from empirical studies of assemblages and over multiple breeding seasons. The results that have been published show that failure rates are generally low. One assemblage-wide study found 2% of nests (2 from 122) were lost to storms in eastern Australia (McLean *et al*. 2005). In North America, Best and Stauffer (1980) identified 3% (9 from 302) lost to storms. Thus, my study's results seem comparatively high with 7% (31 from 468). However, the current study included only those nests that experienced a storm. This procedure was not explicitly reported in the other cited studies; thus this may help explain the differences.

Hole nests are widely regarded as safer, being sheltered from the wind (e.g. Lack 1954; Nice 1957; Martin and Li 1992). Yet, these studies have not isolated the function of storms from other factors such as predation as did this study. Additionally, in this study, some cup nests were provided greater protection by being constructed in open cavities such as knot holes or broken branches. None of these nests failed in storms indicating that they are similarly protected from wind. Notably, Nice (1957) found that cup nests in open cavities were intermediately successful between hole and cup nests. While her results provide some support to my findings, her results, like other studies, reported overall success rates without delimiting the proximate causes.

There were no differences in failure rates of cup and pensile enclosed nests. While pensile enclosed nests provide greater thermal benefits compared to cup nests (Martin *et al.* 2017), it has been generalised that they are more susceptible to wind damage, because of their structure and placement—often attached to the tips of terminal tree branches at the periphery of the tree (Chapman 1928; Morton *et al.* 1972; Schaefer 1976). Yet, the positioning of pensile enclosed nests on the periphery of trees is thought to make them less susceptible to arboreal predators with the thin terminal branches unable to support the weight of predators (Kendeigh 1942; Ricklefs 1969; Brosset 1974). At Dryandra, the two most frequent tree-nesting species with pensile enclosed nests (Yellow-rumped Thornbill and Western Gerygone *Gerygone fusca*) placed their nests, on average, less than half way to the periphery of tree-crowns. Such positioning may provide protection from winds or concealment from predators. Parsimony would suggest they may be avoiding predators since predation accounts for most lost nests (Fulton 2018a [Chpt. 1]; Fulton 2019 [Chpt. 2]).

Storm elements: wind, rain and the duration of the storm

Wind

Despite the apparent medium to moderate intensity of the winds recorded here they were responsible for the loss of 10% of cup and pensile enclosed nest assemblage. The sharp increase in the rate of nest failure as wind speeds increased underscores how even relatively moderate winds can become a significant hazard to these birds. This finding has additional significance in light of the climate-change predictions. Australian temperate woodlands are expected to experience an increased intensity of extreme storm events—projected with a high confidence overall and a medium confidence in south-western Australia (Hope *et al.* 2015; CSIRO and Bureau of Meteorology 2017). The wheatbelt of south-western Australia will likely experience a greater proportion of tropical and extra tropical cyclones with their more intense winds (Lim and Simmonds 2002).

Precipitation and the Duration of Storms

Wind was more important than rain in causing nest failure. Three storms had either light or no wind and caused no nest losses, and rainfall did not correlate with nest failure. Few studies have considered the effect of rainfall as a natural hazard on nesting success of above ground nesters. One recent study found heavy rainfall decreased breeding success in two Darwin's finch species, on the Galápagos Islands, where nest predation was minimal. They speculated that rainfall decreased foraging by parents (Cimadom *et al.* 2014). In another study, rainfall was partially correlated with nesting success of the American Redstart *Setophaga ruticilla* in one month, but overall predation accounted for 90% of failures (Sherry *et al.* 2015). Rainfall has been associated with flooding on or near the ground. Bourke (1948) reported that four species that nested close to or on the ground (Banded Lapwing *Vanellus tricolor*, Superb Fairy-wren *Malurus cyaneus*, White-fronted Chat *Epthianura albifrons* and Australasian Pipit *Anthus novaeseelandiae*) had their nests flooded by unusually high rates of precipitation (unspecified), in south-eastern Australia. At Dryandra, only one ground nest was active during a storm, a Painted Button-Quail *Turnix varia*, and it did not fail. Given the scarcity of data on how rainfall affects ground nests future observers might watch for how these nests interact with storms.

Burrow nests reported here were all one species Rainbow Bee-eater *Merops ornatus*, which excavated their burrows in broad flat low-lying areas of the landscape. While none failed to storms in this study they have been reported losing nests when placing their burrows in creeks that flooded (Lill 1993) and on flat and gently sloping landscape when precipitation exceeded 20 mm in 48 hours (Boland 2004). This quantity of rain only fell prior to the commencement of the Rainbow Bee-eater's breeding at Dryandra, which is typically the case each year, suggesting that their late start to breeding may be influenced by the annual rhythm of the Mediterranean climate of south-western Australia. Rainfall before digging their burrows softens the ground, while the decreased frequency of larger storms later in the season diminishes the likelihood of flooding.

The duration of storms in this study did not correlate with nest failure. Even when one storm closely followed another neither the extended duration nor the second storm increased nest failure. Thus, I conclude that this element is unimportant to nesting birds; at least for the durations of storms reported here.

Nest position

Two studies have identified birds orienting their nests in tree crowns away from prevailing or intense winds (Summers *et al*. 2002; Rae and Rae 2014) or towards the sun in the northern crowns of trees (Rae and Rae 2014). In the current study, nests were placed throughout tree crowns, yet significantly more were placed on the windward side of crowns in the face of storm winds indicating that the positioning of the nests was not governed by storm winds. Because this nest placement was non-random it may be better explained as a response to nest predation (Martin and Roper 1988; Martin 1993).

At Dryandra, nests placed in the centre of trees experienced a significant benefit over nests otherwise placed throughout the tree crown and over nests placed in the open (on ground wood or stags). Although 15 species had centrally positioned nests in tree crowns only the Western Yellow Robin commonly nested there. Yet, this species may have another overarching natural history reason causing them to nest there. Nest positioning by yellow robins *Eopsaltria* spp., (basally and centrally) is thought to be an adaptation to avoid nest predators (Debus 2006a; Cousin 2009). However, that does not discount that central positioning may also provide a benefit in relation to protection from the effects of storms.

Horizontal and vertical nest placement

I found no statistically significant evidence that the nests of this assemblage were adversely affected by storms due to their horizontal or vertical position in tree crowns or that they placed their nests differently in response to milder conditions late in the season. Overall these results indicate, for the magnitude of winds reported here, that birds are not responding to storms or wind. This result is somewhat paradoxical, because storms caused 10% of cup and enclosed pensile nests to fail.

However, predation is the most important factor affecting nesting passerines in Australian woodland (Fulton and Ford 2001; Debus 2006b; Fulton 2006a, 2006b, 2006c; Fulton 2018a [Chpt. 1], 2019 [Chpt. 2]). Thus, I hypothesise that this assemblage of birds has positioned their nests in response to nest-predation rather than the effect of storms, because nest-predation is more important to them.

Species most affected

All species of eucalypt forest and woodland birds position their nest differently and uniquely, yet they are all designed essentially for the same purpose. Yellow-plumed Honeyeaters lost more nests with nestlings than any other species. On the basis of these findings their nests may be more susceptible to strong winds than other species in the assemblage reported here. Western Yellow Robins benefitted from the protection of crown vegetation by placing their nests centrally, although this may be a secondary benefit from concealing their nests from predators (Debus 2006a) or seeking a sheltered micro-climate. Cup nests of medium to larger species, varying from Red Wattlebird (a large honeyeater) to Brown Goshawk *Accipiter fasciatus*, with nests constructed from sticks had fewer nest failures than smaller birds that built structures with fine grasses. The durability of larger stick nests may be either related to either longer incubation and brooding periods or may be an artefact of the bird's size—by simply being large it may need a sturdier nest.

CONCLUSION

Nest losses due to inclement weather do occur, although such nest losses are comparably fewer than those attributed to nest predation (Ricklefs 1969; Martin 1992; Remeš *et al*. 2012; Fulton 2018a [Chpt. 1]). Birds do not appear to position their nests within tree crowns to minimise the impact of wind, though wind was found to be the most important storm element in relation to nesting success. Presumably, birds have adapted to the climatic conditions to which they have been exposed over evolutionary time and their nest placement is more focused on avoiding nest predators (Martin 1995; Fulton 2018b). Thus, in terms of weather, they may be more adversely impacted by atypical weather events—whether or not these are naturally occurring or caused by human induced climate change. Yet perhaps most importantly, while discrete weather events may destroy nests the birds will respond by re-nesting.

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5. LOW-LYING LANDSCAPE & SOILS

SPATIAL PLACEMENT OF BIRD NESTS IN EUCALYPT WOODLAND

ABSTRACT

Australia's forest and woodland birds are threatened by habitat loss and degradation, particularly through the disproportionate loss of habitat on better-quality soils. In a disappearing landscape it is critical to know what parts of the landscape must be preserved to support or recover the remaining avifauna. This study surveyed an assemblage of threatened woodland birds and determined that they preferentially nested close to the lowest landscape contours on the more productive and more mesic soils. The location of 413 nests were mapped using a Differential Global Positioning System (DGPS) with sub-metre accuracy. The number of nests increased exponentially with increasing proximity to the lowest contours of the landscape. This results supports the hypothesis that the more mesic and more productive soils of the low-lying areas of the landscape must be preferentially reserved and restored.

Keywords: Landscape, Australia, Dryandra, low-lying areas, most productive soils

INTRODUCTION

The worldwide reduction and modification of forest and woodland habitats for agricultural and pastoral pursuits has resulted in the dramatic decline of bird numbers (Bregman et al. 2014; Betts et al. 2017). Even in large reserves bird declines are forecast to continue through a diminishment of food resources under climate change (Mac Nally et al. 2009). In Australia, temperate eucalypt woodlands were once widespread in what are now vast agricultural expanses (Prober et al. 2002). In Australia, for forty years, the number of woodland birds has declined substantially (Ford and Howe 1980; Garnett 1993; Reid 1999; Ford et al. 2001; Fulton and Majer 2006; Watson 2011; Lindenmayer et al. 2018). This vast removal of the woodland landscape, which has resulted in the widespread losses of bird and other biota has not occurred uniformly—spatially or temporally. The woodlands on the most productive soils, in the low-lying areas of the landscape, were cleared first and most thoroughly (Prober et al. 2002), despite harbouring the greatest abundance and species richness of birds (Bentley and Catterall 1997; Catterall et al. 1997). The surviving fragments of woodland are generally on poorer soils considered unsuitable for agriculture, particularly on rocky slopes and ridge-tops that are limited in size (Ford et al. 2001). Surviving fragments are further degraded by continued grazing and the removal of coarse woody debris (Mac Nally et al. 2000; 2001; 2002). In such an inhospitable environment it is important to understand the life history strategies employed by birds to halt their declines and facilitate their recoveries (Watson 2011; Remeš et al. 2012; Fulton 2018 [Chpt. 1]; Fulton 2019 [Chpt. 2]).

Avian reproduction and juvenile recruitment are fundamental themes in the study of avian life histories (Lack 1954; Martin 1992a; 1992b). The spatial and temporal proximity to food resources is an important ecological requirement for successful reproduction. Nix (1976) aligned bird breeding with the broadscale temporal sequence of plant growth and invertebrate food supply. For example, honeyeaters bred when nectar and invertebrates associated with flowering were available, while frugivorous and granivorous species bred later in the cycle as seed and fruit become abundant. Martin (1987) linked food to reproductive success. He highlighted that food was limited spatially with birds having larger clutch sizes and greater reproductive success in more productive habitats, even when compared to increased food between years and food increases through supplemental feeding. Yet, limiting food may not simply be expressed as starvation of young, it is expressed through smaller or fewer clutches (Martin 1992a). Therefore habitats that provide more abundant and reliable food for birds would be favoured by breeding birds (Martin 1992a).

In Australia, the preferential clearing of the low-lying areas in the landscape was non-random, because well hydrated and richer soils were attractive to agriculture (Catterall et al. 1998).

Likewise, they are productive habitats for native biota. Such an hypothesis has been supported by broad studies, which have found that the richest and most abundant invertebrate faunas have been recorded from sites with the greatest soil fertility (Recher et al. 1996). Watson (2011) developed this hypothesis further and presented a landscape wide productivity based explanation for the decline of woodland birds through a change and diminution in soil nutrients and soil invertebrates. He hypothesised that these decreases resulted in the reduction of invertebrate prey for insectivorous woodland birds, which in turn resulted in their reduced reproductive output. He generated falsifiable predictions, one of which stated, “Abundance, species richness and reproductive output of woodland birds are greater in sites with greater availability of invertebrate prey.” Such hypotheses are testable at Dryandra, because it is a large reserve of undisturbed old growth woodland. It encompasses a mosaic of habitats including large areas of the more productive valley soils (McArthur et al. 1977; DEC 2011) and it shelters an almost intact avifauna (Fulton 2013). As such it provides an opportunity to examine how birds locate their nests in a woodland landscape when many different habitats are available, but also to show how intensely they responded within the low-lying and most productive areas of the landscape, where greater productivity and more nests have been detected (Majer 1985; Majer et al. 2003, Fulton and Rose 2007; Fulton 2013). The aim of this study was to establish if the number of nests increased with proximity to the lowest landscape contours.

MATERIALS AND METHODS

Study site: Dryandra Woodland

Dryandra Woodland (Dryandra) is located about 160 km southeast of Perth (Lat. 32 48' S, Long. 117 0' E) on the western side of the Western Australian wheatbelt (Figure 1). Dryandra is comprised of a series of large woodland fragments, which are separated by agricultural land and scattered over an east-west distance of approximately 35 km (Friend *et al*. 1995; DEC 2011).

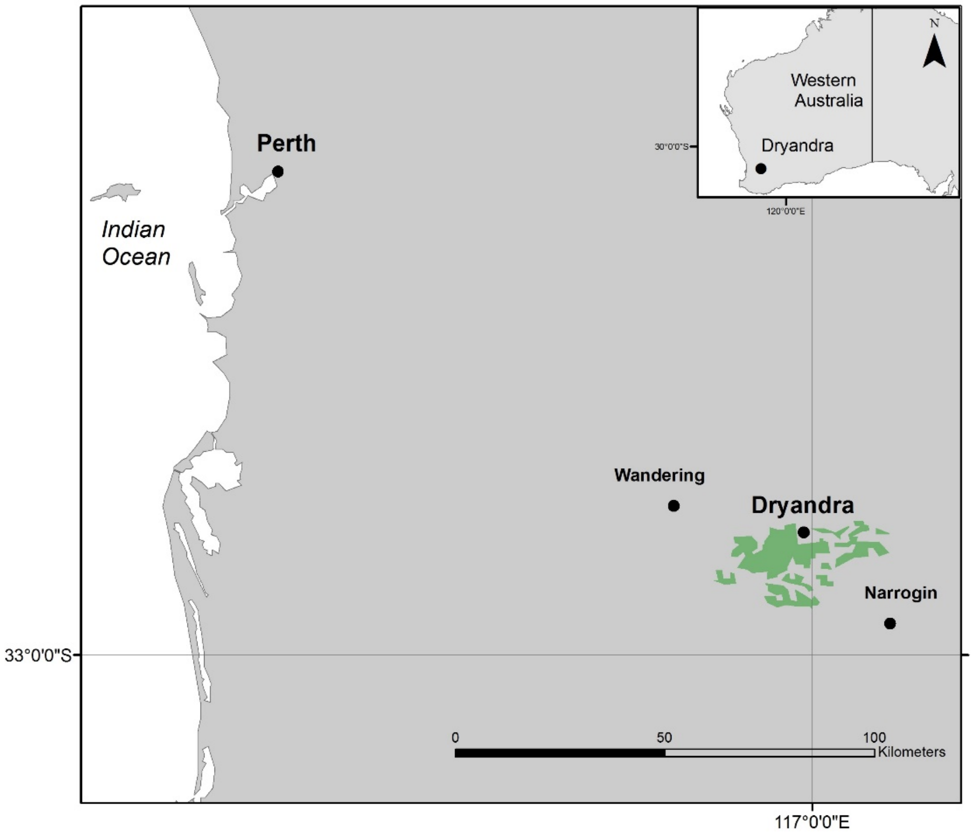

Figure 1. Dryandra in relation to Perth and southwestern Australia

Vegetation, landforms and soil

In general, the woodlands are characterized by Powderbark Wandoo *Eucalyptus accedens*, Jarrah *E. marginata* and Brown Mallet *E. astringens* on the mid and upper slopes, with Wandoo *E. wandoo*, Jam *Acacia acuminata*, (and less commonly Marri *E. calophylla*) on the lower slopes and valleys — Powderbark Wandoo and Wandoo (*E. wandoo*) woodland make up approximately 50 per cent of the total area (McArthur et al. 1977; Coates 1993; Fulton 2013). Hereafter Wandoo (*E. wandoo*) woodland is referred to as *E. wandoo* woodland to avoid confusion with the general term wandoo woodlands, which refer alternatively to Powderbark Wandoo, *E. wandoo* and collectively wandoo woodlands. At Dryandra, the lower levels of the landscape collect the most water and nutrients and thus have the richest and most mesic soils (DEC 2011).

Dryandra lies in the south-western province of the Yilgarn Craton, an ancient plateau (3.0 Ga (a Gigaannum is 10^9 years)) and ranges from 300-400 m ASL (McArthur et al. 1977). Past weathering of the plateau has produced a gently undulating countryside that can be partitioned into three broad landform units: Norrine unit (lateritic uplands), Noombling unit (long gentle valley slopes) and Biberkine unit (moist alluvial soils on central valley floors) (McArthur *et al*. 1977). The vegetation communities of Dryandra are closely linked to these landform units with two landform units linked to the bird breeding areas reported herein: The Noombling unit (lower valley) is associated with Powderbark Wandoo and *E. wandoo* woodland, covering extensive areas within Dryandra and the Biberkine unit (moist sites on the central valley floor) associated with *E. wandoo* woodland and Jam *Acacia acuminata* forest. The latter woodland is less common, covering comparatively smaller areas (DEC 2011). An understorey of grass, herbs and scattered shrubs persists in the *E. wandoo* woodlands throughout Dryandra. There are more than 800 native plant species at Dryandra (Coates 1993; Friend et al. 1995).

Landscape context and management

Dryandra is unlike other temperate woodland remnants in Australia due to a number of factors, including its overall size (27 000 ha), which embraces large areas of undisturbed old-growth woodland (Friend et al. 1995; DEC 2011) and its location on the central western side of the Western Australian wheatbelt where up to 97% of the original native vegetation has been removed (Saunders and Curry 1990, Saunders and Ingram 1995). Dryandra holds an almost intact bird fauna in ecologically functional numbers, including many species lost from remnants of the central wheatbelt (Fulton 2013). It also harbours rare marsupials that have become extinct in the surrounding wheatbelt and some that have been re-introduced (Fulton 2017 [Chpt. 3]). The natural presence of fluoroacetate (natural poison) bearing plants, particularly Sandplain Poison *Gastrolobium microcarpum* has had a major influence on allowing native species to persist at Dryandra (Short et al. 2005). Since the 1980s the control of the Red Fox *Vulpes vulpes* using 1080 (fluoroacetate) baiting has enabled the recovery of marsupials, birds, and reptiles, which were adversely affected by fox predation (Burbidge et al. 1996; Friend and Beecham 2004; Possingham et al. 2004), although subsequent predation by cats *Felis catus* is now known to have reduced the numbers of some of these endemic animals (Marlow et al. 2015). Dryandra has been a focal point of research since 1980s with baseline data accumulated across a wide diversity of biota (Friend et al. 1995; DEC 2011). Its ongoing management as a National Park suggests that this will continue.

Climatic overview

Dryandra experiences a Mediterranean climate with hot dry summers and mild wet winters. The wettest six-month period is May to October, accounting for 80 per cent of the annual precipitation (N = 115 years; 1887-2003). The mean annual rainfall varies across Dryandra with 600 mm in the west to 500 mm in the east (Sutton et al. 1994; Fulton 2013). The annual mean minimum and maximum temperatures range from 8.4°C to 23°C (N = 98 years (N = 102 years; 1901-2003) (Fulton 2013; Fulton unpublished storms).

Nests and Mapping

Nest searches

Bird nests were located and monitored over three breeding seasons from September 2002 through to January 2005. Nests were recorded and contours lines mapped from seven sites within the main block at Dryandra and the most remote and isolated block, 14 Mile Brook, making eight study sites (Table 1). All eight field sites were located in the low-lying areas of the *E. wandoo* woodland where the majority of birds breed (Fulton and Rose 2007; Fulton 2013; Fulton and Possingham Chpt. 6). Search areas were established based on the location of birds. Birds were initially searched for by driving 169 kilometres on access roads and walking 106 kilometres along two and three-kilometre-long transects (plus return = 6 and 4 kms) through the woodlands (Appendix 3). Subsequently, I learnt to search for nests near the lowest hydrological contours, because this is where the birds were found. After establishing that more birds and nests were found in the low-lying areas they were only searched for there.

Low-lying area searches for nests extended outwards from these lowest contours and from the first discovered nests over continuous repeat surveys. The expansion of the search area ceased as the likelihood of discovering a nest approached zero. New nests typically appeared within the search area over the course of the breeding seasons. Nests were detected by observing birds, which were then followed to their nests. On rare occasions new nests were detected whilst monitoring active nests. Descriptions of the nests position, including woodland tree type were written down while in the field and later that night entered into a database. All nests were given a unique identifying code.

Detectability—The repeated, sometimes daily, visits to each site enabled me to know where birds were or should be. I learnt the habits of individual and species. If their behaviour changed, if or one of a pair, or a pair were missing, it would be noticed and a cause searched for. Yet, despite my continued observations some birds remained difficult to detect. Button-quails *Turnix* spp., and the Bush Stone-Curlew *Burhinus grallarius* are not uncommon at Dryandra (Fulton 2013), but their numbers could not be confidently estimated nor their nests frequently found because their detectability was low due to their cryptic appearance. In general, many nests of ground nesting birds were missed. There was some heterogeneity of habitat density; *Gastrolobium* spp. thickets occurred patchily, especially on less fertile laterite breakaways situated at the peripheral margin of *Eucalyptus wandoo* woodland. Birds that frequented this vegetation, e.g. fairy-wrens *Malurus* spp. were more difficult to detect. However, knowing this meant that more careful and prolonged observations were undertaken in these areas. In general, the habitat heterogeneity did not obscure the movement of birds to and from denser patches and all observations led to appropriate nest searches. Despite this some species were too cryptic, which resulted in low detection rates for their nests.

Nest and contour line mapping

At the conclusion of the three-year-survey a Differential Global Positioning System (DGPS) was used to create digital markers for each nest location and to draw lines by carefully following the lowest hydrological contours, at each site. The DGPS system had a sub-metre accuracy. The lowest contours were walked while wearing the DGPS and as it recorded a point every two seconds to thus draw a line. While the sites and their lowest points were known from frequent surveys and nest monitoring, great care was taken to observe carefully, because the lowest contour was easily lost on the generally flat-looking surface (see Figure 2).

