

# **Avian breeding phenology and functional traits in relation to climatic variation**

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“Most of them are doomed to rapid extinction, but a few may make evolutionary inventions, such as physiological, ecological, or behavioral innovations that give these species improved competitive potential.”

— Ernst Mayr

## **Dedication**

I dedicate this thesis to the many ornithologists who freely contribute their time and effort in collecting, compiling, and making data available.

Without their labour, this research would not be possible.

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# General Abstract

The goal of this thesis is to explore how adaptations modulate the influence of climatic extremes in breeding birds. I develop novel methods to collate and analyse breeding observations from conventional and non-conventional data sources and compile the largest dataset of avian breeding observations in Australia. I assess spatial and temporal patterns of breeding phenology for approximately 330 species to evaluate how phenology varies across five biomes, (based on a national classification system where the tropical and equatorial regions were combined). Arising from this was the novel finding that birds in the desert breed significantly earlier than in any other biome. Additionally, phenology calculated from single sightings of juvenile birds or eggs was interchangeable with multi-visit observations, increasing the breadth of data available for breeding-time studies. I tackle a long-standing ecological question about which climatic conditions underpin the timing of opportunistic breeding. I show that inter- and intra-specific breeding niches differ systematically across tropical, subtropical, grassland, desert, and temperate biomes, and over temperature and aridity gradients. A key finding is that hot temperatures constrain breeding in arid regions, but the effect of rainfall is not as universal as commonly assumed. I further examine the relationship between breeding and climate, exploring variation in phenology in relation to the El Niño–Southern Oscillation (ENSO). Australian birds breed for longer and with greater intensity during the La Niña phase of ENSO, providing an outstanding opportunity for well-timed conservation initiatives. Finally, I demonstrate that the distribution of egg shape and nest types reflects selective pressures of critical environmental parameters such as temperature and the drying capacity of the air. In hot/dry areas with sparse plant canopies, mean egg elongation decreased, and the proportion of species with covered nests increased. Predicting which species may cope with extreme climate from measurable phenology, climatic niches and traits provide a timely solution for assessing vulnerability from climate change.

# Declaration

I do declare that this thesis constitutes my original work, and has not been submitted or accepted for the award of a higher degree at another institution. No persons have contributed to this work that have not been given credit, and all the work of previous scholars influencing this work are cited in the appropriate manner.

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Daisy Englert Duursma

20<sup>th</sup> September 2017



# List of Original Publications

This thesis is based on the following original manuscripts that are in various stages of publication; they are referred to in the text as Chapters two to five. Original publications are reproduced with permission from their copyright holders.

Chapter 2 **Englert Duursma, D.** , R. V. Gallagher, and S. C. Griffith (2017).

Characterizing opportunistic breeding at a continental scale using all available sources of phenological data: An assessment of 337 species across the Australian continent. *The Auk*:**126**,509–519. doi: 10.1642/AUK-16-243.1

Chapter 3 **Englert Duursma, D.**, R. V. Gallagher, and S. C. Griffith (in review). Climatic conditions that inhibit and promote egg-laying in opportunistically breeding birds. *Ecography*.

Chapter 4 **Englert Duursma, D.**, R. V. Gallagher, and S. C. Griffith (in review). Effects of El Niño Southern Oscillation on avian breeding phenology. *Diversity and Distributions*.

Chapter 5 **Englert Duursma, D.**, R. V. Gallagher, Price, J. J. and S. C. Griffith (in review). Variation in egg shape and nest structure modulates the effects of climate extremes. *Proceedings of the Royal Society, London, Series B*.

Appendix 1 Garnett ST, **Englert Duursma D.**, Ehmke G, Guay PJ, Stewart A, Szabo JK, Weston MA, Bennett S, Crowley GM, Drynan D, Dutson G et al. (2015) Biological, ecological, conservation and legal information for all species and subspecies of Australian bird. *Scientific Data*, **2** 150061.

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# Division of labour for chapters

Contribution by co-authors of the thesis, my own percentage contribution is provided in brackets. Co-authors key: DED – Daisy Englert Duursma, SCG – Simon C. Griffith, RVG – Rachael V. Gallagher, JJP – Jordan J. Price. For Appendix 1, the contributions of individual co-authors are not noted, due to large amount of co-authors.