Figure 2. *Eucalyptus wandoo* woodland at Marri Road, in Dryandra. There are descending altitudinal gradients from the centre foreground to the rear and from the left and right to the centre, of the photo. The lowest mesic contour is slightly to the right of the large *E. wandoo* tree near the centre.

ArcGIS analyses

ArcGIS Pro 2.2.3 was used to map the nests sites, including marking up nest locations and measuring distances. Bird nests (as points) and the lowest contours (as lines) were added to a map in ArcGIS. Straight line measurements were made from points representing nests to the closest points on the lowest contour lines. These distances were recorded to the nearest centimetre then tabulated for later evaluation.

Nest distribution pattern and statistical analyses

Nest locations relative to the lowest contours

To discern if more nests were clumped closer to the lowest landscape contours the distance between the contour (zero) and the furthest nest (after deleting two outliers) was established and divided by 10. The number of nests in each tenth of this distance was then tabulated and graphed for analysis. This procedure was repeated for all eight sites, but divided into fifths, then tabulated and graphed.

The division of data into tenths and fifths was undertaken arbitrarily for convenience and to correctly gain the shape of the distribution. Quadratic regression was used to assess the strength of the overall relationship for the pattern detected between the number of nests (dependent variable) and their distance from the lowest contours (independent variable). All individual sites were graphed to compare their distribution of nests to that of the combined data.

Table 1. Location of field sites within Dryandra: approximate centres given.

Site name	**Coordinates**
1. Marri Road	32°46'27.6"S 116°55'18.7"E
2. Gura Crossroads	32°44'48.6"S 116°56'32.8"E
3. Spider Orchid	32°47'03.7"S 116°56'55.3"E
4. Gura Road	32°45'26.2"S 116°57'09.0"E
5. Old Mill Dam	32°47'10.8"S 116°58'03.3"E
6. 14 Mile Brook	32°49'55.4"S 117°05'44.3"E
7. Congellin	32°49'17.0"S 116°53'14.1"E
8. Site 33: Tomingley Rd	32°47'52.9"S 116°54'02.1"E

RESULTS

Nest locations

Overall the numbers of bird nests increased with increasing proximity to the lowest contours (Figure 3). This general pattern of a sharp increase in nests with increasing proximity to the lowest contours was observed at all eight sites, although a variation between curvilinear and linear distributions was detected (Figures 4a-h). An overall significant quadratic effect was observed with the combined data for all sites with the number of bird nests increasing with proximity to the lowest contour $R^2 = 0.89$, $F(2, 7) = 28.20$, $\beta = 518.18$, $t = 4.43$, $p < 0.01$, with the relationship was described by a single curve $Y = 253.87 + 518.18x^2$ (Figure 3).

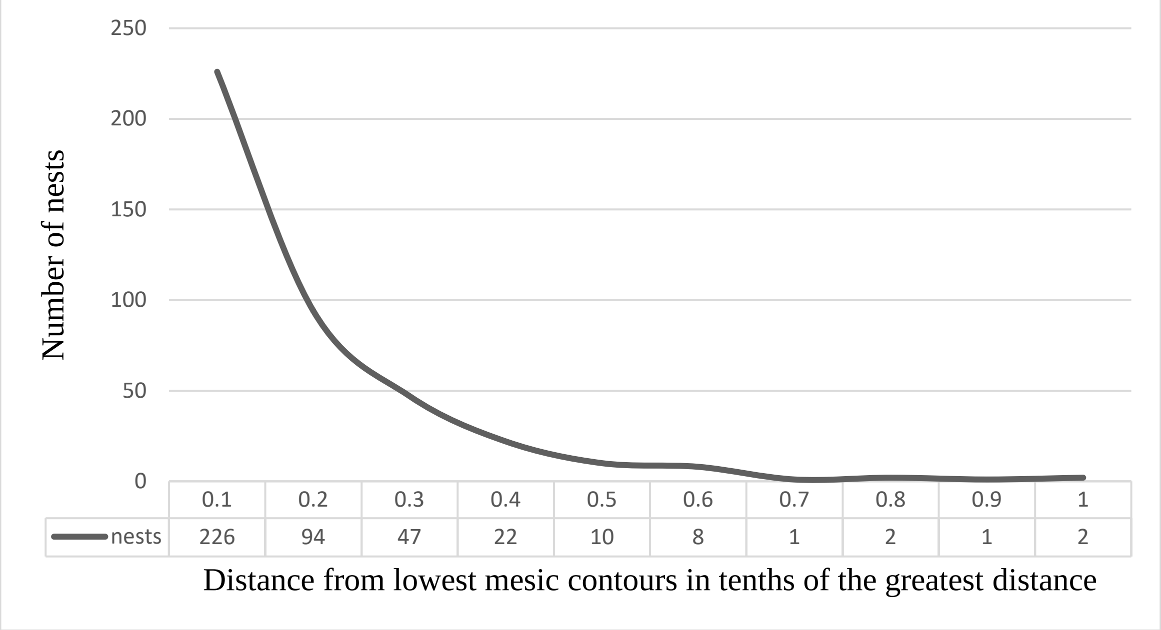

Figure 3. Number of nests decreasing with greater distance from the lowest contours, for all eight sites combined: N = 413 nests in total with the greatest distance at 463 m.

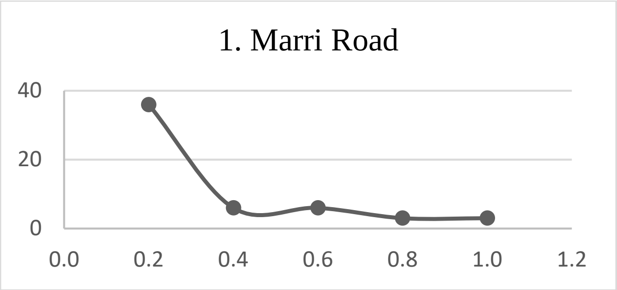

Fig.4a: N = 54 nests with greatest distance at 287m

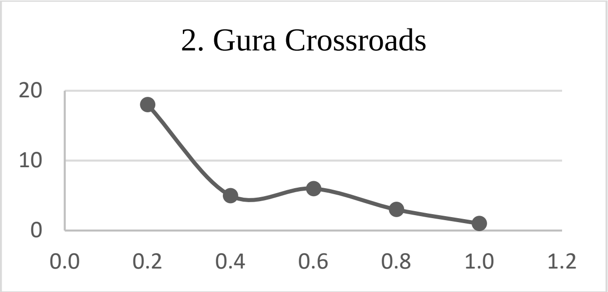

Fig.4b: N = 33 nests with greatest distance at 88m

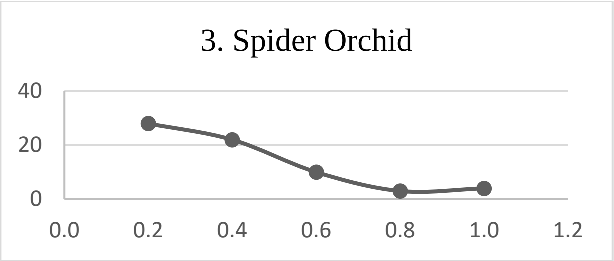

Fig.4c: N = 67 nests with greatest distance at 219m

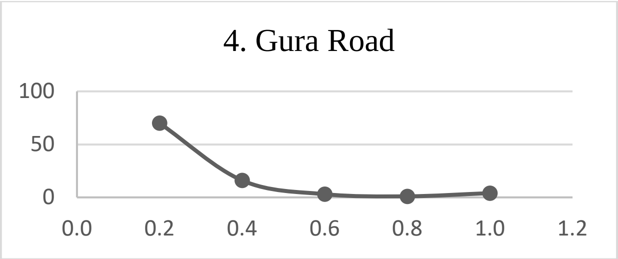

Fig.4d: N = 94 nests with greatest distance at 463m

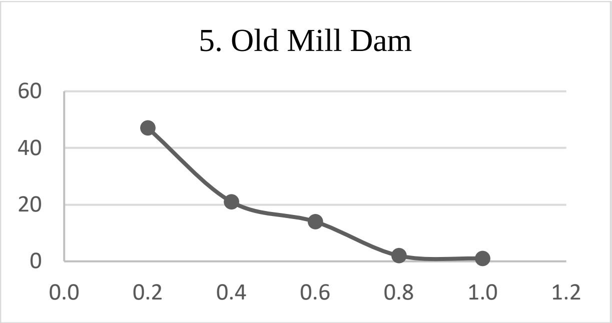

Fig.4e: N = 85 nests with greatest distance at 381m

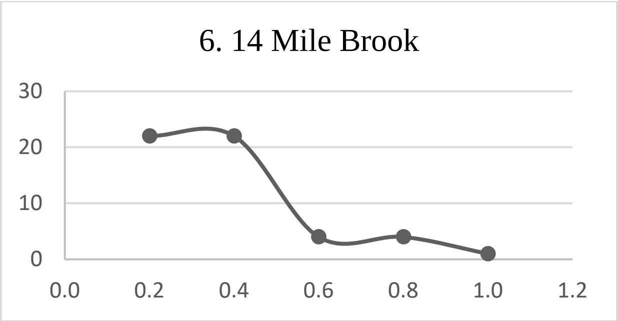

Fig.4f: N = 53 nests with greatest distance at 151m

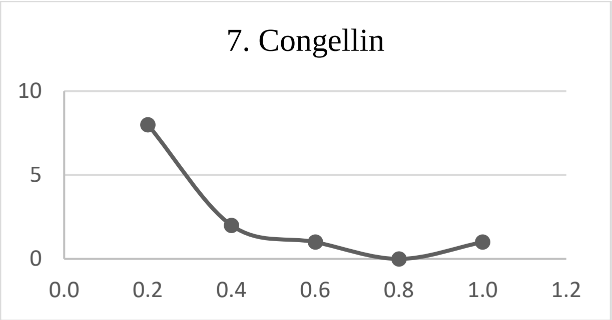

Fig.4f: N = 12 nests with greatest distance at 113m

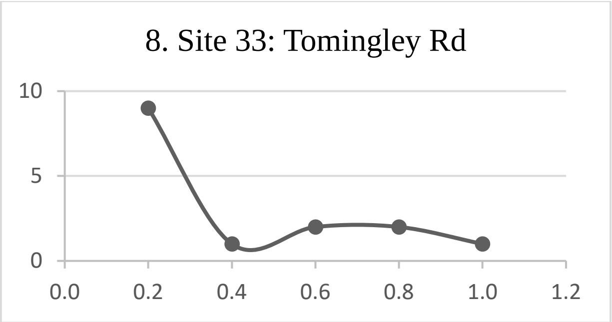

Fig.4h: N = 15 nests with greatest distance at 156m

Figures 4a-h. Number of nests decreasing with greater distance from the lowest contours for all eight sites presented individually. Y-axes give the numbers of nests and X-axes give distance from lowest contours in fifths of the greatest distance.

DISCUSSION

Nests located in low-lying areas

It is widely accepted that the preferential clearing of woodland from the low-lying areas of the landscape has exacerbated the loss of woodland birds (Bentley and Catterall 1997; Catterall et al. 1997; Bennett and Watson 2011; Watson 2011). It is hypothesised that the loss of this more fertile habitat has led to decreases in nectar and invertebrate prey, which in turn has reduced the reproductive success of woodland birds (Watson 2011). Herein this scenario was examined in an old growth woodland, Dryandra, which has retained a mosaic of habitats including the low-lying areas of the landscape with their higher soil moisture and greater productivity.

At Dryandra, a threatened assemblage of nesting birds clumped their nests in the low-lying areas on the Biberkine soil unit. With the numbers of nests increasing significantly with increasing proximity to the lowest lying or more mesic contours in the landscape. This pattern of nest placement is consistent with the hypothesis that the assemblage is responding to attributes found there—higher soil moisture, which leads to greater primary productivity. At Dryandra, the Biberkine soil unit is recognised as the most productive soil type within the Murray River Catchment Area that encompasses Dryandra (McArthur et al. 1977). The soil's higher productivity is due to its position in the landscape, its composition of depositional material of alluvial origin (McArthur et al. 1977) and moisture from its position in the central valley floors (Friend et al. 1995).

At Dryandra, invertebrate studies conducted on vegetation of this soil unit, *E. wandoo* woodland, have reported increases in both abundance and species richness (Majer 1985; Majer et al. 2003). More precisely they have reported: a positive correlation between the abundance and species richness of canopy arthropods with foliage and soil nutrients (Majer et al. 2003). Additionally, *E. wandoo* woodland was found to support more invertebrates than Powderbark Wandoo woodland (Majer et al. 2003); while ground and litter invertebrates counts were higher at sites with greater moisture, and soil moisture was highest in the low-lying area (Majer 1985).

Numbers of bird nests increased with increasing proximity to the lowest contours. Yet ephemeral running water, of about 2cm depth, was only observed on one survey in the low-lying area of the Gura Road transect and never at Marri Road. Nonetheless, the lowest contours are where moisture is greatest. Such a clear gradient supports a strong response to productivity, yet the slope or gradient in the study areas is very gentle ranging from 1:300 to 1:500 (McArthur et al. 1977 and see Figure 2).

Overall, the discussion above highlights an association between more productive soils, in this study, the Biberkine soil unit, with *E. wandoo* woodland and the nests of an assemblage of threatened woodland birds. This association appears rooted in the more productive and moister soils, supporting Watson's hypothesis that the loss of woodland bird habitat on better quality soils will diminish food resources and thus reduce reproductive output of woodland birds (Watson 2011).

Patterns of nest location

While the overall pattern of nest placement increased at an increasing rate with proximity to the lowest contours, this was not the case for all field sites. Some field sites were observed with a more linear distribution. What they shared was a quick drop-off in nests as the distance from the lowest contour increased. This suggests that factors other than soil must be involved in the placement of nests. Notably, Fulton and Possingham (Chpt. 6) shows that the availability of concealment in *E. wandoo* trees, at Dryandra, is significantly related to nest placement and nesting success highlighting that the vegetation type and its characteristics are also important. Presumably the width of the low-lying area may also affect the distribution of nests with sites on narrow low-lying areas less likely to have a long tail of more widely spaced nests. Yet, at Dryandra, narrow sites (e.g. Gura Crossroads: Figure 4b) still demonstrated the pattern of most nests close to the lowest contour.

Conservation implications

A threatened assemblage: A conservation priority

Woodland birds have seriously declined across southern Australian with local extinctions reported in many areas (e.g. Garnett 1993; Garnett and Crowley 2000; Garnett et al. 2011). Overall, woodland birds have decreased on average by 53% since 2000 (TSX 2018). Within the paradigm of woodland bird decline a recurring pattern emerges with the same birds and bird groups being iteratively reported across the continent as the most effected. For example, Catterall et al. (1998) identified a strong correspondence between woodland bird declines in the lowlands south-eastern Queensland to other studies of regional decline; they highlighted whistlers, pardalotes, thornbills, gerygones (acanthizids), robins, and small honeyeaters. Reid (1999) cited the selective clearance of vegetation types on fertile soils as the ultimate cause of decline in the sheep and wheatbelt of NSW; highlighting a predominance of insectivores and ground feeders and emphasising whistlers, acanthizids, robins and babblers having most declined. Across the continent in the wheatbelt of south-western Australia, whistlers, robins, acanthizids, flycatchers, quail-thrush, Rufous Tree-creeper and honeyeaters, particularly the Yellow-plumed Honeyeater were reported in significant decline (Saunders and Curry 1990; Saunders and Ingram 1995). The same groups of birds have been reported in decline in other temperate Australian woodlands, for example, the Fleurieu Peninsula/Mount Lofty Ranges, in South Australia (Szabo et al. 2011) and the northern plains of Victoria (Bennett and Ford 1997). Yet, Dryandra presents a contrasting picture to this decline with the usual declining species persisting there (Fulton 2013). Dryandra retains an almost full community of birds, most of which have increased in abundance—Rufous Tree-creeper *Climacteris rufa* and Yellow-plumed Honeyeater are common, contrasting with to their declines reported from the surrounding wheatbelt (Fulton 2013). Most notably, the assemblage of birds recorded in this study and nesting in *E. wandoo* woodland on the more mesic soils is the threatened assemblage of woodland birds iteratively reported in greatest decline across the continent. This study supports the hypothesis that they are the assemblage most in decline because they nest on the soils that are most frequently cleared of their natural vegetation. A prudent step would be to preferentially conserve and revegetate these areas of the landscape.

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6. CONCEALMENT IN COMPLEX TREE FOLIAGE

NEST CONCEALMENT IN COMPLEX TREE FOLIAGE PROVIDES GREATER NESTING SUCCESS IN OLD GROWTH WOODLAND: A STUDY USING DIGITAL COVER PHOTOGRAPHY

ABSTRACT

The nest is a critical stage in avian life histories, its success or failure impacts on the recruitment of new generations of adult birds. Some studies have found that birds may conceal their nests in tree foliage to avoid detection by predators. Yet such studies have used subjective judgments to infer this association based on how much of the nests are visible to the human eye. We used an objective measurement of foliage cover, known as digital cover photography, which counts sky and foliage pixels to determine the extent of foliage cover or conversely the accumulated gaps between the foliage. This is an overall assessment of the tree crown's foliage not simply above or beside the nest. Foliage cover included the architectural complexity of tree crowns and not merely leaves. We measured the north and south foliage cover on 267 trees that had had bird nests with known outcomes. There was on average 12 percent greater foliage cover on the northern side of a tree's crown - 76% of trees had greater foliage cover on the northern side. More nests were placed on the northern crown projections (north 120, South 74, centre 51, while 21 nests were placed almost exactly at 090° or 270°). Nests placed in the centre had greater nests success than those in the north by 17% while those in the north had greater success than those in the south by 18%. Overall 24 out of 29 species of birds placed their nests in trees which had greater foliage cover in their northern crown projections. These findings support the hypothesis that birds derive a concealment benefit from placing their nests where there is greater foliage cover and may derive a positive fitness benefit from nesting there.

KEY WORDS: Digital Cover Photography, temperate woodland birds, tree crown asymmetry, temperate Eucalyptus woodland, Australia

INTRODUCTION

Global reduction and modifications of forest and woodland habitats have caused bird numbers to decline (Bregman et al. 2014; Betts et al. 2017), declines that are exacerbated by climate change (Mac Nally et al. 2009). Hence it is important to understand the life history strategies employed by birds that could halt their declines and facilitate their recoveries (Remeš et al. 2012; Fulton 2018 [Chpt. 1]; Fulton 2019 [Chpt. 2]). Avian reproduction and juvenile recruitment are fundamental themes in the study of avian life histories (Martin 1992a; Martin 1995). Among these two themes nest predation has long been recognised as the major cause of nest failure in birds (Lack 1954; Skutch 1966; Ricklefs 1969). The heterogeneity of nest types and their placement highlights both the struggle birds experience with nest predation and the variety of anti-predator responses they have evolved to that predation (Collias and Collias 1984; Fulton unpublished a). Specific anti-predator responses may include hollow or burrow nests that are difficult for some nest predators to penetrate (Nice 1937; Fulton 2019 [Chpt. 2]; Fulton unpublished a), colonial nesting—where birds find safety in numbers (Rolland et al. 1998), or adults with cryptic plumage that are difficult to differentiate from their surroundings (Rae and Rae 2014). One general response is thought to involve concealing the nest, hereafter “concealment” (e.g. Martin and Roper 1988; Filliater et al. 1994).

In order to quantify and study concealment various techniques have been used by researchers to assess the vegetative cover around nests. For example, Remeš (2005) experimentally removed foliage to lessen concealment at some nests and compared rates of predation with undisturbed nests, Debus (2006) used a levy pole to assess vegetative complexity at different heights, while others have used subjective visual estimation of the vegetation at the nest (Filliater et al. 1994; Lambert and Kleindorfer 2006; Colombelli-Négrel and Kleindorfer 2009). Typically these assessments consider the nest’s concealment from different directions: above, below and beside. Yet another approach has used visual assessments at the nest combined with assessments and/or measurements of the vegetation surrounding the nest site (Kelly 1993; Lambert and Kleindorfer 2006). Direct visual assessment of the immediate vegetative cover at the nest remains a subjective approach, dependent on the observer. Levy poles (Majer 1981) and clump density measures (where a transparency with printed dots is held between the foliage and the observer’s eye) probably reduces the subjectiveness of the observers’ visual assessments, yet they still rely on the observer to be consistent in method and in judgment. Such subjective measures are unlikely to be consistent between observers.

Digital cover photography is an objective approach that photographs a tree’s foliage and provides accurate measures of foliage cover and its inverse, the gap fraction (sometimes called crown porosity). The gap fraction is the amassed gaps between stems and leaves. Digital cover photography has evolved from the need for objective estimations of the leaf area index of canopies. In particularly, to estimate attributes of forest canopies and develop models of vegetation canopy response to global environmental change (Jonckheere 2004; Alivernini et al. 2018). The procedure has advanced from using specialised fisheye to non-fisheye digital photography along with the software to analyse the images (Macfarlane et al. 2007; Macfarlane 2011). In this study, the procedure was adapted to compare the density of foliage between fractions of the canopy—specifically the north and south crown projections (otherwise known as hemispheres), to determine the degree of concealment available to birds on either side of a tree. This was done because significantly more birds were found nesting in the northern crown projections of trees, at my field site (North 171—South 105: north = 62%) (Fulton unpublished b).

This study aimed to test three related hypotheses: 1. examine if northern crown projections of trees, that were known to have had birds' nests, had greater foliage cover than the southern crown projections of the same trees; 2. to assess birds preferentially locate their nests in the northern crown projections; and 3. to assess nests experience greater nesting success than those in the southern crown projections.

MATERIALS AND METHODS

Study site: Dryandra Woodland

Dryandra Woodland (Dryandra) is located about 160 km southeast of Perth (Lat. 32 48' S, Long. 117 0' E) on the western side of the Western Australian wheatbelt (Figure 1). Dryandra is comprised of a series of large woodland fragments, which are separated by agricultural land and scattered over an east-west distance of approximately 35 km (Friend *et al*. 1995). The woodland is characterised by Powderbark Wandoo Eucalyptus *accedens*, Jarrah *E. marginata*, Marri *E. calophylla* and Brown Mallet *E. astringens* on the mid and upper slopes, with Wandoo *E. wandoo* on the lower slopes and valleys – Powderbark and Wandoo woodland make up approximately 50 per cent of the total area (Coates 1993; Friend *et al*. 1995).

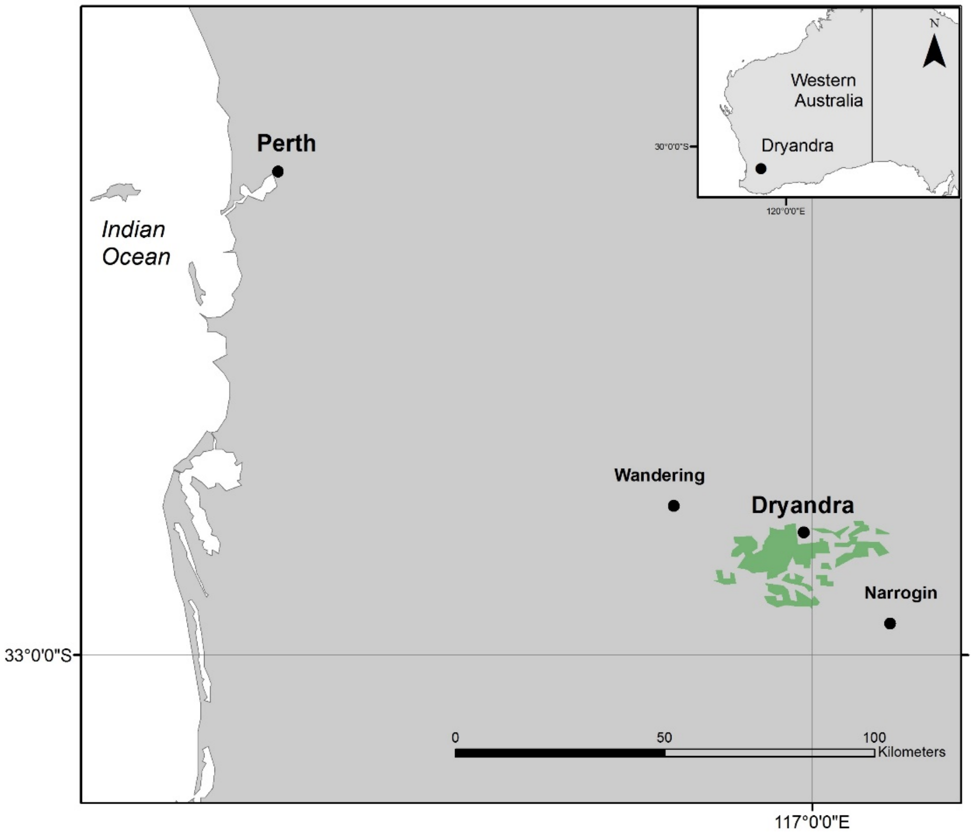

Figure 1
Dryandra in relation to Perth and southwestern Australia

Dryandra is unlike other woodland remnants, in Australia, due to a number of factors including its overall size (27 000 ha), which embraces large areas of undisturbed old-growth woodland (Friend *et al*. 1995) and its location on the central western side of the Western Australian wheatbelt where up to 97% of the original native vegetation has been removed (Saunders and Curry 1990, Saunders and Ingram 1995). Dryandra holds an almost full complement of bird species present in ecologically functional numbers, including many lost from remnants of the central wheatbelt (Fulton 2013; Fulton unpublished a). It also harbours rare marsupials that have become extinct in the surrounding wheatbelt and some that have been re-introduced (Fulton 2017 [Chpt. 3]). The natural presence of fluoroacetate (a natural poison) bearing plants, particularly Sandplain Poison *Gastrolobium microcarpum* has had a major influence on allowing native species to persist at Dryandra (Short et al. 2005). Since the 1980s the control of the Red Fox *Vulpes vulpes* using 1080 (fluoroacetate) baiting has enabled the recovery of marsupials, birds, and reptiles, which were adversely affected by fox predation (Burbidge et al. 1996; Friend and Beecham 2004; Possingham et al. 2004). However, subsequent predation by cats *Felis catus* is now known to have reduced the numbers of some of these endemic animals (Marlow et al. 2015). Dryandra has been a focal point of research since 1980s with baseline data accumulated across a wide diversity of biota (Friend et al. 1995). Its ongoing management as a National Park suggests that this might continue.

Climatic overview

Dryandra experiences a Mediterranean climate with hot dry summers and mild wet winters. The wettest six-month period is May to October, accounting for 80 per cent of the annual precipitation (N = 115 years; 1887-2003). The mean annual rainfall varies across Dryandra with 600 mm in the west to 500 mm in the east (Sutton et al. 1994; Fulton 2013). The annual mean minimum and maximum temperatures range from 8.4°C to 23°C (N = 102 years; 1901-2003) (Fulton unpublished b).

Wind, tree crown projection and shoot growth

At Dryandra, the canopy is open and the tree crowns generally do not meet or overlap. The study sites were in gently rolling hills without higher landscape features. Thus, light was available in all directions to enable growth in any direction. The trees have an asymmetrical crown projection to the north with greater foliage density. Foliage includes living and dead branches. Crown asymmetry was caused by the wind and harsh conditions coming predominately from the north during the tree's growth phase. Wind and harsh conditions may abscise leaves or damage apical meristems, causing greater lateral growth and epicormic sprouting (bushiness), which develops as an asymmetrical crown projection with greater foliage density (pers. comm. Alison Specht). In September, at Dryandra, the wind is predominantly from the north (Figure 2) and frequently associated with storms and thus colder conditions (Fulton unpublished b). This corresponds with the start of new growth (phenophases) in September and is followed by strong shoot growth in October (Specht 1981; Specht and Specht 1999).

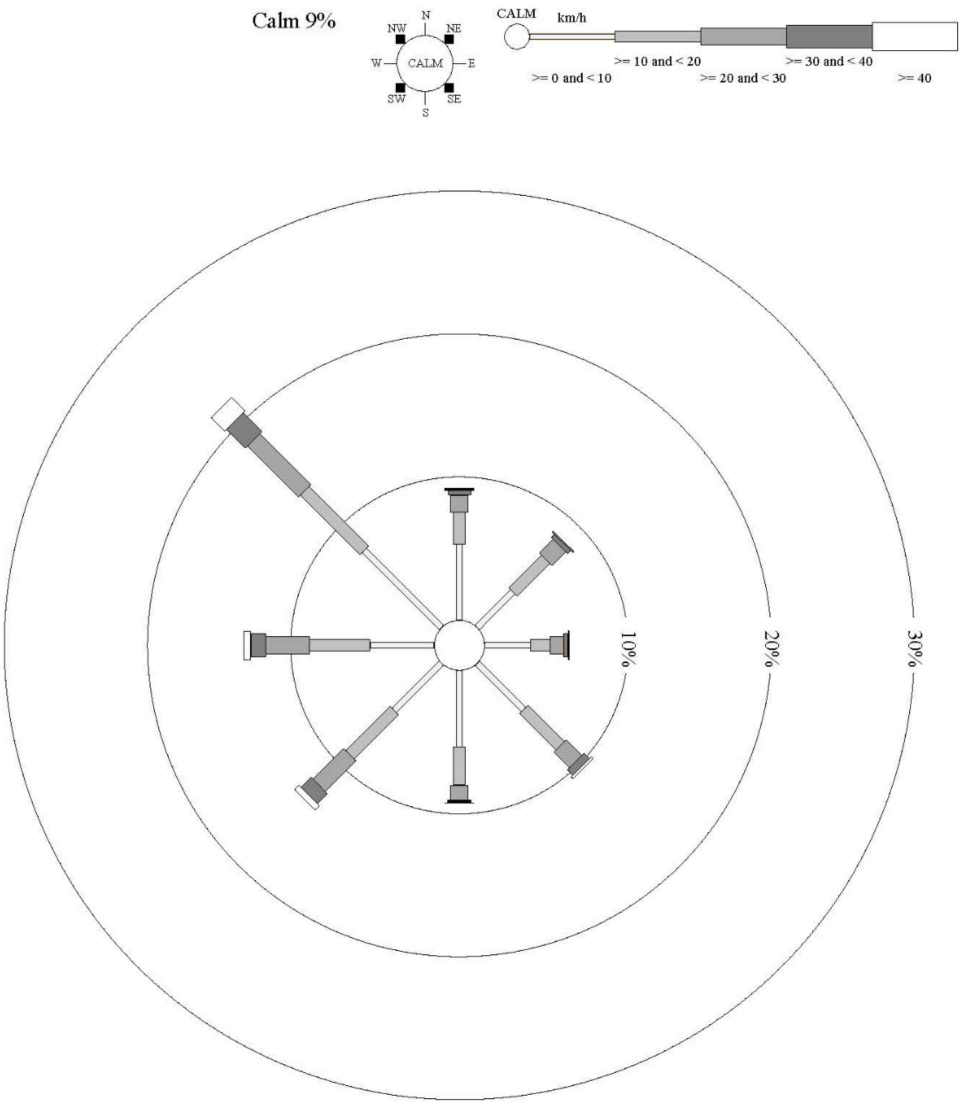

Figure 2. September wind rose, adapted from the Bureau of Meteorology's weather station, Wandering Comparison, situated 25 km west of the centre of Dryandra from data accumulated over the years 1901 to 2003. Wind speed is given in km/h.

Nest searches, mapping and monitoring

Bird nests were located and monitored over three breeding seasons from September 2002 through to January 2005. All site searches were within low lying areas of the *Eucalyptus wandoo* woodland where the majority of birds breed (Fulton and Rose 2007; Fulton 2013; Fulton unpublished a). See Fulton (unpublished a) for a detailed explanation of the site searches and monitoring. Once encountered, nests were marked with dark green surveyor's tape, chosen because it was difficult to see, minimising interference to the nest. Markers had shorthand text that gave the position of the nest tree and were always placed on shrubs or trees 10-20 m away from the nest tree. Descriptions of the nests' positions were written down while in the field and later that night entered into a database. All nests were given a unique identifying code. At the conclusion of each nest, following fledging or failure, a 10 cm length of the dark green surveyors tape was tied to a small 5 cm stick and placed on the ground directly under each nest's location. In instances where birds reused their nests for sequential broods the nests were flagged this way after the final brood had fledged. If it was thought the marker could be moved by running water the stick was pushed into the ground. At the conclusion of the three year monitoring survey a Differential Global Positioning System (DGPS) was used to create digital markers for each nest location. The DGPS system had a sub-metre accuracy. The ground markers were used in confirming the exact position of each nest at this time.

Detectability—The repeated, sometimes daily, visits to each site enabled me to know where birds were or should be. I learnt the habits of individual and species. If their behaviour changed it or one of a pair or a pair were missing it would be noticed and a cause searched for. Yet, despite my continued observations some birds remained difficult to detect. For example, I sat beside Tawny Frogmouths *Podargus strigoides* without noticing them causing then to fly away, but never found their nests. Button-quails *Turnix* spp., and the Bush Stone-Curlew *Burhinus grallarius* are not uncommon at Dryandra (Fulton 2013), but their numbers could not be confidently estimated nor their nests frequently found because their detectability was low. In general many nests of ground nesting birds were missed. There was some heterogeneity of habitat density; *Gastrolobium* spp. thickets occurred patchily, especially on less fertile laterite breakaways situated above *Eucalyptus wandoo* woodland. Birds that frequented this vegetation, e.g. fairy-wrens *Malurus* spp. were more difficult to detect. However, knowing this meant that more careful and prolonged observations were undertaken in these areas. In general, the habitat heterogeneity did not obscure the movement of birds to and from denser patches and all observations led to appropriate nest searches. Despite this some species were too cryptic, which resulted in low detection rates for their nests.

Nest monitoring and within crown positional assessment

Nest sites were visited daily seven days per week, in all daylight hours, throughout the three breeding seasons. Nests were never approached closely to avoid laying a scent trail that could be used by olfactory predators. Nests were checked daily, when close to fledging or hatching, otherwise every three to five days, rarely longer. A fuller description of nest monitoring is given by (Fulton unpublished a; Fulton unpublished b). The position of nests within tree crowns were recorded as compass bearings to the nearest five degrees, using a hand held compass and by standing at the main stem of the tree. For analysis of the categorical nest locations within tree crowns (north, south and centre) bearings for north were taken as greater than 270° and less than 090°, while south was greater than 090° and less than 270°. Those bearings recorded as 090° and 270° could not evaluated as either north or south.

Digital Cover Photography

Timing of image acquisition

Nest locations were revisited in October 2016 when the crown shape was assessed and the tree foliage photographed. October (mid-spring) was chosen because it coincides with the peak nesting period of the birds at Dryandra (Fulton unpublished a; b). It was also chosen to catch the same seasonal growth of the trees. The shoot growth of temperate southern-Australian *Eucalyptus* spp., begins in September with growth continuing through October and November, before decreasing in mid-December (Specht 1981; Specht and Specht 1999). There was a gap of between 11 to 14 years since the nests concluded. Some growth undoubtedly occurred in this period. Yet the growth differences between the north and south crown projections is governed by the long term climatic conditions, particularly the prevailing wind direction. It is a forest wide phenomenon—14 or 40 years ago the crown projections would still be in the same ratio. Nonetheless, future studies might try to photograph nests sooner after their conclusion.

Digital cover photography

Digital Cover Photography measures the foliage density, it is a measure that is independent of crown size or crown projection. Thus the comparison of the foliage density can establish if one side of the canopy has denser foliage than the other. In this study, the photographs were to capture the density of foliage on the north and south crown projections (hemispheres), for comparison. The comparisons were of the foliage density of the tree crown and not focus on foliage at nest locations.

A Nikon digital single-lens reflex camera (DSLR camera) was used to photograph the tree crowns. The camera had a 15-55 mm lens, flip-out LCD screen, and two opposed bubble levels to photograph consistently plumb and level. The camera was attached to a bracket and monopod stand, which allowed the camera to face upwards and be quickly positioned under trees. The camera settings remained unchanged for both hemispheres, including the height of the monopod. Images were captured in NEF (RAW) format and converted to JPG for analysis. Images were collected in the early morning, late afternoon or under overcast and almost windless conditions. The intention was to avoid having the sun appearing in the photographs, and avoid flaring from white wandoo trunks and branches. Photographs were not taken if the wind was visibly moving the leaves. The camera was placed under the north and south crown projections of each tree and images were captured with the camera pointed vertically and levelled. North and south crown projections refer to the north and south of the main stem, and not the north and south halves (50%) of the tree crown. The image was captured at the same distance (north and south) from the main stem on each side of the tree, but this distance varied between trees because trees have different sizes and heights. The camera's field-of-view was optimised to photograph the most foliage on each side. The field of view was controlled using the zoom through monitoring the flip-out LCD screen. This was done to avoid photographing too much sky beyond the perimeter of the tree crown. However, the software used eliminates the surrounding sky from the quantitative measurement of leaf cover and gap density. Photographs used to assess the foliage cover, or conversely the gap fraction, ideally had their crown hemispheres filling the entire field of view without gaps outside the crown boundary. Nonetheless, the software used to analyse the foliage cover was able to exclude light around the edges of the tree crowns.

Subjective assessments

Eucalyptus wandoo clumps and nests on dead ground-wood

Some birds nested in clumps (groups) of *Eucalyptus wandoo* trees. These trees were not photographed if the nest tree did not have a crown developed enough to stand out from the group of trees in the clump. Clumps consisted of a tightly clustered group of trees that had germinated simultaneously usually from a fallen mature tree. In such cases, a mature tree has fallen to the ground and all its seeds are dehisced simultaneously on that spot resulting in a tightly grouped clump of trees of the same age and species. Clumps were mostly, but not exclusively, young trees of *Eucalyptus wandoo*. Much larger and older trees shading a clump were photographed when they were considered to provide the primary shade and concealment for a nest. Clumps were subjectively considered to generally provide greater concealment in all directions and were used by various species, although no species used them exclusively (Table 1). In contrast, Jacky Winter *Microeca fascinans* and Willie Wagtail *Rhipidura leucophrys* often positioned their nests on dead ground-wood without apparent foliage cover or concealment (Table 1). This ground-wood appeared to have been a branch that had fallen from the northern side of a tree crown (uncounted). Thus these nests were shaded by the northern crown projection, from which the nest probably derived some concealment. However, nests on dead ground wood were subjectively considered to have less concealment than nests in trees and clumps of trees. Digital cover photographs were only taken if the nests were considered to be clearly under the crown of a shading tree. A half (n=26 from clumps) and a third (n=3 from ground-wood) had a covering tree's digital cover photographs taken (Table 1).

North-south visual and comparative crown assessment

A total of 287 trees were visually assessed for their ratio of north/south crown projection. Trees were visually assessed from the east or west, from as close as possible to 090º or 270º and far enough away to easily view the whole crown of the tree. An estimate of the fraction of the crown present on each side of the main stem, north and south, was made and recorded. A tree's crown was treated as 100% and divided into 10% fractions based on how much was present north and south. The following fractions 100/0, 90/10, 80/20, 70/30, 60/40 or 50/50 were recorded against the trees identity: an assigned code. The first number in the fraction represents the northern hemisphere. If the southern side of the crown had a greater proportion of the whole crown the ratio would be reversed e.g., 20/80, where the north is 20%.

Nesting success

While many trees had had monitored nests, only 216 were evaluated for their success in combination with their location in trees. Nests located in the centre were within hollows in the main stem or the nest abutted the main stem. Only nests that had successfully fledged young, been depredated, abandoned or had been parasitised by cuckoos were considered. Nests were excluded from analyses because: their location was recoded as either 090° or 270° and they could not be assigned to either north, south or centre; they had failed due to inclement weather or disease; they were completely exposed on dead branches without crown cover; they were in clumps without cover from a single and dominant tree, they were not monitored until their conclusion, and one was abandoned on the first day due to known non-predatory reasons. Thus, three fractions were derived for the three categories north, south and centre—where the numerator gave the numbers of successful nests and the denominator gave the total number of nests for that category.

Statistical analyses

Unless otherwise stated analyses were carried out in SPSS version 25.

Digital Cover Photography and foliage cover

Digital cover photography software DCP 3.14 (developed and supplied by Craig Macfarlane at CSIRO: WA) was used to analyse the images by counting pixels and deriving percentages of foliage cover and its inverse the gap fraction. A paired-samples t-test was conducted to compare foliage cover on the northern and southern hemispheres of 267 trees that had had monitored nests. A simple count was also conducted to establish the numbers and percentages of trees with greater foliage cover on their north and south hemispheres.

Visual assessment of the crown projection

To determine if the trees overall had more crown on the north, I used a single-sample confidence interval calculator that used the z-statistic. I obtained the 95% confidence interval of the sample mean of the data to test if there was significantly more canopy to the north than 50%.

Nest placement and success

To test if more nests were present in the northern crown projections than the two other sections of tree crowns, south and centre, I used a chi-square one-dimensional goodness of fit test on the VassarStats statistical website (Lowry 1998-2019). Additionally, a paired-samples McNemar exact two-sided test (using binomial distribution) was used to assess the difference between the number of nests placed only in north and south crown projections.

No nest or nest-tree was counted twice in any of the analyses, although some trees had more than one nest (though rarely simultaneous nests)—the first nest monitored in a photographed tree was chosen to use in calculations of nest success. A Chi-square test of independence was performed using SPSS version 25 software to assess associations between the categorical variables north, south and centre, against the frequency of success and failure of nests.

Eucalyptus wandoo clumps and nests on dead ground-wood

These nests were not subjected to statistical analyses, because those that had their covering trees photographed were analysed within the digital cover photography component of this study. Beyond this the subjective assessments regarding their degree of concealment are not considered reliable, or consistent with this studies assessment of concealment—nonetheless their results are presented in Table 1.

RESULTS

Foliage cover and nest placement

Overall the average foliage cover (or density) on the northern crown projections exceeded that on the southern by 61% to 49%, a 12% difference: A paired-samples t-test gave foliage cover north (M = 0.61, SD = 0.14) significantly greater than foliage cover south (M = 0.49, SD = 0.17); t (266) = 11.07, P < 0.001. In total, 204 of 267 trees (76%) had greater foliage cover in their northern crown projections. Of 266 nests that had locations associated with photographed trees (one nest had no within-crown location data), more nests (north 120) were located in the northern crown projections than each of the other two sections of the tree crowns: south 74, centre 51 ($\chi^2 = 30.23$, df = 2, P < 0.001); while 21 were recorded as east 090° and west 270° and could not be assigned to north and south. Considering only north and south nest placement: 120/194 = 62% of nests were placed in north while 74/194 = 38% were placed in the south of tree crowns—a 24% difference: twice that of the average difference in foliage cover between north and south crown projections was found. A paired-samples McNemar exact two-sided test (using binomial distribution) found the difference was significant $n = 194$, P < 0.001. A total 24 out of 29 (83%) species of birds nested in trees that had greater average foliage cover in their northern crown projections (Table 2).

Nesting success

The location and success of 216 nests were evaluated, from three categories (north, south and centre), of which 33 from 43 (77%) were recorded as successful in the centre of the tree crown while 67 from 111 (60%) were recorded as successful in the northern crown projections and 26 from 62 (42%) were recorded as successful in the southern crown projections (Table 2). Thus, a 17% difference was detected with centre > north and an 18% difference with north > south. Also, more nests failed than succeeded in the southern crown projection with the opposite result in the north and centre. The relationship between the categorical variables north, south and centre was significant ($\chi^2 = 13.043$, df = 2, P < 0.01) and the relationship between the categories variables north and south was also significant ($\chi^2 = 5.432$, df = 1, P = 0.02).

Subjective visual assessments

Visual assessment of the north-south crown projection

More trees (60%) had a dominant northward crown projection, than a dominant southward crown projection (6%), while 34% were assessed with equal north/south projections. Overall, nearly two thirds of the canopy projection was to the north (63.6%, SE=1.08: 95% CI 61.5% – 65.7%), 50% fell outside this 95% CI (Figure 3).

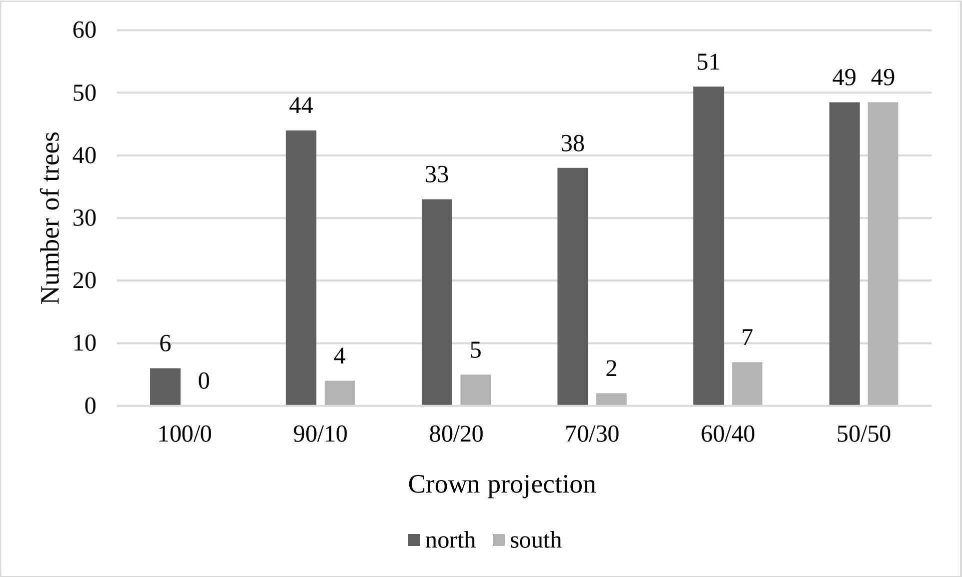

Figure 3.
The north/south crown projection of 287 trees that had bird nests. A tree’s crown was treated as 100% and divided into 10% fractions based on how much was present north and south.