	CHAPTER ONE	CHAPTER TWO	CHAPTER THREE	CHAPTER FOUR	CHAPTER FIVE	CHAPTER SIX	APPENDIX ONE
<b>CONCEPTION AND PLANNING</b>	DED (100%)	DED (80%), SCG, RVG	DED (80%), SCG	DED (80%), SCG	DED (80%), SCG, RVG	DED (100%),	DED (20%)
<b>DATA COLLECTION</b>	NA	DED (90%), SCG	DED (100%)	DED (100%)	DED (80%), SCG, JJP	NA	DED (5%)
<b>DATA ANALYSIS</b>	NA	DED (90%) RVG	DED (100%)	DED (100%)	DED (100%)	NA	DED (30%)
<b>INTERPRETATION AND WRITING</b>	DED (100%)	DED (90%), SCG, RVG	DED (80%), SCG, RVG	DED (90%), SCG, RVG	DED (80%), SCG, RVG, JJP	DED (100%)	DED (10%)

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I have the greatest appreciation for the many field ornithologists that contribute to the Handbook Of Australian, New Zealand & Antarctic Birds (HANZAB), as well as, observational repositories. In addition, I would like to thank the following organizations and establishments for making data available: Australia Bird and Bat Banding Scheme, Australian Museum, Australian National Wildlife Collection, BirdLife Australia, eBird, Museum and Art Gallery of the Northern Territory, Museum Victoria, Online Zoological Collections of Australian Museums (OZCAM), Queen Victoria Museum and Art Gallery, Queensland Museum, South Australian Museum, Tasmanian Museum and Art Gallery, and Western Australian Museum.

Finally, I would again like to express my deepest gratitude to Remko and Rachael who have foremost been amazing friends, forever offering support and encouragement. I would also like to thank my parents who provided an upbringing that resulted in an inherent love of nature.

# Chapter 1

## General Introduction

Birds are one of the most well studied classes of all animals, and have fascinated philosophers and scientists for thousands of years (e.g. Schneider 1864, Morton and Colonial Society of Massachusetts 1940, Harrison 1954). Yet there remain many questions and uncertainties as to why traits (e.g. clutch size, egg shape, breeding systems, nest types) and phenology (e.g. start, peak and conclusion of the breeding season, timing of migration) vary geographically and temporally (Bennett and Owens 2002). Aristotle wrote about variation in the timing of breeding and clutch size in 350 BC (Schneider 1864), and he proposed that bird species morphed into new species with the change of the season. It wasn't until the 17<sup>th</sup> century that Charles Morton recognised that birds migrated; however, he believed they migrated to the moon over a period of 60 days (Morton and Colonial Society of Massachusetts 1940, Harrison 1954). Even much more recently some widely accepted ideas to explain trait variation have proved to be quite wrong. For instance, it was widely accepted that the pear-shaped eggs of the Common Guillemot (*Uria aalge*) prevent them from rolling off cliff ledges (Birkhead et al. 2017). However, very few species lay eggs on cliff edges, and the Common Guillemot's egg shape is similar to that of many other species of birds. In fact, the rolling arc of the Common Guillemot's eggs is not that different from other species (Birkhead 2016, Birkhead et al. 2017). Therefore, this widely accepted, text-book example of an adaptive capacity of egg shape has recently been shown to not be correct.

Birds have the highest species richness and greatest global distribution of any terrestrial vertebrates (Claramunt and Cracraft 2015), providing a unique opportunity to examine variation in traits and phenology across assemblages of species in relation to climatic and environmental conditions. They have long been the focus of professional and non-professional interest, with their diurnal nature and high visibility making them easy to study. As a result, compared to other vertebrate groups, we have a more comprehensive understanding of their biodiversity, distributions, morphology and behaviour. This thesis is formulated around the hypothesis that traits and behaviours of

birds are optimized for the environments in which they occur, and large-scale geographic variation in traits reflects this.