Nests in Eucalyptus wandoo clumps and on dead ground-wood

Twelve species nested in clumps of *Eucalyptus wandoo* and two species nested on dead ground-wood. Of those that nested in clumps with known outcomes related to success, predation or abandonment 16 out of 44 (36%) were successful, while 6 out of 10 (60%) of those that nested on dead ground wood were successful (Table 1).

Table 1. Numbers of birds that nested in clumps of *Eucalyptus wandoo* or on dead ground-wood, and the number of north-south crown density photographs taken. Photos were not taken if sufficient foliage cover was not provided by a single tree. Success is given as a fraction where the numerator is the number of successful nests and the denominator gives the number of nests evaluated. Nests chosen for evaluation were successful, depredated, abandoned or parasitised by cuckoos, not failed through inclement weather or disease.

Species	*Eucalyptus wandoo* clumps	Success	N-S photos	Ground-wood	Success	N-S photos
Australian Raven *Corvus coronoides*	1	1/1	1			
Australian Magpie *Gymnorhina tibicen*	1	0/1	1			
Dusky Woodswallow *Artamus cyanopterus*	4	2/2	3			
Grey Fantail *Rhipidura albiscapa*	5	0/5	1			
Jacky Winter *Microeca fascinans*	1	0/1	1	1	1/1	
Restless Flycatcher *Myiagra inquieta*	2	N/A	1			
Rufous Treecreeper *Climacteris rufa*	1	3/3	1			
Western Gerygone *Gerygone fusca*	1	0/1	1			
Willie Wagtail *Rhipidura leucophrys*	8	1/7	4	11	5/9	3
Western Yellow Robin *Eopsaltria griseogularis*	10	2/9	2			
Yellow-plumed Honeyeater *Lichenostomus ornatus*	12	5/12	9			
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*	2	2/2	1			
Total	48	16/44	26	12	6/10	3

Table 2. Nest placement in relation to foliage cover and nest success by species. Nests located in the centre were within hollows in the main stem or the nest was abutted against the main stem. Nests categorised as north and south were in the northern and southern crown projections. Success is given as a fraction where the numerator is the number of successful nests and the denominator gives the number of nests evaluated. Empty cells have no data to show. The ‘n’ gives the sample sizes for the number of nest-trees analysed and the total number of successful and failed nests. The column with the inequality sign shows which of the crown projections, north of south, was the greater. Only 216 nests were evaluated in the success and failure categories with nests that had successfully fledged young, been depredated, abandoned or had been parasitised by cuckoos considered.

	FOLIAGE COVER				SUCCESSFUL NESTS			
Species	n	% North	% South	>	n	north	south	centre
Australian Magpie *Gymnorhina tibicen*	6	0.79	0.62	N>S	6	3/3	1/2	1/1
Black-faced Cuckoo-shrike *Coracina novaehollandiae*	11	0.58	0.42	N>S	11	5/10	0/1	
Brown Goshawk *Accipiter fasciatus*	1	0.39	0.77	S>N	1	1/1		
Common Bronzewing *Phaps chalcoptera*	2	0.59	0.58	N>S	1		0/1	
Dusky Woodswallow *Artamus cyanopterus*	40	0.60	0.48	N>S	30	6/10	4/13	6/7
Grey Fantail *Rhipidura albiscapa*	4	0.60	0.60	N=S	3	1/2	1/1	
Grey Shrike-thrush *Colluricincla harmonica*	3	0.69	0.35	N>S	2	0/1		1/1
Jacky Winter *Microeca fascinans*	3	0.57	0.44	N>S	0			
Laughing Kookaburra *Dacelo novaeguineae*	1	0.58	0.75	S>N	1			1/1
Purple-crowned Lorikeet *Glossopsitta porphyrocephala*	1	0.29	0.45	S>N	1			1/1
Red-capped Robin *Petroica goodenovii*	4	0.51	0.45	N>S	3		1/2	1/1
Restless Flycatcher *Myiagra inquieta*	15	0.52	0.36	N>S	13	5/10	2/3	
Regent Parrot *Polytelis anthopeplus*	1	0.47	0.54	S>N	1			0/1
Rufous Treecreeper *Climacteris rufa*	14	0.59	0.39	N>S	13	2/2	1/1	9/10
Rufous Whistler *Pachycephala rufiventris*	1	0.59	0.71	S>N	1	1/1		
Red Wattlebird *Anthochaera carunculata*	18	0.66	0.57	N>S	15	6/10	0/2	3/3
Southern Boobook *Ninox novaeseelandiae*	1	0.74	0.63	N>S	1	1/1		
Sacred Kingfisher *Todiramphus sanctus*	1	0.47	0.39	N>S	0			
Striated Pardalote *Pardalotus striatus*	6	0.65	0.31	N>S	4	2/2	1/1	1/1
Scarlet Robin *Petroica boodang*	6	0.53	0.47	N>S	6	1/1	2/3	2/2
Tree Martin *Petrochelidon nigricans*	13	0.65	0.51	N>S	9	6/6	2/2	1/1

Varied Sittella *Daphoenositta chrysoptera*	2	0.62	0.44	N>S	0			
Western Gerygone *Gerygone fusca*	11	0.59	0.51	N>S	11	3/6	3/3	0/2
White-naped Honeyeater *Melithreptus lunatus*	1	0.65	0.35	N>S	0			
Willie Wagtail *Rhipidura leucophrys*	23	0.64	0.50	N>S	17	4/10	0/3	3/4
White-winged Triller *Lalage sueurii*	3	0.68	0.52	N>S	3	0/1	0/2	
Western Yellow Robin *Eopsaltria griseogularis*	10	0.57	0.45	N>S	10	0/3	2/4	1/3
Yellow-plumed Honeyeater *Lichenostomus ornatus*	52	0.62	0.52	N>S	42	19/25	5/15	1/2
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*	13	0.63	0.50	N>S	11	1/6	1/3	1/2
Totals and means	267	$\overline{X}$ 61	$\overline{X}$ 49	N(24)>S(5)	216	67/111	26/62	33/43

DISCUSSION

Digital Cover Photography, foliage cover, concealment and nest placement

Digital cover photography was used in this study to avoid the subjective estimations inherent in visual assessments. In this study, I found greater foliage cover in three quarters (76%) of the northern crown projections and more trees with a greater crown projection on the northern side. All these trees had had a bird nest associated with them. In research on the same trees, Fulton (unpublished b) more birds were detected nesting in their northern hemispheres (62% in the north), yet at the same time winter storm winds blew from that direction. This finding was unexpected, thus we hypothesised that these nests may be using concealment to avoid nest predators since they appeared not to be avoiding the winter storm winds. With predation being the most important cause of nest failure (Ricklefs 1969; Martin 1995; Fulton 2018 [Chpt. 1]; Fulton 2019 [Chpt. 2]) we hypothesised that greater concealment may be available to the nests in the northern crown projections of these trees. In this study, the concealment hypothesis was supported by finding a positive association between nest placement and denser foliage cover. While there is a general expectation of finding more randomly placed nests with more foliage, in equal proportions, in this case there were unequal proportions—with 24 percent more nests on the northern crown projections compared with only 12 percent more foliage cover. The finding that nesting birds may use concealment to enhance nest success is not new, for example, Nice (1922) found Mourning Doves *Zenaida macroura* re-position their nests in trees in response to growing foliage cover—leaf-growth associated with deciduous trees. While Filliater et al. (1994) searched fruitlessly for a concealment/success relationship, with the Northern Cardinal *Cardinalis cardinalis*, using subjective categories of concealment that were related to the extent of foliage cover close to the nests. What is different and new in the current study is firstly the method used to determine concealment—Digital cover photography was used to quantify foliage cover, which provided an objective measure of concealment. Secondly the survey was undertaken across the assemblage of woodland bird species that used the trees for nesting. Unlike, Filliater et al. (1994), significant positive associations were found between foliage cover and nest placement highlighting that this assemblage uses the greater foliage cover in the northern crown projections to guide nest placement within the tree.

Nesting success and concealment

More nests were associated with greater foliage cover and more nests were successful when associated with the greater foliage cover. These associations support this study’s hypothesis that birds preferentially nests where greater concealment is available and they benefited from this concealment with greater nesting success. However, while these associations provide a compelling and plausible hypothesis they cannot conclusively demonstrate that the increased nest success was caused partly or wholly by concealment. Other anti-predator strategies are surely involved. Indeed concealment alone is unlikely to provide a panacea for all predatory strategies aimed at all nests or for any one species. Filliater et al. (1994) proposed that a high incidence of predation by a rich guild of nest predators precluded them finding a single or multiple predictor of nesting success. Yet concealment has been shown to increase nest success in some bird species (e.g. Martin and Roper 1988; Lambert and Kleindorfer 2006) and to increase nest success while acting in concert with other anti-predator strategies. For example, Colombelli-Négrel and Kleindorfer (2009) examined nest height, concealment and predator type: they found that predators relying on visual cues were affected by concealment whereas predators relying on olfactory cues were unaffected.

At Dryandra, foliage cover and concealment for birds was not simply about surrounding a nest with more leaves in a leafier side of the tree, a tactic employed by many honeyeater species (pers obs). Foliage cover is also provided by branches, alive or dead, thick or thin, green or grey, or blackened by fire. This diversity of foliage cover provides concealment for different nest types, placed differently in the tree-crown. Trees at Dryandra are considered to be old growth—such growth provides an architectural complexity that can support a myriad of nest that are concealed in different ways. For example, Varied Sittella *Daphoenositta chrysoptera* build their nests at the tips of high dead branches in the canopy (Pizzey and Knight 1997). The presence of dead branches without leaves may therefore be critical to them in concealing their nests. More dead branches surely aids their concealment. The variety of hollows, shapes and sizes, in an architectural complex tree crown projection also adds concealment opportunities to the various hollow nesting species. Tree Martin *Petrochelidon nigricans* Rufous Treecreeper *Climacteris rufa* both nested in hollows, some of which were in dead branches of the northern crown projections, others were positioned in the main stem. At Dryandra, most bird species known to have become threatened or extinct regionally have increased their abundance (Fulton 2013). It is plausible that the old growth of Dryandra's trees, with their age-related architectural complexity, has facilitated this response. Thus, I suggest that foliage cover be considered for its density and for its architectural complexity to understand concealment across an assemblage of species nesting in different ways.

Centrally placed nests

More nests were successful in the northern side of tree crowns than the southern side. Yet, the most successful nests by percentage were located in the centre of the tree. Nests placed centrally included those that consistently nested in hollows, which are known to be less affected by nest predation

(Lack 1954; Fulton 2019 [Chpt. 2]) and those that nested there inconsistently in other hollows such as knot holes and broken branches with hollows (spouts). For example, Dusky Woodswallow *Artamus cyanopterus* typically locate their nests on branches though, less frequently, they nest in knot-holes or in broken branches (Pizzey and Knight 1997). In this study Dusky Woodswallow's greatest success came from nests located centrally (Table 2). Centrally located nests may derive a concealment advantage from being simultaneously under both sides of the tree crowns whilst gaining additional concealment from the main stem, including the opportunities provided by partial and complete hollows.

Nest placement: a discussion of predation versus micro-climate and inclement weather

Evolution has generated a great variety nest structures and nesting strategies. For a long time the primary functions thought to be underlying this diverse array of structures and strategies was the need to provide warmth and safety for the developing eggs and young (Collias and Collias 1984). In this dogma, the emphasis rested with protection from climatic elements, particularly because altricial young hatch in a helpless state—featherless and blind (Heinroth 1922; Collias and Collias 1984). However, the importance of nest predation rose in prominence following the quantitative work of Robert Ricklefs (e.g. Ricklefs 1969) and later by Thomas Martin (e.g. Martin 1992b). Nest predation is now known to be the most important cause of nest failure (Ricklefs 1969; Martin 1995) and therefore parsimoniously linked as an important factor driving the evolution of nest placement. Concealment of nests is also known to be an important anti-predator response (Collias and Collias 1984; Martin and Roper 1988). Still many birds, particular small passerines, have evolved to position and construct their nests to avoid or ameliorate the adverse effects of inclement weather (Collias 1997). In Australia, where cold weather is less intense than North America or Europe, a consistent response to climate was perhaps not be expected. Nonetheless, the local climatic conditions were shown to affect the materials used in the construction of Australian bird nests and across a large geographical gradient (Heenan et al. 2015). This indicates that Australian birds do respond to climatic conditions and may react by placing nests in more or less exposed positions. However, a study of nest positioning within tree crowns, across an assemblage of birds at Dryandra, did not detect any changes in the degree of either horizontal or vertical nest placement between the winter storm and summer dry seasons (Fulton unpublished b). Thus, concealment as an anti-predator strategy in concert with other considerations such as food availability and local climatic conditions may best predict nest placement in Eucalypt forest and woodlands, in temperate Australia.

Nests in Eucalyptus wandoo clumps and on dead ground-wood

Not all birds use concealment the same way and therefore cannot be evaluated the same way as those that placed their nests within tree crowns. At Dryandra some species, although not exclusively, nested in clumps of eucalypt vegetation. Others placed their nests in seemingly exposed positions on dead ground wood; such positions may have gained concealment from tree crowns directly above. Yet others nest exclusively in shrubs, for example Blue-breasted Fairy-wren *Malurus pulcherrimus* nest in *Gastrolobium microcarpum* (Rowley and Russell 2002; pers obs). While contrastingly the Rainbow Bee-eater *Merops ornatus* excavated tunnels on flat ground, gaining concealment by being underground (Fulton and Rose 2007).

Conclusion

More trees had a greater crown projection to the north compared to the south and digital cover photography identified more foliage cover in the north. More bird nests were found in the northern than the southern crown projections and they experienced greater nesting success there and in the centre. Branches (alive and dead) and leaves make up the foliage and this architectural complexity explains why a diverse array of species are more successful in complex tree crowns and in old growth woodland in general. I suggest conservation efforts consider this old growth and crown architectural complexity when conservation of assemblages and communities is required.

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7. DISCUSION

NEST ECOLOGY IN THE CONTEXT OF AN INTACT ASSEMBLAGE OF THREATENED WOODLAND BIRDS: A DISCUSSIVE SYNTHESIS FROM DRYANDRA

OPENING NOTE: ON CONTEXT AND STRUCTURE OF THIS DISCUSSION

This discussion is meant to be published as an opinion piece—a stand-alone paper. It was never intended to be a typical thetic discussion. As such, it draws on my body research from Dryandra and not simply the chapters of this thesis. But, being an opinion piece, it is intended to provoke discussion. It is intended to draw a long bow and present thought-provoking ideas. Note: This discussion is not intended to be publishing without all the material cited and drawn upon being published.

ABSTRACT

Dryandra is a large old growth woodland reserve that retains an intact assemblage of threatened birds in what is now a vast agricultural landscape. This paper discusses research findings (including novel results) from this threatened avian assemblage in the context of its intact community where invasive species have been controlled. At Dryandra, many avian species have increased their abundance over the 54 years from 1953 to 2008, in contrast to a worldwide trend of declining bird numbers. Life history attributes of these woodland birds was studied using cameras, direct observations and an artificial nests. Nest predators formed a heterogeneous group of animals. While specialist nests predators were present nest success was high. High nest success is hypothesised to be a result of the presence of these threatened birds in ecologically functional numbers. Prey responses are reported, including canopy nesters concealing their nests in denser foliage cover, measured using digital cover photography. Birds aggregated their nests close to the low-lying and more mesic contours of the landscape with their numbers increasing exponentially at close proximity to the contours. Overall, the assemblage of threatened birds was found to be very sensitive to more productive and more mesic soils.

KEYWORDS

Landscape ecology, low-lying contours, review, long-term research, concealment, nest-predation, nest success, preferential clearing, conservation, productive soil, group mobbing,

INTRODUCTION

The worldwide reduction and degradation of forests and woodlands for agriculture has resulted in the dramatic decline of bird numbers; even in large reserves bird declines are forecast to continue through a diminishment of food resources due to climate change (Mac Nally et al. 2009). In Australia, temperate eucalypt woodlands were once widespread in what are now vast agricultural expanses (Prober et al. 2002). This vast change in the landscape has resulted in extensive bird declines—declines that continue from legal clearing (Reside et al. 2017; Lindenmayer et al. 2018) and illegal clearing (Fulton and Majer 2006; Ward et al. 2019). Notably, woodland birds have decreased on average by 53% since 2000 (TSX 2018).

In Australia, for forty years, the number of woodland birds has declined substantially (Ford and Howe 1980; Garnett 1993; Reid 1999; Ford et al. 2001; Fulton and Majer 2006; Watson 2011; Lindenmayer et al. 2018). This vast removal of the woodland landscape, which has resulted in the widespread losses of bird and other biota has not occurred uniformly—spatially or temporally. The woodlands on the most productive soils, in the low-lying areas of the landscape, were cleared first and most thoroughly, because well hydrated and more productive soils were attractive to agriculture (Prober et al. 2002; Watson 2011), despite harbouring the greatest abundance and species richness of birds (Bentley and Catterall 1997; Catterall et al. 1998). The surviving fragments of woodland are generally on poorer soils considered unsuitable for agriculture, particularly on rocky slopes and ridge-tops that are limited in size (Ford et al. 2001). Surviving fragments are further degraded by continued grazing and the removal of coarse woody debris (Mac Nally et al. 2000; 2001; 2002).

In such a vastly modified environment it is important to understand the life history strategies employed by birds to halt their declines and facilitate their recoveries (Remeš et al. 2012; Fulton 2018a [Chpt. 1]; Fulton 2019 [Chpt. 2]). There are two major factors influencing the life histories of birds: nest predation and food availability (Lack 1954; Ricklefs 1969; Martin 1992). Both factors are critically important to breeding birds (Lack 1954) and interact in complex ways for nesting birds (Collias and Collias 1984; Martin 1992). Yet many life histories studies are regularly undertaken in highly disturbed environments. Such studies are therefore unlikely to accurately represent natural or endemic life histories. They will certainly lack the influence of all the naturally interacting factors available in undisturbed habitats. In contrast, to many other studies, this thesis promotes conservation through understanding the effects inherent in a natural assemblage of birds within the *context* of an intact community—Dryandra. But what does context mean and what is an intact community?

Context

Herein, I provide a synthesis of studies on the nesting ecology of an intact assemblage of temperate woodland birds, at Dryandra Woodland National Park, in south-western Australia. These studies are discussed within the context of Dryandra's high quality old-growth woodland, which is managed for invasive species. The intact avian assemblage is comprised of a full complement of species—in ecologically functional numbers (Fulton 2013). It exists within the broader context of an intact biotic community that has been minimally disturbed since European colonisation and managed for invasive predators (Friend and Beecham 2004; Friend et al. 1995; DEC 2011). Data derived from this assemblage looks more specifically into the life histories of Australian woodland birds than recently published reviews and meta-analyses that have addressed continent-wide findings (Remeš et al. 2012; Fulton 2018a [Chpt. 1]; Fulton 2019 [Chpt. 2]). These reviews reported findings from a broad context of forests types, generally from within disturbed landscapes and frequently in association with invasive predators—exotic and endemic. Context is important: reporting and discussing results from within a specific context facilitates a refined understanding of the results. For example, studies that ignored context and investigated nest success based on distances to forest edges produced highly equivocal results (Fulton 2018a [Chpt. 1]). Those studies typically had disparate contexts in terms of: fragment size, structure and faunal assemblage. Their simple distance-to-edge measurement was too broad to capture a consistent result. More complex paradigms may have better explained the presence or absence of changes to nest predation at their various edges (Fulton 2018a [Chpt. 1]). Brooker and Brooker (2001) invoked size as an explanatory context when accounting for lower nest predation found in smaller forest fragments of the Western Australian wheatbelt. They suggested that small forest fragments may not support nest predators that required large territories. In such examples, context is used in an *ad hoc* fashion, coming after the data, to explain the results. At Dryandra, I took an *a priori* approach and considered the intact community when gathering and reporting the data.

Dryandra's intact context does not preclude contrasts and comparisons with disturbed habitats. Correlative studies of habitat features and species abundance/richness have long been used in ecological hypothesis testing (Jones 2001). More specifically, results derived from Dryandra's intact context may be used as baseline data to formulate conservation strategies and recognise targets when trying to mimic natural outcomes in disturbed environments. They may shed light on interactions lost from depleted assemblages and communities elsewhere.

Avian assemblages

In Australia, studies that have garnered large sample sizes of nesting birds have typically focused on a single species (e.g. Rowley et al. 1991; Brooker and Brooker 2001). Few observations have come from empirical studies of avian assemblages (Fulton 2018a [Chpt. 1]; Fulton 2019 [Chpt. 2]). Yet, the strategies and definitive targets required for the conservation and management of threatened species and assemblages may be best informed by life history data taken from natural assemblages. Quantifying metrics within assemblages may highlight behaviours employed by subsets of the assemblage or by the whole assemblage; such wide-ranging data can generate broad and useful theories and inform conservation targets well beyond the species level (Fulton 2018a [Chpt. 1]). For example, the suite of threatened birds that preferentially use the low-lying more mesic and productive parts of the landscape (Fulton and Possingham [Chpt. 5]). Conserving a threatened assemblage through actions that impact on assemblages rather than a single species is surely advantageous to conservation managers, and administrators, and to biodiversity. Conversely, baseline data from threatened species, acquired within the context of a natural assemblage, is surely critical for guiding effective recovery plans—A recovery plan might ask: What are the desired levels or targets needed for the management of that species? Where would this data come from if all habitats are disturbed?

Assemblages have evolved in parallel in response to the same predators, thus to study individual species or species groups without the full context of their assemblage may provide an incomplete representation of their natural history. Within a context of parallel evolution repeated patterns of behaviour might be expected. For example, on a continental scale Australian birds generally experience higher levels of nest predation than North American birds, thus they generally nest more frequently with smaller clutches and have shorter nesting cycles (Woinarski 1985; Martin 1995). Assemblages may share nest predators that act to organize assemblages: Nest predators may be density dependent responding spatially and temporally to the density of nests (Martin 1988; Martin 1993). Nest predators may specialise on certain types of nests making those nests more vulnerable, notably cup nests are more frequently depredated than hole nests (Fulton 2019 [Chpt. 2]). Likewise, they may specialise on a particular nest stage or hunt within a particular substrate. An important nest predator, the Tiger Snake *Notechis scutatus* (Fulton 2019 [Chpt. 2]), preys preferentially on nestlings because is thought to be unable to break the shells of undamaged eggs (Bonnet et al. 1999). Likewise, small mouthed Brown Antechinus *Antechinus stuartii* were unable to break large quail eggs, although they consume smaller eggs (Fulton and Ford 2003).