Assessing traits, and how they are shared across assemblages of species, is a way to assess ecological strategies that improve fitness under a set of environmental conditions. It has been demonstrated that geographic variation in functional traits across assemblages of species can largely be explained by environmental factors (Liu et al. 2013, Foden et al. 2013). In this thesis I deliberately focus our analyses on the role of contemporary climate conditions in shaping the phenology of egg-laying and variation in traits whilst acknowledging the complementary role that shared evolutionary history may also play in determining patterns. Australia provides a unique opportunity to assess variation in traits and phenology because of its wide range of environmental conditions, distinct biogeography and phylogeny. It encompasses a large landmass, making it the easiest place in the world to sample across a whole continent. Australia extends over 35° of latitude (9–44° S) and 42° of longitude (112–154° E). Although a large portion of the country is covered by arid vegetation, there are also tropical, equatorial, subtropical, grassland and temperate biomes (Stern et al. 2000, Bureau of Meteorology 2006). Australian birds are globally distinct in their opportunism and nomadism, with 30% of Australian desert birds displaying opportunistic breeding (Morton et al. 2011), and more than 50 species of waterbirds breeding irregularly in response to periodic flooding (Kingsford et al. 1999). There is also a high degree of cooperative breeding when compared to other continents (Cockburn and Russell 2011). For these reasons Australia and the birds that breed on it, presents a unique opportunity to study avian traits such as nest type, egg shape and colour, body size, preferred food type, and phenology.

Australia is the driest inhabited continent in the world (Coleman 1980), but it was once much wetter. During the late Palaeocene (55 M years before present), seasonal aridity developed and by the end of the Pliocene (2 M years before present) modern climate existed (Martin 2006). Organisms have shifted their ranges and assemblages of species have changed in response to these climatic changes (Morton et al. 2011). Certain traits make particular groups (e.g. species, families, orders, or functional types) better adapted to survive under a set of climatic and environmental conditions. For instance, it is widely accepted that certain species of arthropods, amphibians, reptiles, and mammals have physiological adaptations that help them survive in the desert

(Willmer and Stone 2009, Moyes 2015). There is also evidence that desert birds have lower rates of metabolism, reduced oxygen consumption at the tissue level, and decreases respiratory water loss when compared to bird species in wetter environments (Williams and Tieleman 2005).

### ***Phenological records in Australia***

The US/IBP Phenology Committee defines phenology as "the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces and the interactions among phases of the same or different species" (see Lieth 1974). Historical interest in phenology, particularly in plants peaked between 1850 and 1950 (Sparks and Menzel 2002). In the late 20<sup>th</sup> century there has been a resurgence of interest because phenological observations are key in assessing how species have responded to past climatic events and current changes in the climate (Sparks and Menzel 2002). Research on multi-species bird breeding phenology, particularly in relation to anthropogenic climate change, is dominated by examples from the Northern Hemisphere temperate region (Crick 2004, Carey 2009, Both 2010, Møller et al. 2010). The United Kingdom's Nest Record Scheme (NRS) is the longest running NRS in the world and has been used in numerous publications that characterise breeding phenology and impacts from environmental and climatic changes (Crick et al. 2003, Crick 2004, Newton 2004, Gregory et al. 2004). Additionally, many of the most detailed studies of birds' breeding responses to climate change (e.g. Visser et al. 1998, 2010, 2015; Both and Visser 2005, Visser and Both 2005, Both 2010) come from just a few Northern Hemisphere temperate region species which have been extensively monitored for many decades (e.g. Great tits *Parus major* and pied flycatchers *Ficedula hypoleuca*). The dominance of the Northern Hemisphere temperate region in phenological studies is presumably due to the lack of long-term monitoring programs in other areas, such as Australia (Hughes 2003), rather than an absence of impacts from climate change.

Although many regions of the world do not have the long-term time series (greater than 30 years) of ornithological data available for studying avian populations, there are many potential sources of phenological and distributional observations that can be utilised (Møller and Fiedler 2010). The first avian breeding observations in Australia

come from James Cook's voyage to Australia in 1770. During this trip, bird observations were recorded, and specimens, including avian eggs, were collected. These eggs show that breeding was occurring on and at a particular date and location. Most of Australia's major museums have egg collection records, including many thousands of samples, that are an invaluable source of phenological observations but have yet to be used in large-scale studies. The Australian nest records scheme is the longest running bird survey in Australia (1939 – present) and records include all aspects of different breeding stages. Nests are often visited multiple times, allowing for accurate calculations of the timing of breeding events such as the date the first egg is laid in a clutch. Other sources of breeding data include Birdlife Australia Atlas, which records if observations were of breeding birds, online repositories such as eBird where lifecycle stage may be recorded, and bird banding records that include if the banded bird was a juvenile. In this thesis, I combine these various large-scale data sources to study the relationship between phenology and climate and to establish the breeding ranges.

Many difficulties need to be overcome when combining data from different sources. The quality and availability of the previously described data are highly variable, and each dataset has its own set of potential errors and biases (Møller and Fiedler 2010). To effectively use these data as a combined source of phenological records: 1) reduce the effect of variation in sampling intensity due to sampling method (i.e. a day of intensive mist netting in one location that results in 100 banding observations of a single species should have the same value as a single nest record observation or one record of a species breeding along a survey transect), 2) methods need to be developed so all the data measure the same distinct point in time (i.e. back-calculating to the date of first-egg lay in a clutch or date of egg hatch) and 3) phenological estimates from different sources should be calculated to cross validate estimates. Once these challenges are overcome, spatial and temporal variation in phenology can be studied.

### ***Breeding phenology and climate***

Modern day increases in climate extremes are already having direct consequences for ecosystems, including shifts in species distributions (Walther et al. 2002, Parmesan and Yohe 2003, Walther et al. 2005), and mass die off events due to heat stress and drought (Welbergen et al. 2008, Allen et al. 2010, McKechnie et al.



2012). For birds, the impact of climate change is already apparent in changes to the timing of breeding and migration (e.g. Crick, 2004; Crick and Sparks, 1999; Dunn and Winkler, 2010) and distributional range shifts (Shoo et al. 2006, La Sorte and Thompson 2007, Huntley et al. 2008, McClure et al. 2012, VanDerWal et al. 2013). Despite these documented changes, most avian species continue to breed successfully even under extreme conditions such as those found in the Australian desert (i.e. hot and dry). Identifying traits that may be advantageous for successful breeding in hot and arid regions may indicate groups (e.g. species, families, orders, or functional types) that may cope successfully with changing climates.

The timing of reproduction in birds most often corresponds to when food resources are most abundant and environmental conditions are suitable (Lack 1968). Food abundance is a crucial cue for breeding which can inhibit, drive, or maintain breeding activity (Zann et al. 1995, Visser et al. 1998, Both 2010) and, therefore, determine reproductive success (Visser et al. 2015)). Many species of birds have the greatest energy expenditure during reproduction, and the nestling rearing and fledging period is adjusted to coincide with peak food availability (Both 2010). For much of the world, this results in an annual cycle with breeding occurring at the same time every year, and even species that breed opportunistically do have some degree of seasonality (Sharp 1996, Tökölyi et al. 2011). Seasonal breeding can also result from the avoidance of detrimental environmental conditions. For example, excessive rainfall can flood nest burrows and saturate nests. Too much moisture in the nest can reduce hatching of eggs (Walsberg and Schmidt 1992). If extreme rainfall is an annual occurrence (i.e. in tropical and subtropical regions during monsoon season), it would be advantageous avoid breeding during those times.

In Australia, dry periods are well known to lead to the disruptions of seasonal breeding. During long lasting dry periods the reduction of food resources such as insect, fruit, and nectar can result in species refraining from breeding altogether. Such breeding depression has been observed in the tropics and subtropics (Williams and Middleton 2008), and arid regions (Morton et al. 2011). In desert regions bird species breed seasonally, opportunistically, or are interruptive (Zann et al. 1995). Australian desert waterbirds and some passerines have especially pronounced opportunistic and interruptive breeding (Kingsford et al. 1999, Morton et al. 2011). Given that Australia is

the world's driest continent (Coleman 1980), it is no surprise that the timing of reproduction appears to be strongly linked to rainfall (Zann et al. 1995, Gibbs et al. 2011, Morton et al. 2011). However, the link between rainfall and breeding has not been systematically studied for a wide range of species across the continent.