Similarly, prey responses are likely to be evolved with members of assemblages acting in uniform ways. At Dryandra three such responses were recognised: the assemblage aggregated their nests in the more productive sections of the landscape (Fulton and Possingham Chpt. 5) and further responded to predators either by mobbing them with a mixed species group comprised of nesting birds (Fulton 2006a; Fulton 2007) or by concealing nests within areas of greater foliage density

(Fulton and Possingham Chpt. 6). Such evolved responses from the assemblage reinforce the notion of investigating life histories from within the context of an intact assemblage and community, particularly where the biota is in ecologically functional numbers.

Aims

This study aimed to synthesise and discuss/hypothesise avian life history findings within the subset of on nest ecology, but moreover within the context of the intact avifaunal assemblage, at Dryandra. More specifically to –provide a broad estimate of the success and failure rates of bird nests –quantify nest failure caused by storms; –identify nest predators, –hypothesise how nest placement in the landscape and systematic concealment within tree-crowns might interact with the nest ecology of Dryandra's woodland birds.

STUDY SITE & METHODS

General overview

The study site description and methods provided herein give only a brief summary, for detailed methods, statistical analyses and results follow the references given. Dryandra Woodland National Park (Dryandra) is located about 160 km southeast of Perth (Lat. 32 48' S, Long. 117 0' E) on the western side of the Western Australian wheatbelt (Figure 1). Dryandra is comprised of a series of large woodland fragments, which are separated by agricultural land and scattered over an east-west distance of approximately 35 km (Friend *et al*. 1995; DEC 2011; Fulton 2013).

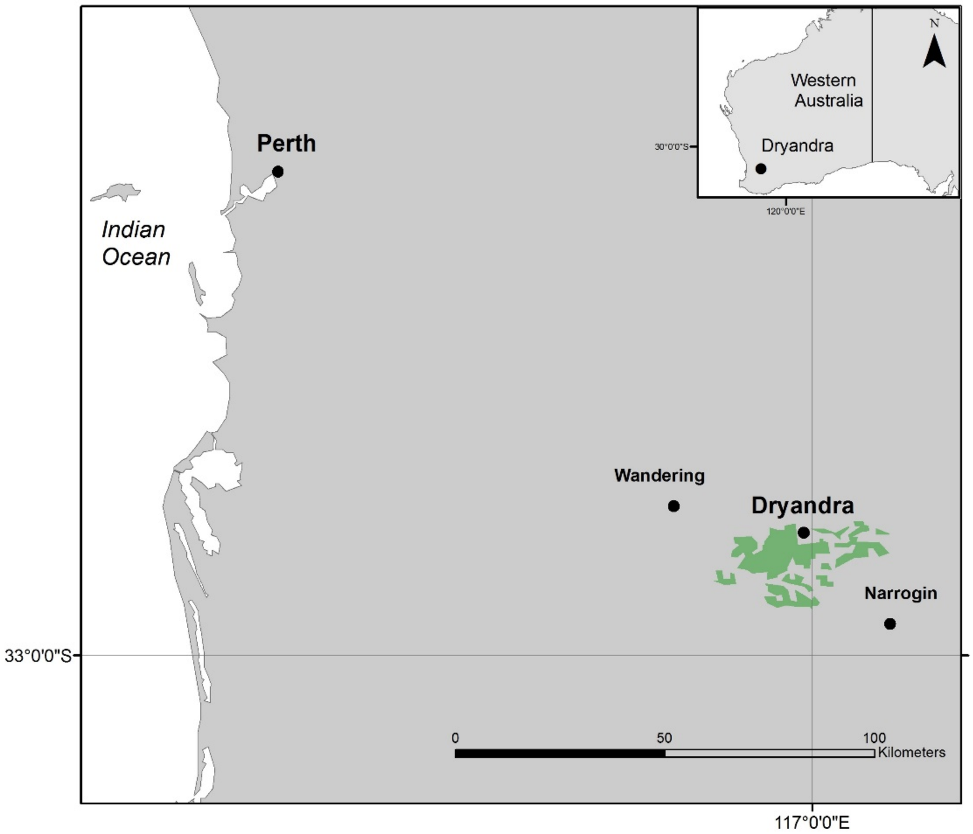

Figure 1. Dryandra in relation to Perth and southwestern Australia

Dryandra is unlike other woodland remnants, in Australia, due to a number of factors including its overall size (28 000 ha), which embraces large areas of undisturbed old-growth woodland (DEC 2011) and its location on the central western side of the Western Australian wheatbelt where up to 97% of the original native vegetation has been removed (Saunders and Curry 1990, Saunders and Ingram 1995). Dryandra holds an almost full complement of bird species in ecologically functional numbers, including many lost from remnants of the central wheatbelt (Fulton 2013). It possesses rare marsupials that have been extirpated from the region and/or mainland Australia, some of which have been re-introduced (DEC 2011; Fulton 2017 [Chpt. 3]).

The natural presence of fluoroacetate (a natural poison) bearing plants, particularly Sandplain Poison *Gastrolobium microcarpum* has had a major influence on allowing native species to persist at Dryandra (Short et al. 2005). Since the 1980s the control of the Red Fox *Vulpes vulpes* using 1080 (fluoroacetate) baiting has enabled the recovery of marsupials, birds, and reptiles, which had been adversely affected by fox predation (Burbidge et al. 1996; Friend and Beecham 2004; Possingham et al. 2004). Dryandra has been a focal point of research since 1980s with baseline data accumulated across a wide diversity of biota (Friend et al. 1995; DEC 2011). Its ongoing management as a National Park suggests that this might continue.

Vegetation, landforms and soil

The woodlands are characterized by Powderbark Wandoo *Eucalyptus accedens*, Jarrah *E. marginata* and Brown Mallet *E. astringens* on the mid and upper slopes, with Wandoo *E. wandoo*, Jam *Acacia acuminata*, (and less commonly Marri *E. calophylla*) on the lower levels (McArthur et al. 1977; Coates 1993). The lower levels of the landscape are the most mesic and most productive (DEC 2011; Fulton and Possingham Chpt. 5 and references cited therein). The trees have an asymmetrical crown projections with the north having significantly greater foliage density, which includes living and dead branches (Fulton and Possingham Chpt. 6).

Climatic overview

Dryandra experiences a Mediterranean climate with hot dry summers and mild wet winters. The mean annual rainfall varies across Dryandra with 600 mm in the west to 500 mm in the east (Sutton et al. 1994; Fulton 2013). The wettest six-month period occurs from May to October and accounts for 80 per cent of the annual precipitation (N = 115 years; 1887-2003). The annual mean minimum and maximum temperatures range from 8.4°C to 23°C (N = 102 years; 1901-2003) (BOM 2006; Fulton Chpt. 4). Weather metrics were taken from the Bureau of Meteorology’s automatic weather station.

Nest: searching, monitoring and measuring

At each site I developed a detailed knowledge of the birds from spending most daylight hours in the field, throughout three breeding seasons. This was facilitated by living in a hut within the woodland. Many of the birds were known to me individually, some through the three seasons, by their behaviour and individual characteristics and by their association with their nests and territories. Such knowledge helped me find nests quickly, many after the first cobwebs on the nests’ foundations were wiped in place. However, the lower detectability of cryptic species and species that used denser habitats meant fewer of their nests were found.

Bird nests were located and monitored over three breeding seasons; direct observation of predation and camera trials occurred during this time (Fulton 2006a; Fulton 2006b; Fulton 2006c). Nest sites were visited daily, seven days per week, in all daylight hours. Nests were not approached closely to avoid laying a scent trail that could be used by olfactory predators. All nests were given a unique identification code. Measurements of the nests, trees and shrubs were made after the nests were had failed or fledged. All 18 storms occurring at Dryandra over three years were monitored with all nests checked immediately following each storm.

Artificial ground nests

Over two years, 100 artificial ground nests were placed centrally within Dryandra: 50 per year. Nest-sites were spaced 50m apart east-west and 100m apart north-south. The nests were modelled closely on the Painted Button Quail *Turnix varius*. Complex and numerous human scent trails were used to confound olfactory predators. Two imprint receptive eggs and two fresh Common Quail *Coturnix coturnix* eggs were used at each nest. The nests were check daily (Fulton 2017 [Chpt. 3]).

Camera trials

Cameras used film and were triggered by micro-switches under clay eggs within an artificial cup nest or a re-used natural nest. Two camera setups were moved through 15 locations, totalling 256 camera days. Each nest contained a single Common Quail egg. These set-ups were checked daily (Fulton 2006b).

Digital cover photography

Digital cover photography measured the foliage density. Tree foliage included all branches and leaves dead or alive but not the main stem (trunk). Photographs captured the density of foliage on the north and south crown projections (hemispheres). DCP 3.14 software was used to analyse the foliage density in the photographs (Fulton and Possingham Chpt. 6). Photographs were taken in October (mid-spring), because it coincides with the peak nesting period (Fulton and Possingham Chpt. 6).

Nest and contour line mapping

A Differential Global Positioning System (DGPS) was used to create digital markers for each nest location and to draw lines by carefully walking the lowest hydrological contours, at each site. The DGPS system had a sub-metre accuracy. ArcGIS Pro 2.2.3 was used to measure the distances from each nest to the nearest point of the site’s lowest contour (Fulton and Possingham Chpt. 5).

Figure 2. *Eucalyptus wandoo* woodland at Marri Road, in Dryandra. There are descending altitudinal gradients from the centre foreground to the rear and from the left and right to the centre, of the photo. The lowest mesic contour is slightly to the right of the large *E. wandoo* tree near the centre.

RESULTS AND DISCUSSION

NEST PREDATION

Nest Success and Failure

Across the assemblage 47% of nests failed while 53% fledged (n = 274 out of 519). Within the subset of failed nests: predation and abandonment were overwhelmingly the most frequent causes of nest failure with storms and disease far less frequent (Table 1a). Further, within the subset of depredated and abandoned nests: depredated nests predation were approximately 2.5 times greater than abandoned nests (Table 1b), then within the subset of depredated nests: eggs were depredated 6% more frequently than nestlings (Table 1c). Hole nests were almost twice as successful than the more exposed cup and enclosed nests. Nests in burrows and platform nests (of larger birds) also experienced greater success the cup and enclosed nests (Table 1d).

Storms caused more nests to fail than disease. Disease resulted in three nest failures from 520 nests with known outcomes (0.006%). Storms caused 31 nests to fail (7%) from 468 nests active during storms (Fulton Chpt. 4). There was a significant relationship between wind speed and nest losses, but no significant associations between nest losses with the amount of precipitation or the duration of the storm (Fulton Chpt. 4). Cup and enclosed nests failed at the same rate of 10% yet no hole nest failed (Fulton Chpt. 4). There are no directly comparable empirical studies. However, two similar assemblage-wide studies Best and Stauffer (1980) [North America] and McLean *et al.* (2005) [eastern Australia] reported 3% and 2% nest losses respectively. Fulton (Chpt. 4), included only those nests that experienced a storm. Yet, this procedure was not explicitly reported in the other cited studies, which may therefore explain the differences.

Table 1a. Quantity of nests that failed by cause. *Not all nests were active during storms. N = the number of nests.

	%	N
Predation and Abandonment	.86	211
Storms	.13*	31
Disease	.01	3
Total	1.00	245

Table 1b. Quantity of nests that failed through predation and abandonment. N = the number of nests.

	%	N
Predation	.71	150
Abandoned	.29	61
Total	1.00	211

Table 1c. Quantity of nests that failed through predation only. N = the number of nests.

	%	N
Eggs	.53	80
Nests	.47	70
Total	1.00	150

Table 1d. Nest type: percentage success and fail rates. N = the number of nests.

Nest type	Success %	Fail %	N
hole	85	15	68
platform	76	24	17
burrow	58	42	59
cup	45	55	319
enclosed	44	56	52
ground	40	60	5

Can predation and abandonment and lost energy be considered in nesting success?

This is an argument for including the theft of nest material, abandonment and the nest building stage to more fully understand energy stresses on nesting birds. The above combined abandonment and predation result was most important with regard to nest failure. Most nest abandonment occurred during the building stage. The two most frequent causes of abandonment are the presence of a nest predator that has discovered the nest (e.g. Berger-Tal et al. 2010) and the theft of nest material from active nests (e.g. Ley et al. 1997; Rowley and Russell 2002; Fulton 2006b; Fulton 2006c). Brood parasites, cuckoos, were less frequently detected at Dryandra, although cuckoos may cause abandonment and inflict energy losses on the host species, particularly when the hosts don’t abandon the net, but do fledge the cuckoo (Brooker and Brooker 1989). Energy is used to build nests, thus abandoning a nest amounts to a loss of energy without a successful result; a result equivalent to nest predation in that energy is lost without gain. The theft of nest material may or may not cause birds to discontinue their nests and it is not limited to the building stage of nests. At Dryandra, a Rufous Treecreeper *Climacteris rufa* broke eggs to take nest material from an active Willie Wagtail *Rhipidura leucophrys* nest, yet while doing so it did not consume any of the eggs (Fulton 2006c). The energy lost in this instance included energy invested in the eggs and the nest building. Since direct observations of such events are rare (Brown and Veltman 1987—a single nest predation event in 2000 hours of observations), many more such events undoubtedly occur without being witnessed. Yet, modern digital cameras will undoubtedly detect more occurrences. At Dryandra, birds risked injury or death to either steal nest material or defend nests, which suggests that the energy involved is highly valued by them (Fulton 2006c). Thus, a more precise quantification of the overall nest-predatory impact will be obtained by considering both predation and abandonment collectively, particularly by quantifying the energy (and time) lost. But to do this the inclusion of the frequently overlooked nest-building stage is required to more fully understanding nesting success.

The context of lower nest predation—are an intact assemblage and group mobbing important in understanding nest predation?

Even when incorporating abandonment, the overall nest predation rate at Dryandra is low compared to other regions in Australia. Remeš et al. (2012) reviewed nest predation rates across Australia and found rates were lower in temperate regions than the tropics with the lowest rates in south-western Australia. They found that nest predation on average resulted in a total nest failure of 72%. They speculated that the control of invasive nest-predatory species and the absence of the Pied Currawong *Strepera graculina* brought about the lower result in south-western Australia. The Pied Currawong is noted as Australia's top nest predator (Major et al. 1996; Fulton and Ford 2001a; Fulton and Ford 2001b; Fulton 2018b; Fulton 2019 [Chpt. 2]). Yet, consideration of the complete context at Dryandra may better explain the lower nest predation rate observed there. Notably, while the Pied Currawong is absent other observed nest predators are present, including: Grey Currawong *Strepera versicolor,* Square-tailed Kite *Lophoictinia isura,* Brushtail Possum *Trichosurus vulpecula* and Tiger Snake *Notechis scutatus*. Thus, with specialists and generalist nest predators present, why might the nest predation rate be comparative low compared to other regions in Australia?

One hypothesis might be that there is more food in the more productive old-growth landscape at Dryandra. Another hypothesis is group mobbing by a range of different species, which stems from the assemblage aggregating their nests around the low-lying more mesic contours of the landscape (Fulton and Possingham Chpt. 5). Members of this assemblage group-mobbed nest-predators (Fulton 2006a; Fulton 2007). Group mobbing is a response to nest predators with individuals defending their own nests and thus reciprocally supporting each other in ameliorating nest predation. The response has likely been overlooked in the past, because the threatened birds comprising the assemblage are rare or extirpated elsewhere (Bentley and Catterall 1997; Catterall 1997; Fulton and Possingham Chpt. 5). Yet, at Dryandra, the assemblage remains in ecologically functional numbers (Fulton 2013). Notably, an analogous yet inutile response has been reported from Noisy Miner *Manorina melanocephala* territories, where Noisy Miners excluded other birds and thereby increased the success of artificial nests (Fulton and Ford 2001; Robertson et al. 2014). Similarly, yet with greater utility, Yellow-throated Miners *Manorina flavigula* defend their territories by selectively mobbing birds, while allowing Grey Butcherbirds *Cracticus torquatus* or Pied Butcherbirds *C. nigrogularis* to nest alongside them, with both miner and butcherbirds benefitting from the close association of nests (Fulton 2008). In a broad review, Fulton (2018) asserted that more complex paradigms rather than simple or single effects (e.g. edge-effects) control nest predation rates. Thus, at Dryandra, the overall high quality of the habitat and the control of introduced invasive animals, along with the interactions of the endemic biota, support the suggestion that group mobbing, may help explain the comparatively low predation rate recorded there. It is unlikely to be as simple as the absence of a single, albeit notorious, nest predator.

A broad array of nest predators at Dryandra

Reviews of nest predation call for more information on the role and identity of nest predators (Remeš et al. 2102; Fulton 2018a [Chpt. 1]). Thus far studies seeking the identities of nest predators in Australia, have found a very broad range of animals are involved (Fulton 2018a [Chpt. 1]). In a meta-analysis of nest predation in temperate Australian forests and woodlands 94 nest predators and 95 prey species were identified (Fulton 2019 [Chpt. 2]). The largest avian nest-predator was the 4kg Wedge-tailed Eagle *Aquila audax* and the smallest the 11g Eastern Spinebill *Acanthorhynchus tenuirostris*. Prey varied even more from the 37kg Emu *Dromaius novaehollandiae* to Australia's smallest bird the 6g Weebill *Smicrornis brevirostris* although, prey species must surely include all birds (Fulton 2019 [Chpt. 2]).

At Dryandra; when incorporating the theft of nest material, 21 nest predators were identified, some of which were new identities (Table 2). Nest predators varied from marsupials to ants. Three threatened marsupials were recorded depredating ground nests (Fulton 2006a; Fulton 2017 [Chpt. 3]). While a range of 14 birds were identified as nest predators using cameras and from direct observations (Table 2). These birds varied from small Restless Flycatcher *Myiagra inquieta* and Willie Wagtail *Rhipidura leucophrys* to the larger Brown Goshawk *Accipiter fasciatus*. The heterogeneous range of nest predators recorded, particularly the new identities, compared well with other studies attempting to discover nest predator identities, in that a heterogeneous array of animals were responsible including some that were unexpected. A body of literature is building on unsuspected marsupials as nest predators, for example Koala *Phascolarctos cinereus* (Fulton and Ford 2003) and Quokka *Setonix brachyurus* (Stevenson 2011; Dundas *et al*. 2014; Fulton 2017 [Chpt. 3]).

Table 2. Number and type of predatory events are given. An event refers to a single incident, which can comprise multiple eggs or chicks. Predators were identified using direct observations, cameras and artificial nests. The numbered superscripts denote the paper from which the data was drawn (Fulton 2006a[2], b[1], c[3]; Fulton 2010[4]; Fulton 2017[5] [Chpt. 3]). The asterisk * denotes an unsuccessful predatory attempt, “nm” denotes nest material. The superscript question mark highlights that the exact species of bettong could not be determined. Percentage results (not the number of events) are given for artificial nests under the column headed Art.[5]. They do not sum to 100%, because not all predators were identified and not all nests were depredated. These artificial nests were ground nests. Artificial cup nests, placed in vegetation were used with the cameras and the number of photographed events are given.

Evidence type	Cameras[1]		Art.[5]	Direct Observations [2 & 3]				
Event type	nm	egg	% egg	nm	egg	nestling	adult	other
MARSUPIALS								
Brushtail Possum *Trichosurus vulpecula*		20	35					
Woylie *Bettongia penicillata*			30					
Boodie *B. lesueur*			5					
B. sp.[?]			2					
Bilby *Macrotis lagotis*						1		
BIRDS			3					
raptorial								
Brown Goshawk *Accipiter fasciatus*						1		
Southern Boobook *Ninox novaeseelandiae*								1 *Antechinus flavipes* [4]
non-raptorial								
Rufous Treecreeper *Climacteris rufa*				1				
Red Wattlebird *Anthochaera carunculata*	6	6		1				
Singing Honeyeater *Lichenostomus virescens*		1						
Yellow-plumed Honeyeater *Lichenostomus ornatus*	3	2			1			
Brown-headed Honeyeaters *Melithreptus brevirostris*				1				
White-browed Babbler *Pomatostomus superciliosus*	3							
Grey Shrike-thrush *Colluricincla harmonica*	1	9			2			2*
Australian Magpie *Gymnorhina tibicen*	3	2					3	1*
Grey Currawong *Strepera versicolor*	2	17						
Willie Wagtail *Rhipidura leucophrys*	4							
Australian Raven *Corvus coronoides*	1	1						

Evidence type	Cameras[1]		Art.[5]	Direct Observations [2 & 3]				
Event type	nm	egg	% egg	nm	egg	nestling	adult	other
Restless Flycatcher *Myiagra inquieta*		1						
REPTILES								
South-western Carpet Python *Morelia spilota imbricata*						1	3	
INVERTEBRATES								
Black-headed Sugar Ant *Camponotus nigriceps*						1		
Greenslade's Meat Ant *lridomynnex greensladei*					1	2		

The Dryandra context—the context of nest predators

Four nest predators were identified more frequently than others, at Dryandra: Brushtail Possum, Grey Currawong, Grey Shrike-thrush *Colluricincla harmonica* and Red Wattlebird *Anthochaera carunculata* (Table 2). All are known to be important nest predators (Fulton 2018a [Chpt. 1]; Fulton 2019 [Chpt. 2]). Yet, two of the usual suspects Tiger Snake and Square-tailed Kite were present at Dryandra, but they were not observed or recorded as nest predators there. Understanding the context of each predator sheds light on their relative roles. The Square-tailed Kite, is a specialist nest-predator (Griffiths *et al*. 2002; Fulton 2019 [Chpt. 2]), but did not frequent the breeding territories studied at Dryandra, thus it did not depredate nests of the threatened assemblage. Likewise, the Tiger Snake was rarely observed at field sites contrasting with the South-western Carpet Python *Morelia spilota imbricata*, which was common at all sites and subsequently observed at four predatory events (Table 2). It took ground and arboreal prey (Fulton 2006a) whereas the Tiger Snake typically takes prey from close to the ground (Cogger 2018). Thus, the Python is a greater threat to the arboreal nesting birds, at Dryandra. The Grey Currawong is known to depredate natural nests (Colombelli-Négrel et al. 2009). At Dryandra, it was only locally sympatric with the studied assemblage outside the nesting season. During their nesting season Grey Currawongs undertook a home range shift and were not present in the study areas and were thus not a threat to the studied breeding assemblage (Fulton 2006b; also see Fulton *et al*. 2008 re nesting range shift).

At Dryandra, patch specific conditions included the mass flowering of Brown Mallet *Eucalyptus astringens* plantation. This mass flowering event, the only one observed during the principal three year survey, attracted large numbers of Red Wattlebirds *Anthochaera carunculata*. This is the only time they were common and corresponded both spatially and temporally with their predatory activity (Fulton 2006b). The Brushtail Possum is a recognised nest predator (Garnett et al 1999; Smith et al. 2016). At Dryandra, it was the most prolific nest predator and was observed at most field sites, though it was likely present at all field sites. Its predatory events were not directly observed, because the species is largely nocturnal. It was observed at arboreal camera nests and its teeth imprints were captured at the artificial ground nests (Fulton 2017 [Chpt. 3]). Yet, it is not considered a threat to native birds with whom it has evolved alongside (Fulton 2107 [Chpt. 3]). The Grey Shrike-thrush is a well-recognised nest predator (Major et al. 1999; Fulton 2006b; Fulton 2006c; Fulton 2018a [Chpt. 1]; Fulton 2019 [Chpt. 2]). It was observed depredating eggs and nestlings, and was photographed at camera nests throughout the woodland, but was not detected in the village in any survey (unpublished data). It may have avoided human disturbance. Its context is perhaps the most important as its breeding territory was shared with the threatened assemblage that aggregated their nests in the low-lying areas (Fulton 2006b).

Three novel nest predators were detected, Bilby *Macrotis lagotis*, which dug a Rainbow Bee-eater *Merops ornatus* nest burrow with nestlings, Woylie *Bettongia penicillata* and Woylie and Boodie *B. lesueur,* the latter two are both threatened bettongs; they were identified depredating over a third of the 100 artificial ground nests (Fulton 2006a; Fulton 2017 [Chpt. 3]). Bettongs are thought to be primarily mycophagous and omnivorous (Van Dyck and Strahan 2008; Eldridge and Frankham 2015), but both Woylie and Boodie are also known to take live prey, including small birds and show clear carnivorous tendencies (Fulton 2017 [Chpt. 3]). They were not previously regarded as nest predators, because the biology of rare Australian marsupials is not fully understood due to its rarity (Fulton 2017 [Chpt. 3]). At Dryandra, the novel finding of bettongs as nest predators could only be detected due to the long-term control of Cats *Felis catus* and Foxes *Vulpes vulpes* using 1080 poisoning (Friend et al. 1995). The long-term control of these invasive predators has allowed the Woylie to thrive while the Boodie was reintroduced (Fulton 2017 [Chpt. 3]). This unexpected result highlighted that the re-introduction of a threatened bettong might negatively impact on ground nesting birds, which strongly suggests that more research is required on the impacts of reintroductions to avoid deleterious effects on resident species (Fulton 2017 [Chpt. 3]).

The nearest neighbour hypothesis

At Dryandra, the most important nest predators are those that shared the low-lying areas with the threatened assemblage of breeding birds—their nearest neighbours. Nearest neighbours include birds, mammals and others that forage or nest locally. Neighbouring insectivorous birds may not be broadly carnivorous, yet they may destroy nests to steal nest material (Fulton 2006b; Fulton 2006c). Southern Boobook *Ninox novaeseelandiae* (Fulton 2010), Grey Shrike-thrush and Brushtail Possum were three recognised nest predators that shared the low-lying areas with the threatened assemblage, suggesting they are likely to be important nest-predators to this threatened avifauna. Yet, the assemblage has evolved with them. Thus, their predatory impact may not be a threat to Dryandra’s birds without human disturbance causing their numbers to inflate, as is the case for Australia’s most prolific nest predator the Pied Currawong (Fulton and Ford 2001; Fulton 2019 [Chpt. 2]).

NEST PLACEMENT

Nest placement in the low-lying more mesic and productive area of the landscape

Nest success is not solely governed by predation, but also by the availability of food and nest sites (Lack 1954; Martin 1987). Nix (1976) proposed that nesting birds respond to the temporal sequence of plant growth and thus food supply: firstly honeyeaters nest when nectar associated with flowering becomes available and then frugivorous and granivorous species follow as seed and fruit become abundant. Yet, food is distributed spatially as well as temporally with birds having greater reproductive success in more productive habitats (Martin 1987; Luck 2002a; 2002b; Fulton and Possingham Chpt. 5). Thus, more reliable and productive habitats are favoured by breeding birds (Martin 1992). Conversely, as productive habitats are lost through broadscale clearing reproductive success will decrease and species numbers decline (Ford et al. 2001). In Australia, clearing of the low-lying areas in the landscape has been non-random with well hydrated and nutrient rich soils preferentially cleared for agriculture (Catterall et al. 1998; Watson 2011). This preferential clearing has resulted in the disproportionate loss of forests and woodland birds that were found in these lowing-lying areas (Bentley and Catterall 1997; Ford et al. 2001; Fulton and Possingham Chpt. 5). A recurring pattern has emerged with the same birds and bird groups being iteratively reported lost and threatened across the continent (Saunders and Curry 1990; Saunders and Ingram 1995; Bennett and Ford 1997; Catterall et al. 1998; Reid 1999; Szabo et al. 2011). Yet, these birds persist at Dryandra and they aggregated their nests tightly around the lowest lying contours of the landscape—on the most productive soils (Fulton and Possingham Chpt. 5). The overall aggregation of nests followed an exponential pattern, increasing exponentially with increasing proximity to the low-lying and more mesic contours (Fulton and Possingham Chpt. 5). This response is perhaps more remarkable considering the very gentle gradient in the study area ranging from 1:300 to 1:500 (McArthur et al. 1977; see Figure 2 for a visual interpretation). Such sensitivity highlights why this assemblage contains so many of the most threatened woodland birds. Indeed such sensitivity highlights how and why they have been lost elsewhere.

Nest placement and prey response: concealing an assemblage of nests

Bird nests tightly clumped around the low-lying contours provide a target for density dependent nest predators that respond to the spatial and temporal increases in the density of nests (Martin 1988; Martin 1993). In response, prey must develop behavioural answers to ameliorate the risk of such predation. One response, from the group of canopy nesting species, was to conceal their nests in the denser foliage cover found in the northern crown projections of old growth *Eucalyptus wandoo* trees (Fulton and Possingham Chpt. 6). Significantly more nests were positioned within the northern crown projections of these trees and these nests experienced significantly greater nesting success than those positioned in the southern crown projections with their less dense foliage (Fulton and Possingham Chpt. 6). The measured foliage cover of the trees included the architectural complexity of tree crowns and not merely leaves. This complexity is typical of old growth woodland and stands in contrast to newer regrowth without age complexity. Such age or old growth complexity includes branches that are dead and alive, thick or thin, green or grey, or blackened by fire, and the greater density of leaves. Such architecturally complexity affords concealment, not just through its denser foliage cover, but through its mottled colours and textural differences. Its complexity provides not only greater concealment, but a greater range of camouflaged nest sites for a wide range of birds with their heterogeneous range nest types (Fulton and Possingham Chpt. 6).

Conclusion

Dryandra’s intact context—the soils, vegetation and animals being only minimally disturbed while being managed for exotic and invasive species, allows research to extract baseline life history data to inform conservation and management strategies for fragmented and disturbed habitats. For example, the threatened assemblage nested in the low-lying, more mesic and more productive parts of the landscape, which have been preferentially cleared elsewhere. Thus, highlighting the importance of this landscape element to the threatened assemblage of breeding birds.

The fact that Dryandra has a full complement of birds, mammals, reptiles and other biota to act as nest predators yet experiences comparatively low rates of nest predation among its threatened birds, suggests that the usually important nest predators are in balance with their prey. Identification of nest predators at Dryandra found that they were frequently the victim’s nearest neighbours or that they shared the same local patch. However, while predator and prey remain in a balanced condition this will not pose a threat. Birds at Dryandra showed prey-responses such as group mobbing and nest concealment within denser foliage.

Within Dryandra the threatened assemblage of birds studied nested and foraged in the low-lying and more productive parts of the landscape. More mesic and more productive soils in the low-lying sections of the landscape provided enough resources to support this threatened assemblage of birds—Resources and birds which are missing from what are now agricultural landscapes. Many individual metrics can be taken from Dryandra to inform the management of small reserves or whole landscapes. Yet, the most overarching message must be to put back the mosaic of vegetation, particularly the old-growth woodlands on the most productive soils, re-introduce the biota as required and control the invasive species.

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APPENDICES

APPENDIX X_1 (DRAFT ETHICS APPROVAL)

26th September 2002 **Animal Ethics Committee**

Mr Graham Fulton
Natural Science
Joondalup Campus

Dear Mr Fulton

Code: 02-A15
Project Title: *Avian nest depredation in Eucalyptus woodland*

This proposal was reviewed by members of the Animal Ethics Committee.

I am pleased to advise that the proposal complies with the provisions contained in the University's policy for the conduct of ethical research, and your application for ethics clearance has been approved.

Period of approval: **From** 24th September 2002 **To** 28th February 2005

With best wishes for success in your work.

Yours sincerely

Derril Tennant
EXECUTIVE OFFICER
Phone 9273 8170
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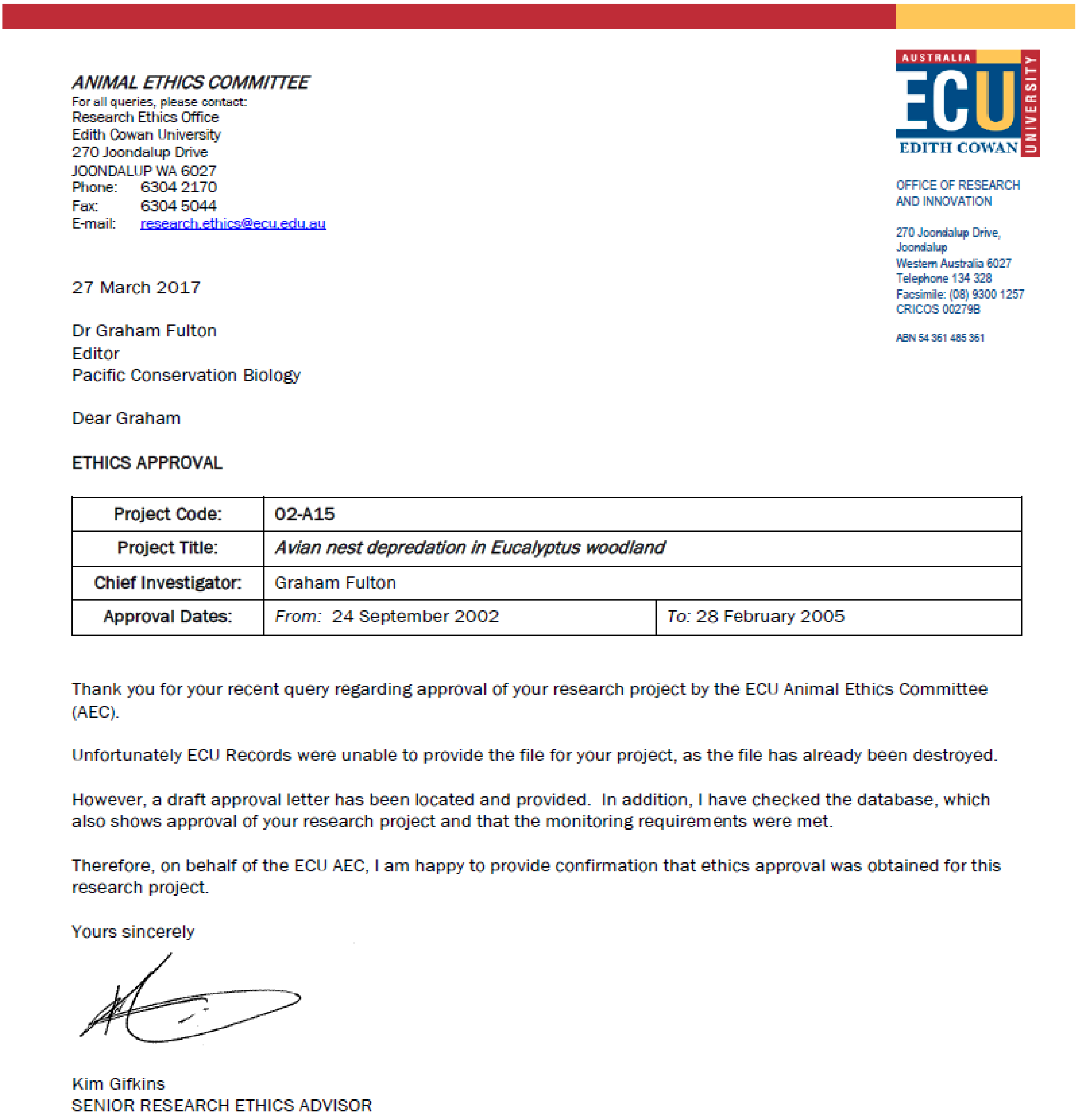
Email: d.tennant@ecu.edu.au

APPENDIX X_2 (LETTER ETHICS APPROVAL)



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27 March 2017

Dr Graham Fulton
Editor
Pacific Conservation Biology

Dear Graham

ETHICS APPROVAL

Project Code:	**02-A15**	
Project Title:	***Avian nest depredation in Eucalyptus woodland***	
Chief Investigator:	Graham Fulton	
Approval Dates:	*From:* 24 September 2002	*To:* 28 February 2005

Thank you for your recent query regarding approval of your research project by the ECU Animal Ethics Committee (AEC).

Unfortunately ECU Records were unable to provide the file for your project, as the file has already been destroyed.

However, a draft approval letter has been located and provided. In addition, I have checked the database, which also shows approval of your research project and that the monitoring requirements were met.

Therefore, on behalf of the ECU AEC, I am happy to provide confirmation that ethics approval was obtained for this research project.

Yours sincerely

Kim Gifkins
SENIOR RESEARCH ETHICS ADVISOR

APPENDIX 1

NEST PREDATORS AND PREY

Nest predators are given in bold. The quantity of predation events are given as the number of nests unless otherwise stated. Nest type: species: is the type of nest used by the species. Nest type: as reported: refers specifically to what was published or to if it is either an artificial or natural nest—an empty cell indicates a natural nest. Artificial nests are given as "art". Under nest contents: young = a precocial chick one to a few days after hatching. The abbreviation nm = nest material taken not eggs or nestlings. The asterisk (*) before the name of a prey species denotes an artificial nest constructed to approximate that species. Abbreviations giving the type of evidence used to identify nest predators are: camera = any device including video that can capture an image at the nest during predation; d. obs = direct observation of the event; report = not an explicit direct observation, although it reads as though it was based on observations (as opposed to assumptions without evidence); reference = a record that was taken from primary source and presented in a secondary source, typically in a review paper; sign = evidence at the nest, typically the type of damage to the nest or egg, especially imprints in clay eggs; stomach = the contents of the oesophagus, crop, gizzard, stomach and intestines; pellet = a regurgitated mass of food remnants; trap = a trap used to capture a predator. Other abbreviations are: indet. = indeterminate—not identified; unkwn = unknown; pers comm. = a personal communication in a published paper, typically a direct observation, but not by the author/s. Nomenclature and taxonomic order follow: for birds, Christidis and Boles 2008; for mammals, Jackson and Groves 2015; for frogs and reptiles Cogger, H. G. 2014; and for hymenoptera, Andersen 2002.

Only species known to occur in forest and woodland were included, but not those that only frequent water courses within. For example, Silver Gulls *Chroicocephalus novaehollandiae* frequent water courses in forests and were found to be an important predators of beach and island bird nests (e.gs. Wheeler and Watson 1963; Hulsman 1977), but were excluded from Appendix 1.

Citations: 1 Allison 1993; 2 Arnold 2000; 3 Ashby 1927; 4 Ashton 1986; 5 Aston 1978; 6 Aston and Aston 1988; 7 Barnes *et al.* 2001; 8 Bell 1960; 9 Bell 1985; 10 Bennett 1881; 11 Berney 1905; 12 Berry 2002; 13 Bischoff *et al.* 2000; 14 Boland 2004a; 15 Boland 2004b; 16 Bourke 1948; 17 Bridges 1994; 18 Brooker 1998; 19 Brown and Veltman 1987; 20 Brown *et al.* 2000; 21 Buchanan 1989; 22 Campbell 1927; 23 Campbell and Barnard 1917; 24 Carter 1913; 25 Carter 1924; 26 Chaffer 1945; 27 Chisholm 1928; 28 Cleland *et al.* 1918; 29 Colombelli-Négrel and Kleindorfer 2009; 30 Colombelli-Négrel *et al.* 2009; 31 Cooper 1948; 32 Cooper 1953; 33 Crowe 1978; 34 Cupper 1977; 35 Davis and Recher 1993; 36 Debus 2006; 37 Debus and Czechura 1992; 38 Emery 1988; 39 Fitzsimons 2003; 40 Ford 1999; 41 Fulton 2006a; 42 Fulton 2006b; 43 Fulton 2006c; 44 Fulton and

Ford 2001a; 45 Fulton and Ford 2001b; 46 Gardner 1988; 47 Garnett *et al.* 1999; 48 Griffiths *et al.* 2002; 49 Guppy *et al.* 2014; 50 Guppy *et al.* 2016; 51 Guppy *et al.* 2017; 52 Hausmann *et al.* 2005; 53 Hindwood 1947; 54 Hobbs 1990a; 55 Hobbs 1990b; 56 Holland 2001; 57 Hunt and Hunt 1995; 58 Jack 1949; 59 Langmore and Mulder 1992; 60 Lashmar 1946; 61 Laurance and Grant 1994; 62 Laurance *et al.* 1993; 63 Legge 1901; 64 Lenz 1990; 65 Lepschi 1993; 66 Ley *et al.* 1997; 67 Lord 1936; 68 Luck 2003; 69 Lutter *et al.* 2003; 70 Lutter *et al.* 2004; 71 Major 1990; 72 Major 1991a; 73 Major 1991b; 74 Major and Gowing 1994; 75 Major *et al.* 1994; 76 Major *et al.* 1996; 77 Major *et al.* 1999; 78 Major *et al.* 2015; 79 Manuel 1992; 80 Marchant 1974; 81 Marchant 1981; 82 Marchant 1989; 83 Matthews *et al.* 1999; 84 McDonald *et al.* 2009; 85 McFarland 1986; 86 McKilligan 1987; 87 Metcalf 1988; 88 Mo and Waterhouse 2016; 89 Morris and Burton 1994; 90 Mueller 1991; 91 North 1912 (citing Gould 1840); 92 Piper and Catterall 2006a; 93 Piper and Catterall 2006b; 94 Poiani 1991; 95 Portbury 1992; 96 Pratt 1972; 97 Prawiradilaga 1994; 98 Priddel and Wheeler 1994; 99 Recher and Schulz 1983; 100 Robinson 1990; 101 Rose and Banks 2007; 102 Rowley 1973; 103 Rowley and Vestjens 1973; 104 Rowley *et al.* 1991; 105 Russell *et al.* 2004; 106 Saunders 1991; 107 Sefton 1988; 108 Shine 1991; 109 Smith *et al.* 2016; 110 Stojanovic *et al.* 2014; 111 Trost and Olsen 2016; 112 Van Bael and Pruett-Jones 2000; 113 Vellenga 1968; 114 Vellenga 1980; 115 Vestjens 1977a; 116 Vestjens 1977b; 117 Vestjens and Carrick 1974; 118 Warham 1958; 119 White 1992; 120 Whitmore 1981; 121 Winter 1966; 122 Wood 1988; 123 Wood 1998a; 124 Wood 1998b; 125 Wood and Wilson 1997; 126 Wyndham 1981; 127 Zanette 1997; 128 Zanette 2002.

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
BIRDS						
indet. raptor						
Malleefowl *Leipoa ocellata*	sign	young	ground	reintroduced young	8	98
***Accipiter* sp.**						
Yellow-faced Honeyeater *Lichenostomus chrysops*	camera	nestling	cup		1	49
Square-tailed Kite *Lophoictinia isura*						
Pallid Cuckoo *Cacomantis pallidus*	stomach	egg	N/A		1	24
Australasian Pipit *Anthus novaeseelandiae*	stomach	egg	ground		1	24
indet. sp.	pers comm	nestling			1	89
indet. spp.	pellet	nestling			17	48
Eastern Yellow Robin *Eopsaltria australis*	report	nestling	cup		1	48
indet. honeyeater	report	nestling			1	48
Varied Sittella *Daphoenositta chrysoptera*	report	nestling	cup		1	48
Willie Wagtail *Rhipidura leucophrys*	report	nestling	cup		1	48
indet. flycatcher	report	nestling			4	48
Spotted Dove *Streptopelia chinensis*	pers comm	nestling	cup		1	13
Silvereye *Zosterops lateralis*	pellet	nestling	cup		1	20
indet. egg	pellet	egg			52 pellets	7
indet. nestling	pellet	nestling			54 pellets	7
Crested Pigeon *Ocyphaps lophotes*	pellet	nestling	cup		2	7
New Holland Honeyeater *Phylidonyris novaehollandiae*	pellet	nestling	cup		2	7
Eastern Yellow Robin	pellet	nestling	cup		1	7
Rufous Whistler *Pachycephala rufiventris*	pellet	nestling	cup		1	7
Red-browed Finch *Neochmia temporalis*	pellet	nestling	dome		1	7

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Brown Honeyeater *Lichmera indistincta*	pellet	nestling	cup		1 whole nest	7
Dusky Honeyeater *Myzomela obscura*	pellet	nestling	cup		1 whole nest	7
Little Friarbird *Philemon citreogularis*	pellet	nestling	cup		1 whole nest	7
Rufous Whistler	pellet	nestling	cup		1	7
indet. spp.	pellet	egg			12 eggs	7
indet. spp.	pellet	nestling			17 nestlings	7
indet. pigeon or dove	pellet	egg & nestling			1	69
indet. finch	pellet	nestling			1	69
Rufous Whistler	pellet	nestling	cup		1	69
indet. dove	pellet	nestling			2	70
Spotted Dove	pellet	nestling	cup		1	70
Crested Pigeon	pellet	nestling	cup		2	70
Red Wattlebird *Anthochaera carunculata*	pellet	nestling	cup		2	70
Little Wattlebird *Anthochaera chrysoptera*	pellet	nestling	cup		3	70
Noisy Miner *Manorina melanocephala*	pellet	nestling	cup		1	70
indet. honeyeater	pellet	nestling			3	70
Black-breasted Buzzard *Hamirostra melanosternon*						
Emu *Dromaius novaehollandiae*	d. obs	egg	ground		1	11
Emu	reference	egg			>1	91
Magpie Goose *Anseranas semipalmata*	pers comm	egg	ground		>1	37
Black Kite *Milvus migrans*	reference	nestling	platform		1	37
Nankeen Kestrel *Falco cenchroides*	d. obs	nestling	platform		>1	34
Galah *Eolophus roseicapillus*	d. obs	nestling	hollow		>1	34
Brolga *Grus rubicunda*	sign	egg	ground		1	23
Australian Bustard *Ardeotis australis*	sign	egg	ground		>1	10
goshawk Accipter spp.						

predator and prey	evidence	contents	Nest type: species	as reported	# nests	cite no.
Superb Fairy-wren *Malurus cyaneus*	camera	nestling	dome		1	51
Brown Thornbill *Acanthiza pusilla*	camera	egg	dome		1	51
Brown Goshawk *Accipiter fasciatus*						
Willie Wagtail	d. obs	nestling	cup		1	43
Australian Magpie *Cracticus tibicen*	d. obs	nestling	cup		1	43
Magpie-lark *Grallina cyanoleuca*	d. obs	nestling	cup		1	65
Eastern Yellow Robin	camera	nestling	cup		1	49
Yellow-faced Honeyeater	camera	egg & nestling	cup		1	51
Collared Sparrowhawk *Accipiter cirrocephalus*						
Brown Thornbill	camera	nestling	dome		1	49
Spotted Harrier *Circus assimilis*						
New Holland Honeyeater	camera	egg & young	cup	natural with art egg	1	74
Swamp Harrier *Circus approximans*						
Wild Turkey *Meleagris gallopavo*	report	egg & nestling	N/A	farm	>1	60
Little Grassbird *Megalurus gramineus*	stomach	nestling	ground		1	116
art	sign	egg			2	78
Wedge-tailed Eagle *Aquila audax*						
Little Raven *Corvus mellori*	report	nestling	cup		>1	102
Little Raven	d. obs	nestling	cup		1	102
Brown Falcon *Falco berigora*						
Noisy Miner	d. obs	nestling	cup		1	2
Purple Swamphen *Porphyrio porphyrio*						
Noisy Miner	d. obs	nestling	cup		1	39
Pheasant Coucal *Centropus phasianinus*						
indet. spp.	report	egg & nestling			>1	32
Buff-banded Rail *Gallirallus philippensis*	d. obs	nestling	ground		1	96

predator and prey	evidence	contents	Nest type: species	as reported	# nests	cite no.
indet. spp.	report	nestling			>1	96
Bronze-Cuckoo *Chalcites* spp.						
Brown Gerygone *Gerygone mouki*	camera	nestling	dome		1	51
Shining Bronze-Cuckoo *Chalcites lucidus*						
indet. sp.	stomach	egg			1	28
Fan-tailed Cuckoo *Cacomantis flabelliformis*						
Brown Thornbill	camera	egg	dome		1	49
Brown Thornbill	camera	nestling	dome		2	49
Brown Thornbill	camera	nestling	dome		1	51
Superb Fairy-wren	camera	nestling	dome		1	51
Superb Fairy-wren	camera	egg	dome		2	51
Variegated Fairy-wren *Malurus lamberti*	camera	egg	dome		1	49
White-browed Scrubwren *Sericornis frontalis*	camera	egg & nestling	dome		3	51
Southern Boobook *Ninox novaeseelandiae*						
Common Myna *Sturnus tristis*	d. obs	nestling	hollow		1	111
Noisy Pitta *Pitta versicolor*						
*(chicken egg)	camera	egg		art	3	61
Laughing Kookaburra *Dacelo novaeguineae*						
Bell Miner *Manorina melanophrys*	d. obs	nestling	cup		1	94
Pacific Black Duck *Anas superciliosa*	d. obs	nestling	hollow		1	6
Magpie-lark	d. obs	nestling	cup		1	22
Rufous Whistler	d. obs	nestling	cup		1	58
*Willie Wagtail	d. obs	egg		art	2	76
New Holland Honeyeater	d. obs	nestling	cup		1	85
art	sign	egg		art	>1	92
Scarlet Robin *Petroica boodang*	d. obs	nestling	cup		1	31
Golden Whistler *Pachycephala pectoralis*	d. obs	nestling	cup		1	31

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Yellow-faced Honeyeater	camera	nestling	cup		1	49
Silvereye	camera	nestling	cup		1	49
Superb Fairy-wren	camera	nestling	dome		1	51
Rufous Treecreeper *Climacteris rufa*						
Willie Wagtail	d. obs	nm	cup		1	43
Spotted Catbird *Ailuroedus melanotis*						
*(chicken egg)	camera	egg		art	7	61
art	sign	egg		art	58	52
Green Catbird *Ailuroedus crassirostris*						
Common Bronzewing *Phaps chalcoptera*	d. obs	nestling	cup	aviary	1	8
Satin Bowerbird *Ptilonorhynchus violaceus*						
White-bibbed Ground-Dove *Alopecoenas jobiensis*	d. obs	nestling	N/A	aviary	>1	8
Striated Pardalote *Pardalotus striatus*						
Regent Honeyeater *Anthochaera phrygia*	d. obs	nm	cup		1	66
Eastern Spinebill *Acanthorhynchus tenuirostris*						
Brown Thornbill	camera	egg	dome		2	50
Brown Thornbill	report	nm	dome		5	50
Yellow-faced Honeyeater	camera	egg			1	50
Rufous Whistler	report	nm	cup		1	50
Singing Honeyeater *Lichenostomus virescens*						
art	camera	egg		art	1	41
White-browed Babbler *Pomatostomus superciliosus*	d. obs	nm	dome		1	66
Yellow-tufted Honeyeater *Lichenostomus melanops*						
White-bellied Cuckoo-shrike *Coracina papuensis*	d. obs	nm	cup		1	82

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Yellow-plumed Honeyeater *Lichenostomus ornatus*						
art	camera	egg		art	2	41
art	camera	nm		art	3	41
*Painted Button-quail *Turnix varius*	d. obs	egg		art	1	43
Fuscous Honeyeater *Lichenostomus fuscus*						
Regent Honeyeater	d. obs	nm	cup		1	66
Black-chinned Honeyeater *Melithreptus gularis*	d. obs	nm	cup		1	66
Eastern Yellow Robin	d. obs	nm	cup		1	66
White-plumed Honeyeater *Lichenostomus penicillatus*						
Regent Honeyeater	d. obs	nm	cup		1	66
Noisy Miner						
*Willie Wagtail	d. obs	egg		art	14	76
art	sign	egg		art	>1	92
Spiny-cheeked Honeyeater *Acanthagenys rufogularis*						
Hooded Robin *Melanodryas cucullata*	d. obs	nestling	cup		1	54
Weebill *Smicrornis brevirostris*	d. obs	nestling	dome		1	54
Splendid Fairy-wren *Malurus splendens*	d. obs	nm	dome		1	112
Regent Honeyeater						
Regent Honeyeater	d. obs	nm	cup		1	66
Noisy Friarbird *Philemon corniculatus*	d. obs	nm	cup		1	66
Fuscous Honeyeater	d. obs	nm	cup		1	66
Red Wattlebird						
art	camera	egg		art	12	41
Yellow-plumed Honeyeater	d. obs	nm	cup		1	43
Regent Honeyeater	d. obs	nm	cup		1	35
Black-chinned Honeyeater						

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Brown-headed Honeyeater *Melithreptus brevirostris*	d. obs	nm	cup		1	66
Brown-headed Honeyeater						
Red-capped Robin *Petroica goodenovii*	d. obs	nm	cup		1	43
Eastern Yellow Robin	d. obs	egg	cup		1	127
Red-capped Robin	d. obs	egg	cup		1	54
indet. spp.	report	nm			>1	54
White-naped Honeyeater *Melithreptus lunatus*						
Noisy Friarbird	d. obs	nm	cup		1	66
Noisy Friarbird						
Regent Honeyeater	d. obs	nm	cup		1	66
Noisy Friarbird	d. obs	nm	cup		1	66
Common Starling *Sturnus vulgaris*	pers comm	egg & nestling	hollow		>1	26
Indet spp.	d. obs	nestling			>1	81
Grey-crowned Babbler *Pomatostomus temporalis*						
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*	d. obs	nm	dome		3	67
Rufous Whistler	d. obs	egg	cup		1	67
*Red-capped Robin	camera	egg		art	1	77
White-browed Babbler						
*Western Yellow Robin *Eopsaltria griseogularis*	camera	nm		art	3	41
Red Wattlebird	d. obs	nm	cup		1	25
indet. small birds	d. obs	nm			2	25
Red-capped Robin	d. obs	young	cup		1	18
Splendid Fairy-wren	sign	unkwn	dome		1	112
Chestnut-crowned Babbler *Pomatostomus ruficeps*						
Splendid Fairy-wren	sign	unkwn	dome		1	112
Eastern Whipbird *Psophodes olivaceus*						
Brown Thornbill	camera	nm	dome		1	51
Brown Thornbill	camera	egg	dome		2	51

predator and prey	evidence	contents	Nest type: species	as reported	# nests	cite no.
New Holland Honeyeater	camera	egg	cup		2	49
Yellow-faced Honeyeater	camera	egg	cup		2	49
Yellow-faced Honeyeater	camera	egg	cup		1	51
Superb Fairy-wren	camera	egg	dome		1	49
Superb Fairy-wren	camera	egg	dome		1	51
White-browed Scrubwren	camera	egg	dome		1	51
White-browed Scrubwren	camera	nm	dome		1	51
Black-faced Cuckoo-shrike *Coracina novaehollandiae*						
small cup nest	pers comm	unkwn			1	36
Rufous Whistler						
*Red-capped Robin	camera	egg		art	1	77
Grey Shrike-thrush *Colluricincla harmonica*						
*Red-capped Robin	camera	egg		art	25	77
art	camera	egg		art	9	41
Rufous Treecreeper	pers comm	egg	hollow		1	41
Restless Flycatcher *Myiagra inquieta*	d. obs	nestling	cup		1	43
*Willie Wagtail	d. obs	egg		art	1	43
Common Bronzewing	d. obs	eggs	cup		1	43
art	camera	egg		art	15	12
Rufous Whistler	d. obs	nestling	cup		1	17
Rufous Whistler	d. obs	egg	cup		1	17
*Willie Wagtail	camera	egg		art	3	46
Flame Robin *Petroica phoenicea*	d. obs	egg	cup		1	100
Zebra Finch *Taeniopygia guttata*	d. obs	egg	dome		1	55
*Bell Miner	sign	egg		art	4	84
small cup nest	pers comm	unkwn			1	36
Western Yellow Robin	d. obs	nestling	cup		1	105
Olive-backed Oriole *Oriolus sagittatus*						
Yellow-faced Honeyeater	camera	nestling	cup		1	51
Eastern Yellow Robin	camera	egg	cup		1	51

predator and prey	evidence	contents	Nest type: species	Nest type: as reported	# nests	cite no.
Acanthiza spp.	d. obs	nestling			1	9
butcherbird						
*Willie Wagtail	d. obs	egg		art	2	76
Grey Butcherbird *Cracticus torquatus*						
*Red-capped Robin	camera	egg		art	8	77
Laughing Dove *Streptopelia senegalensis*	d. obs	nestling	cup		1	90
Willie Wagtail	d. obs	nestling	cup		1	80
Laughing Kookaburra	d. obs	nestling	hollow		1	53
*Willie Wagtail	camera	egg		art	1	46
art	sign	egg		art	>1	92
small cup nest	pers comm	unkwn			1	36
Pied Butcherbird *Cracticus nigrogularis*						
*Red-capped Robin	camera	egg		art	1	77
Willie Wagtail	d. obs	nestling	cup		1	80
Budgerigar *Melopsittacus undulatus*	d. obs	nestling	hollow		>1	126
art	sign	egg		art	>1	92
Australian Magpie						
*Red-capped Robin	camera	egg		art	1	77
art	camera	egg		art	3	41
Yellow-plumed Honeyeater	d. obs	nm	cup		1	43
Magpie-lark	d. obs	nm	cup		1	5
Rainbow Bee-eater *Merops ornatus*	d. obs	nestling	burrow		1	4
*Willie Wagtail	d. obs	egg		art	17	76
*Willie Wagtail	camera	egg		art	2	46
Indet sp.	d. obs	nestling			1	19
*Bell Miner	sign	egg		art	2	84
egg shell	stomach	egg			>1	117
Pied Currawong *Strepera graculina*						
*Red-capped Robin	camera	egg		art	1	77
Magpie-lark	d. obs	nm	cup		1	5
Rufous Whistler	d. obs	nestling	cup		3	17
*Willie Wagtail	d. obs	egg		art	69	76
New Holland Honeyeater	d. obs	nestling	cup		1	85
*Willie Wagtail	camera	egg		art	5	46
Indet spp.	pellet	eggshell			7	21

predator and prey	evidence	contents	Nest type: species	Nest type: as reported	# nests	cite no.
Superb Fairy-wren	d. obs	nestling	dome		2	97
Common Starling	d. obs	nestling	hollow		1	113
Common Starling	d. obs	egg & nestling	hollow		>1	114
Common Blackbird *Turdus merula*	d. obs	egg & nestling	cup		>1	114
House Sparrow *Passer domesticus*	d. obs	egg & nestling	dome		>1	114
farm chicken *Gallus gallus*	d. obs	egg	N/A	farm chicken	1	3
White-browed Woodswallow *Artamus superciliosus*	d. obs	egg	cup		1	99
Spotted Dove	d. obs	egg	cup		1	125
White-bellied Cuckoo-Shrike	d. obs	egg	cup		1	57
Black-faced Cuckoo-shrike	d. obs	egg	cup		1	70
Common Starling	d. obs	nestling	hollow		>1	64
Common Blackbird	report	nestling	cup		1	95
Red Wattlebird	report	nestling	cup		1	95
Acanthiza sp.	report	nestling			1	95
Pardalotus sp.	report	nestling			1	95
Spotted Dove	report	nestling	cup		1	95
House Sparrow	d. obs	nestling	dome		1	65
Silvereye	d. obs	nestling	cup		1	65
Red-whiskered Bulbul *Pycnonotus jocosus*	d. obs	nestling	cup		1	122
Red-whiskered Bulbul	d. obs	nestling	cup		1	38
Red-whiskered Bulbul	report	nestling	cup		1	107
Magpie-lark	report	nestling	cup		1	107
Willie Wagtail	report	nestling	cup		1	107
Black-faced Cuckoo-shrike	report	nestling	cup		1	107
Little Wattlebird	report	nestling	cup		1	107
Flame Robin	d. obs	nestling	cup		1	100
Superb Fairy-wren	report	nestling	dome		>1	59
Common Myna	report	nestling	hollow		1	1
Yellow-rumped Thornbill	report	nestling	dome		1	1
House Sparrow	report	nestling	dome		1	1
Australian Magpie	report	nestling	cup		1	1
Common Blackbird	report	nestling	cup		1	1
Silvereye	report	nestling	cup		1	1
Common Starling	report	nestling	hollow		1	1
Australian Magpie	report	nestling	cup		1	1
Red-browed Finch	report	nestling	dome		1	1

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Silvereye	d. obs	nestling	cup		1	123
Spotted Dove	d. obs	nestling	cup		1	123
Noisy Friarbird	d. obs	egg	cup		1	40
Acanthiza spp.	d. obs	nestling			2	9
Acanthiza spp.	d. obs	egg			1	9
Common Blackbird	d. obs	nestling	cup		1	87
Red-browed Finch	d. obs	nest	dome		1	33
Common Blackbird	d. obs	nestling	cup		1	33
Common Starling	d. obs	nestling	hollow		1	33
Green Catbird	d. obs	nestling	cup		1	88
*Bell Miner	sign	egg		art	3	84
Scarlet Robin	d. obs	egg	cup		2	36
small cup nest	pers comm	unkwn			1	36
Silvereye	d. obs	nestling	cup		1	124
art	sign	egg		art	>1	44
Common Bronzewing	camera	nestling	cup		1	51
Variegated Fairy-wren	camera	nestling	dome		1	51
Brown Thornbill	camera	nestling	dome		2	51
Grey Fantail	camera	egg	cup		1	51
Rhipidura albiscapa						
Grey Currawong						
Strepera versicolor						
*Willie Wagtail	camera	egg		art	1	46
art	camera	egg		art	17	41
Splendid Fairy-wren	sign	unkwn	dome		1	112
Superb Fairy-wren	video	egg	dome		1	29
Willie Wagtail						
*Willie Wagtail	camera	nm		art	4	41
Corvus spp.						
*Willie Wagtail	d. obs	egg		art	2	76
*Willie Wagtail	camera	egg		art	1	46
Australian Raven						
Corvus coronoides						
*Red-capped Robin	camera	egg		art	6	77
art	camera	egg		art	2	41
art	camera	egg		art	33	78
Australasian Pipit	d. obs	egg	ground		1	16
Brolga	d. obs	egg	ground		1	119
indet. spp.	stomach	egg			57	103
Wild Turkey	report	egg & nestling	N/A	farm	>1	60
*Bell Miner	sign	egg		art	1	84
indet. spp.	stomach	egg			2	28
indet. sp.	stomach	nestling			1	28

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Forest Raven Corvus tasmanicus						
indet. spp.	stomach	egg			2	103
Little Raven						
indet. spp.	stomach	egg			30	103
art	camera	egg		art	5	12
White-fronted Chat *Epthianura albifrons*	d. obs	unkwn	cup		1	71
Little Crow Corvus bennetti						
indet. spp.	stomach	egg			13	103
Torresian Crow Corvus orru						
indet. spp.	stomach	egg			10	103
Cattle Egret *Ardea ibis*	sign	egg	cup		67	86
art	sign	egg		art	>1	92
Restless Flycatcher						
art	camera	egg		art	1	41
Magpie-lark						
*Willie Wagtail	d. obs	egg		art	2	76
White-winged Chough *Corcorax melanorhamphos*						
*Willie Wagtail	camera	egg		art	2	46
Apostlebird *Struthidea cinerea*						
*Red-capped Robin	camera	egg		art	1	77
Cattle Egret	d. obs	egg	cup		3	86
Magpie-lark	d. obs	egg	cup		1	120
Silvereye						
*Willie Wagtail	d. obs	egg		art	2	76
Common Starling						
*Willie Wagtail	d. obs	egg		art	2	76
indet. sp.	stomach	egg			1	28
Common Myna						
*Willie Wagtail	d. obs	egg		art	5	76
House Sparrow						
*Willie Wagtail	d. obs	egg		art	5	76
Superb Fairy-wren	d. obs	nm	dome		1	16
large bird						
*Eastern Yellow Robin	sign	egg		art	24	83
MAMMALS						
***Antechinus* sp.**						

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Brown Thornbill	camera	nestling	dome		1	49
Eastern yellow Robin	camera	egg	cup		1	51
Yellow-footed Antechinus *Antechinus flavipes*						
Rainbow Bee-eater	d. obs & sign	egg & nestling	burrow		9	15
art	sign	egg		art	3	92
*Rufous Treecreeper	sign	egg		art	25	68
Brown Antechinus *Antechinus stuartii*						
*Eastern Yellow Robin	sign	egg		art	2	83
*New Holland Honeyeater	sign	egg		art	11	75
Southern Brown Bandicoot *Isoodon obesulus*						
art	sign	egg		art	4	92
Northern Long-nosed Bandicoot *Perameles nasuta*						
*(chicken egg)	camera	egg		art	1	61
Greater Bilby *Macrotis lagotis*						
Rainbow Bee-eater	sign	nestling	burrow		1	42
Koala *Phascolarctos cinereus*						
art	sign	egg		art	1	45
Sugar Glider *Petaurus breviceps*						
Swift Parrot *Lathamus discolor*	camera & sign	egg	hollow		24	110
Tree Martin *Petrochelidon nigricans*	camera & sign	egg	hollow		3	110
Eastern Yellow Robin	camera	egg	cup		1	49
Brown Thornbill	camera	nestling	dome		1	51
Eastern Yellow Robin	camera	nestling	cup		1	51
Squirrel Glider *Petaurus norfolcensis*						
Common Bronzewing	d. obs	egg	cup		1	56
Magpie-lark	d. obs	egg	cup		1	121
Common Ringtail Possum *Pseudocheirus peregrinus*						

predator and prey	evidence	contents	Nest type: species	as reported	# nests	cite no.
*Eastern Yellow Robin	sign	egg		art	2	83
Common Brushtail Possum *Trichosurus vulpecula*						
art	camera	egg		art	20	41
art	sign	egg		art	2	92
art	sign	egg		art	1	93
*Eastern Yellow Robin	sign	egg		art	2	128
*New Holland Honeyeater	sign	eggs		art	12	109
*Rufous Treecreeper	sign	egg		art	18	68
Glossy Black-Cockatoo *Calyptorhynchus lathami*	camera	egg	hollow		1	47
Glossy Black-Cockatoo	sign	egg	hollow		11	47
Fawn-footed Melomys *Melomys cervinipes*						
*(chicken egg)	camera	egg		art	5	61
Giant White-tailed Rat *Uromys caudimaculatus*						
*(chicken egg)	trap	egg		art	23	62
*(chicken egg)	camera	egg		art	205	61
art	sign	egg		art	>1	52
House Mouse *Mus musculus*						
*Eastern Yellow Robin	sign	egg		art	1	128
*New Holland Honeyeater	sign	egg		art	2	75
*Bell Miner	sign	egg		art	48	84
Superb Fairy-wren	video	nestling	dome		1	29
rodent						
art	sign	egg		art	>1	92
*Superb Fairy-wren	sign	egg		art	20	30
rat						
Variegated Fairy-wren	camera	nestling	dome		1	49
Rattus sp.						
*(chicken egg)	camera	egg		art	3	61
*Eastern Yellow Robin	sign	egg		art	10	83
Variegated Fairy-wren	camera	nestlings	dome		1	51

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Bush Rat *Rattus fuscipes*						
*(chicken egg)	trap	egg		art	11	62
*(chicken egg)	camera	egg		art	49	61
art	sign	egg		art	>1	52
Superb Fairy-wren	video	nestling	dome		2	29
Cape York Rat *Rattus leucopus*						
*(chicken egg)	camera	egg		art	5	61
art	sign	egg		art	>1	52
Black Rat *Rattus rattus* and Bush Rat						
*New Holland Honeyeater	sign	egg		art	41	75
Black Rat						
art	sign	egg		art	>1	101
*White-fronted Chat & Scarlet Robin	camera	eggs		art	15	72
*White-fronted Chat & Scarlet Robin	camera	nestling		art	2	72
*New Holland Honeyeater	sign	eggs		art	35	109
New Holland Honeyeater	camera	egg & young	cup	natural with art egg	27	74
*Bell Miner	sign	egg		art	6	84
Dingo *Canis familiaris dingo*						
Rainbow Bee-eater	sign	egg & nestling	burrow		54	15
Red Fox *Vulpes vulpes*						
Malleefowl	sign	young		reintroduced	15	98
Superb Fairy-wren	camera	nesting	dome		2	51
Domestic Cat *Felis catus*						
Carnaby's Black-Cockatoo *Calyptorhynchus latirostris*	sign	nestling	hollow		>1	106
Grey Butcherbird	d. obs	nestling	cup		1	63
Red-tailed Black-Cockatoo Calyptorhynchus banksii	d. obs	nestling	hollow		1	106
Red-tailed Black-Cockatoo	sign and trap	nestling	hollow		27	106
Splendid Fairy-wren	sign	eggs	dome		32	104
Splendid Fairy-wren	sign	nestling	dome		33	104

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
*Willie Wagtail	d. obs	egg		art	3	76
Brown Thornbill	camera	egg	dome		1	51
FROGS AND REPTILES						
Cane Toad *Rhinella marinus*						
Rainbow Bee-eater	d. obs	egg & nestling	burrow		107	14
lizard						
Australasian Pipit	d. obs	nestling	ground		1	16
Eastern Water Dragon *Physignathus lesueurii*						
art	sign	egg		art	7	92
Bearded Dragon *Pogona barbata*						
art	sign	egg		art	>1	92
Rosenberg’s Goanna *Varanus rosenbergi*						
Stubble Quail *Coturnix pectoralis*	stomach	egg	ground		>1	60
Lace Monitor Varanus varius						
*(chicken egg)	camera	egg		art	1	61
Rainbow Bee-eater	sign	egg & nestling	burrow		25	15
art	sign	egg		art	>1	92
Rainbow Bee-eater	d. obs	egg	burrow		3	115
White-winged Chough	stomach	nestling	cup		1	115
Superb Fairy-wren	camera	egg & nestling	dome		2	51
Golden Whistler	camera	nestling	cup		1	51
Eastern Yellow Robin	camera	nestling	cup		1	51
Carpet Python *Morelia spilota*						
Rainbow Bee-eater	d. obs	nestling	burrow		1	42
Brown tree snake Boiga irregularis						
indet. spp.	stomach	eggs			11	108
indet. spp.	stomach	nestlings			6	108
Tiger Snake *Notechis scutatus*						
Flame Robin	d. obs	nestling	cup		1	100
Australasian Grebe *Tachybaptus novaehollandiae*	d. obs	nestling	ground		1	115

predator and prey	evidence	contents	Nest type:		# nests	cite no.
			species	as reported		
Straw-necked Ibis Threskiornis spinicollis	d. obs	nestling	ground		21	115
Glossy Ibis *Plegadis falcinellus*	d. obs	nestling	cup		1	115
Pacific Black Duck	d. obs	nestling	hollow		1	115
Pink-eared Duck *Malacorhynchus membranaceus*	d. obs	nestling	hollow		1	115
Masked Lapwing *Vanellus miles*	d. obs	nestling	ground		1	115
Crested Pigeon	d. obs	nestling	cup		1	115
Sacred Kingfisher *Todiramphus sanctus*	d. obs	nestling	hollow		1	115
Welcome Swallow *Hirundo neoxena*	d. obs	nestling	cup		1	115
Little Grassbird	d. obs	nestling	ground		1	115
Australian Reed-Warbler *Acrocephalus australis*	d. obs	nestling	cup		2	115
Willie Wagtail	d. obs	nestling	cup		2	115
White-plumed Honeyeater	d. obs	nestling	cup		1	115
White-fronted Chat	d. obs	nestling	cup		1	73
Brown Snake *Pseudonaja textilis*						
Superb Fairy-wren	d. obs	nestling	dome		1	27
Flame Robin	d. obs	nestling	cup		1	100
Splendid Fairy-wren	sign	unkwn	dome		3	112
Superb Fairy-wren	d. obs	nestling	dome		1	118
Red-bellied Black Snake *Pseudechis porphyriacus*						
Brown Thornbill	camera	nestling	dome		1	51
Spotted Pardalote *Pardalotus punctatus*	camera	unkwn	burrow		2	51
HYMENOPTERA						
Black-headed Sugar Ant *Camponotus nigriceps*						
Rainbow Bee-eater	d. obs	nestling	burrow		1	42
Greenslade's Meat Ant *lridomynnex greensladei*						
Common Bronzewing	d. obs	nestling	cup		1	42
Yellow-plumed Honeyeater	d. obs	nestling	cup		1	42

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APPENDIX 2

The complete bird community for temperate and sub-tropical woodland birds

This list was redrawn from Hannah Fraser's unpublished Ph.D. Thesis *Overcoming inconsistency in woodland bird classification* (submitted in 2017 at The University of Melbourne) and to be used in the nomination of a Threatened Ecological Community under the Environment Protection and Biodiversity Conservation (EPBC) Act 1999.

This list below was used to explicitly establish a complete set of temperate woodland birds for comparison to the review data presented in the associated paper "Meta-analyses of nest predation in temperate Australian forests and woodlands". Taxonomy follows: (Christidis and Boles 2008). This list is given in alphabetical order by family.

Family	Common name	Species
Acanthizidae	White-throated Gerygone	*Gerygone olivacea*
Acanthizidae	Western Gerygone	*Gerygone fusca*
Acanthizidae	Southern Whiteface	*Aphelocephala leucopsis*
Acanthizidae	White-browed Scrubwren	*Sericornis frontalis*
Acanthizidae	Chestnut-rumped Heathwren	*Hylacola pyrrhopygia*
Acanthizidae	Weebill	*Smicrornis brevirostris*
Acanthizidae	Western Thornbill	*Acanthiza inornata*
Acanthizidae	Striated Thornbill	*Acanthiza lineata*
Acanthizidae	Yellow Thornbill	*Acanthiza nana*
Acanthizidae	Tasmanian Thornbill	*Acanthiza ewingii*
Acanthizidae	Brown Thornbill	*Acanthiza pusilla*
Acanthizidae	Inland Thornbill	*Acanthiza apicalis*
Acanthizidae	Redthroat	*Pyrrholaemus brunneus*
Acanthizidae	Shy Heathwren	*Hylacola cauta*
Acanthizidae	Chestnut-rumped Thornbill	*Acanthiza uropygialis*
Acanthizidae	Buff-rumped Thornbill	*Acanthiza reguloides*
Acanthizidae	Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*
Acanthizidae	Speckled Warbler	*Chthonicola sagittata*
Accipitridae	Grey Goshawk	*Accipiter novaehollandiae*

Family	Common name	Species
Accipitridae	Brown Goshawk	*Accipiter fasciatus*
Accipitridae	Collared Sparrowhawk	*Accipiter cirrocephalus*
Accipitridae	Wedge-tailed Eagle	*Aquila audax*
Accipitridae	Little Eagle	*Hieraaetus morphnoides*
Accipitridae	Square-tailed Kite	*Lophoictinia isura*
Accipitridae	Swamp Harrier	*Circus approximans*
Accipitridae	Black-breasted Buzzard	*Hamirostra melanosternon*
Aegothelidae	Australian Owlet-nightjar	*Aegotheles cristatus*
Artamidae	Masked Woodswallow	*Artamus personatus*
Artamidae	White-browed Woodswallow	*Artamus superciliosus*
Artamidae	Black-faced Woodswallow	*Artamus cinereus*
Artamidae	Dusky Woodswallow	*Artamus cyanopterus*
Artamidae	Pied Currawong	*Strepera graculina*
Artamidae	Grey Currawong	*Strepera versicolor*
Artamidae	Pied Butcherbird	*Cracticus nigrogularis*
Artamidae	Grey Butcherbird	*Cracticus torquatus*
Artamidae	Australian Magpie	*Cracticus tibicen*
Burhinidae	Bush Stone-curlew	*Burhinus grallarius*
Cacatuidae	Red-tailed Black-Cockatoo	*Calyptorhynchus banksii*
Cacatuidae	Glossy Black-Cockatoo	*Calyptorhynchus lathami*
Cacatuidae	Yellow-tailed Black-Cockatoo	*Calyptorhynchus funereus*
Cacatuidae	Sulphur-crested Cockatoo	*Cacatua galerita*
Cacatuidae	Major Mitchell's Cockatoo	*Lophochroa leadbeateri*
Cacatuidae	Carnaby’s Black-Cockatoo	*Calyptorhynchus latirostris*
Cacatuidae	Western Corella	*Cacatua pastinator*
Cacatuidae	Little Corella	*Cacatua sanguinea*
Cacatuidae	Long-billed Corella	*Cacatua tenuirostris*
Cacatuidae	Galah	*Eolophus roseicapillus*

Family	Common name	Species
Campephagidae	Black-faced Cuckoo-shrike	*Coracina novaehollandiae*
Campephagidae	Ground Cuckoo-shrike	*Coracina maxima*
Campephagidae	White-bellied Cuckoo-shrike	*Coracina papuensis*
Campephagidae	White-winged Triller	*Lalage sueurii*
Casuariidae	Emu	*Dromaius novaehollandiae*
Charadriidae	Banded Lapwing	*Vanellus tricolor*
Climacteridae	Brown Treecreeper	*Climacteris picumnus*
Climacteridae	Rufous Treecreeper	*Climacteris rufa*
Climacteridae	White-throated Treecreeper	*Cormobates leucophaea*
Climacteridae	White-browed Treecreeper	*Climacteris affinis*
Columbidae	Peaceful Dove	*Geopelia striata*
Columbidae	Common Bronzewing	*Phaps chalcoptera*
Columbidae	Brush Bronzewing	*Phaps elegans*
Columbidae	Crested Pigeon	*Ocyphaps lophotes*
Corcoracidae	Apostlebird	*Struthidea cinerea*
Corvidae	Little Crow	*Corvus bennetti*
Corvidae	Forest Raven	*Corvus tasmanicus*
Corvidae	Australian Raven	*Corvus coronoides*
Corvidae	Little Raven	*Corvus mellori*
Cuculidae	Pallid Cuckoo	*Cuculus pallidus*
Cuculidae	Fan-tailed Cuckoo	*Cacomantis flabelliformis*
Cuculidae	Black-eared Cuckoo	*Chalcites osculans*
Cuculidae	Horsfield's Bronze-Cuckoo	*Chalcites basalis*
Cuculidae	Shining Bronze-Cuckoo	*Chalcites lucidus*
Estrildidae	Diamond Firetail	*Stagonopleura guttata*
Estrildidae	Double-barred Finch	*Taeniopygia bichenovii*
Estrildidae	Red-browed Finch	*Neochmia temporalis*
Estrildidae	Red-eared Firetail	*Stagonopleura oculata*
Estrildidae	Black-throated Finch	*Poephila cincta*
Eupetidae	Spotted Quail-thrush	*Cinclosoma punctatum*

Family	Common name	Species
Eupetidae	Chestnut-breasted Quail-thrush	*Cinclosoma castaneothorax*
Eupetidae	Chestnut Quail-thrush	*Cinclosoma castanotum*
Eurostopodidae	White-throated Nightjar	*Eurostopodus mystacalis*
Eurostopodidae	Spotted Nightjar	*Eurostopodus argus*
Falconidae	Australian Hobby	*Falco longipennis*
Falconidae	Brown Falcon	*Falco berigora*
Falconidae	Peregrine Falcon	*Falco peregrinus*
Halcyonidae	Laughing Kookaburra	*Dacelo novaeguineae*
Halcyonidae	Blue-winged Kookaburra	*Dacelo leachii*
Halcyonidae	Red-backed Kingfisher	*Todiramphus pyrrhopygius*
Halcyonidae	Sacred Kingfisher	*Todiramphus sanctus*
Hirundinidae	Welcome Swallow	*Hirundo neoxena*
Hirundinidae	Tree Martin	*Hirundo nigricans*
Maluridae	Superb Fairy-wren	*Malurus cyaneus*
Maluridae	Splendid Fairy-wren	*Malurus splendens*
Maluridae	Blue-breasted Fairy-wren	*Malurus pulcherrimus*
Maluridae	Variegated Fairy-wren	*Malurus lamberti*
Megaluridae	Rufous Songlark	*Cincloramphus mathewsi*
Megapodiidae	Malleefowl	*Leipoa ocellata*
Meliphagidae	Crimson Chat	*Epthianura tricolor*
Meliphagidae	White-naped Honeyeater	*Melithreptus lunatus*
Meliphagidae	White-throated Honeyeater	*Melithreptus albogularis*
Meliphagidae	Black-chinned Honeyeater	*Melithreptus gularis*
Meliphagidae	Strong-billed honeyeater	*Melithreptus validirostris*
Meliphagidae	Brown-headed Honeyeater	*Melithreptus brevirostris*
Meliphagidae	Black-headed Honeyeater	*Melithreptus affinis*
Meliphagidae	Striped Honeyeater	*Plectorhyncha lanceolata*
Meliphagidae	Scarlet Honeyeater	*Myzomela sanguinolenta*
Meliphagidae	Black Honeyeater	*Sugomel niger*

Family	Common name	Species
Meliphagidae	Eastern Spinebill	*Acanthorhynchus tenuirostris*
Meliphagidae	Western Spinebill	*Acanthorhynchus superciliosus*
Meliphagidae	Tawny-crowned Honeyeater	*Glyciphila melanops*
Meliphagidae	White-fronted Honeyeater	*Purnella albifrons*
Meliphagidae	Brown Honeyeater	*Lichmera indistincta*
Meliphagidae	Painted Honeyeater	*Grantiella picta*
Meliphagidae	Pied Honeyeater	*Certhionyx variegatus*
Meliphagidae	Regent Honeyeater	*Anthochaera phrygia*
Meliphagidae	Singing Honeyeater	*Lichenostomus virescens*
Meliphagidae	Fuscous Honeyeater	*Lichenostomus fuscus*
Meliphagidae	Yellow-faced Honeyeater	*Lichenostomus chrysops*
Meliphagidae	Yellow-throated Honeyeater	*Lichenostomus flavicollis*
Meliphagidae	Yellow-throated Miner	*Manorina flavigula*
Meliphagidae	White-eared Honeyeater	*Lichenostomus leucotis*
Meliphagidae	Yellow-tufted Honeyeater	*Lichenostomus melanops*
Meliphagidae	Yellow-plumed Honeyeater	*Lichenostomus ornatus*
Meliphagidae	White-plumed Honeyeater	*Lichenostomus penicillatus*
Meliphagidae	Crescent Honeyeater	*Phylidonyris pyrrhopterus*
Meliphagidae	New Holland Honeyeater	*Phylidonyris novaehollandiae*
Meliphagidae	White-cheeked Honeyeater	*Phylidonyris niger*
Meliphagidae	Noisy Miner	*Manorina melanocephala*
Meliphagidae	Red Wattlebird	*Anthochaera carunculata*
Meliphagidae	Yellow Wattlebird	*Anthochaera paradoxa*
Meliphagidae	Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*
Meliphagidae	Noisy Friarbird	*Philemon corniculatus*
Meliphagidae	Little Friarbird	*Philemon citreogularis*
Meliphagidae	Western Wattlebird	*Anthochaera lunulata*
Meropidae	Rainbow Bee-eater	*Merops ornatus*
Monarchidae	Magpie-lark	*Grallina cyanoleuca*
Monarchidae	Restless Flycatcher	*Myiagra inquieta*

Family	Common name	Species
Monarchidae	Satin Flycatcher	*Myiagra cyanoleuca*
Monarchidae	Leaden Flycatcher	*Myiagra rubecula*
Motacillidae	Australasian Pipit	*Anthus novaeseelandiae*
Nectariniidae	Mistletoebird	*Dicaeum hirundinaceum*
Neosittidae	Varied Sittella	*Daphoenositta chrysoptera*
Oriolidae	Olive-backed Oriole	*Oriolus sagittatus*
Pachycephalidae	Crested Shrike-tit	*Falcunculus frontatus*
Pachycephalidae	Golden Whistler	*Pachycephala pectoralis*
Pachycephalidae	Rufous Whistler	*Pachycephala rufiventris*
Pachycephalidae	Gilbert's Whistler	*Pachycephala inornata*
Pachycephalidae	Grey Shrike-thrush	*Colluricincla harmonica*
Pachycephalidae	Olive Whistler	*Pachycephala olivacea*
Pachycephalidae	Crested Bellbird	*Oreoica gutturalis*
Pardalotidae	Spotted Pardalote	*Pardalotus punctatus*
Pardalotidae	Red-browed Pardalote	*Pardalotus rubricatus*
Pardalotidae	Forty-spotted Pardalote	*Pardalotus quadragintus*
Pardalotidae	Striated Pardalote	*Pardalotus striatus*
Petroicidae	Jacky Winter	*Microeca leucophaea*
Petroicidae	Scarlet Robin	*Petroica multicolor*
Petroicidae	Red-capped Robin	*Petroica goodenovii*
Petroicidae	Flame Robin	*Petroica phoenicea*
Petroicidae	Hooded Robin	*Melanodryas cucullata*
Petroicidae	Dusky Robin	*Melanodryas vittata*
Petroicidae	Eastern Yellow Robin	*Eopsaltria australis*
Petroicidae	Western Yellow Robin	*Eopsaltria griseogularis*
Petroicidae	White-breasted Robin	*Eopsaltria georgiana*
Petroicidae	Southern Scrub-robin	*Drymodes brunneopygia*
Phasianidae	Brown Quail	*Coturnix ypsilophora*
Podargidae	Tawny Frogmouth	*Podargus strigoides*
Pomatostomidae	Grey-crowned Babbler	*Pomatostomus temporalis*

Family	Common name	Species
Pomatostomidae	White-browed Babbler	*Pomatostomus superciliosus*
Psittacidae	Rainbow Lorikeet	*Trichoglossus haematodus*
Psittacidae	Musk Lorikeet	*Glossopsitta concinna*
Psittacidae	Purple-crowned Lorikeet	*Glossopsitta porphyrocephala*
Psittacidae	Little Lorikeet	*Glossopsitta pusilla*
Psittacidae	Superb Parrot	*Polytelis swainsonii*
Psittacidae	Red-winged Parrot	*Aprosmictus erythropterus*
Psittacidae	Regent Parrot	*Polytelis anthopeplus*
Psittacidae	Green Rosella	*Platycercus caledonicus*
Psittacidae	Pale-headed Rosella	*Platycercus adscitus*
Psittacidae	Eastern Rosella	*Platycercus eximius*
Psittacidae	Western Rosella	*Platycercus icterotis*
Psittacidae	Red-capped Parrot	*Purpureicephalus spurius*
Psittacidae	Australian Ringneck	*Barnardius zonarius*
Psittacidae	Red-rumped Parrot	*Psephotus haematonotus*
Psittacidae	Mulga Parrot	*Psephotus varius*
Psittacidae	Blue Bonnet	*Northiella haematogaster*
Psittacidae	Blue-winged Parrot	*Neophema chrysostoma*
Psittacidae	Turquoise Parrot	*Neophema pulchella*
Psittacidae	Elegant Parrot	*Neophema elegans*
Psittacidae	Swift Parrot	*Lathamus discolor*
Psittacidae	Budgerigar	*Melopsittacus undulatus*
Ptilonorhynchidae	Spotted Bowerbird	*Ptilonorhynchus maculatus*
Rhipiduridae	Grey Fantail	*Rhipidura fuliginosa*
Rhipiduridae	Willie Wagtail	*Rhipidura leucophrys*
Strigidae	Southern Boobook	*Ninox boobook*
Strigidae	Barking Owl	*Ninox connivens*
Timaliidae	Silvereye	*Zosterops lateralis*
Turnicidae	Painted Button-quail	*Turnix varius*
Turnicidae	Little Button-quail	*Turnix velox*

Family	Common name	Species
Tytonidae	Eastern Barn Owl	*Tyto javanica*
Tytonidae	Masked Owl	*Tyto novaehollandiae*

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APPENDIX 3

Search efforts for first nests that led to the establishment of study sites

Distances travelled searching for the first nests, before establishing that nests were in *Eucalyptus wandoo* woodland, in the low-lying contours (Table A3-1). This is for the period 1 September 2002 to 18 September 2002 (= 18 days). The 8-day break between the 19th and 27th of September occurred, because I was away from Dryandra, in Perth. Road searches varied in length and were measured from Dryandra Village to the start of the walked transect and return. Walked transects were 3-km or two one-way, though one transect was only 2-km or two one-way. However, all required a return journey so they were 4 and 6 kms in total. Transects were measured with a 100 m tape-measure, while following a hand-held compass bearings, in an attempt to keep them straight. It is unlikely they were straight thus the measurements underestimate the true length walked and searched.

Table A3-1

Breakdown of initial searches giving kms searched and days undertaken with the number of nests found.

Distances searched on motorbike or car: Dryandra Village to… and return			
Road searched	kms return	days driven	nests found
Newel Rd	12.2	7	0
Colac	1.5	4	0
Koomal Rd	11.6	6	0
Spider to Marri	8.2	1	0
Totals	33.5	18	0
Total kms searched	**169.2**		

Walked transects			
Transects	kms return	days walked	nests found
Newel Rd (at Site 1)	6	7	5
Colac	6	4	0
Koomal Rd	6	6	0
Spider to Marri (at Site 1)	4	1	1
Totals	22	18	6
Total kms searched	**106**		

First transects searched and nests found that led to the first formal study sites

Site searches began on the 27th September 2002. They replaced transects that had stretched across vegetation types, because the birds and nests were located almost exclusively in low-lying areas of Dryandra (Table A3-2).

Table A3-2

Nest ID	**Date found**	**Transect / Site**	**notes on the nest location**
WS1	5/09/2002	Newel Rd	Found centrally in *Dryandra sessilis* heath on lateritic soils
PBQ1	6/09/2002	Newel Rd	Site 1: Centre site: in *E. wandoo* at the edge of Powder Bark Wandoo and natural Mallet.
YPHe1	15/09/2002	Newel Rd	Site 1: Centre site: near Newel *E. wandoo* woodland
CRTB1	17/09/2002	Newel Rd	Site 1: Centre site: in *E. wandoo* woodland
PBQ2	17/09/2002	Newel Rd / Site 1: Centre	Site 1: Centre site: in *E. wandoo* at the edge of Powder Bark Wandoo and natural Mallet.
BBFW1	27/09/2002	Spider to Site 1: Centre	Site 1: Centre site: near Newel *E. wandoo* woodland
end of transects			
start of site searches			
WYR1	27/09/2002	Site 1: Centre	*E. wandoo* woodland
BBFW2	3/10/2002	Site 4 / Spider Orchid site	*E. wandoo* woodland
DWS1	3/10/2002	Site 4 / Spider Orchid site	*E. wandoo* woodland
RF1	8/10/2002	Site 4 / Spider Orchid site	*E. wandoo* woodland
WW1	8/10/2002	Site 4 / Spider Orchid site	*E. wandoo* woodland
WYR2	8/10/2002	Site 1: Centre	*E. wandoo* woodland
YPHe2	8/10/2002	Site 1: Centre	*E. wandoo* woodland