There is evidence that climate change is affecting birds in Australia in similar ways as to the Northern Hemisphere (*reviewed in* Chambers et al. 2013). For example, in Australia, earlier spring migration has been linked to warmer spring temperatures. In the temperate zone of Australia 40- 60% of bird species arrive earlier since the 1960's and 1970's (Beaumont et al. 2006, Chambers et al. 2013) Additionally, although results have varied by location, earlier breeding times coinciding with warmer spring temperatures have been reported in south-eastern Australia (Gibbs et al. 2011) with significant trends towards earlier breeding for species assessed in this region. These findings are consistent with those from the northern hemisphere where warmer spring temperatures are related to earlier migration and earlier breeding (Crick and Sparks 1999, Crick 2004, Gordo 2007, Carey 2009). However, most of these studies are limited by low sample size and assess only a small proportion of Australia's bird species.

Large-scale atmospheric phenomena such as the El Niño–Southern Oscillation (ENSO) and the North Atlantic Oscillation influence year to year variation in breeding phenology and intensity in many organisms, including birds (Forchhammer et al. 1998, Crick and Sparks 1999, Weatherhead 2005, Gibbs 2007, Møller et al. 2010, Gibbs et al. 2011). To fully assess spatial and temporal variation in breeding phenology, a comprehensive assessment of the effect of ENSO on Australian bird breeding phenology needs to be performed. In Australia, ENSO causes substantial inter-annual climate variation (Suppiah and Hennessy 1998): the El Niño phase is typically characterised by dry/hot conditions while La Niña is typified by wet/mild conditions. Previous studies investigating effects of ENSO phase on Australian birds have found that during the La Niña phase some species arrive earlier (Chambers and Keatley 2010), breed earlier in the year (Gibbs 2007) and with greater intensity (Gibbs et al. 2011). Understanding the effects of inter-decadal climatic variation on natural fluctuations in breeding phenology will improve our understanding of species' responses to climate (McCain et al. 2016).

## **Aims and thesis outline**

Much of the unique flora, fauna, and ecosystems on the Australian continent are exposed to extreme temporal and spatial variations in precipitation and temperature (Dickman et al. 1999, Holmgren et al. 2013, Wardle et al. 2013). Many studies have shown that fluctuations in precipitation and temperature play an important role in the maintenance of genetic variation and morphological evolution (Bell 2010), complex social behaviour (Jetz and Rubenstein 2011), sexual selection (Botero and Rubenstein 2012), and phenology (Zann et al. 1995, Forchhammer et al. 1998, Chambers and Keatley 2010, Gibbs et al. 2011) in birds. The objective of this thesis was to explore how climate, in addition to the physical environment (e.g. topography, vegetation type, proximity to permanent water bodies), has shaped the phenology and traits of Australia's ~600 mainland bird species, of which ~45% are endemic. Understanding how climate and the physical environment shape the traits and phenology of Australian birds will contribute to the conservation of the Australian avian biodiversity in the face of a changing climate.

The majority of the first six months of my thesis was spent collating species trait data and occurrence records of bird species. I assembled life history and functional trait data for Australian bird species using information available from books such as the Handbooks of Australian New Zealand and Antarctic Birds (see Chapter 2 for more detail) and from other databases. Much of these data are now published as a Nature Data Descriptor (Appendix 1). I played a major role in getting these data released by contributing not only several columns of data but also formatting and vetting for accuracy the data that is included. Due to this, I am a principal co-author on this paper, and although I have included this as an appendix, it is an important part of my thesis and represents an extensive amount of work.

One of the greatest challenges in studying phenology outside of the northern Hemisphere temperate region is the lack of reliable long-term baseline data. The data that does exist is typically specific to a particular location or region and has a taxonomic bias towards passerines. This is potentially problematic for inferring species responses to climate change in less seasonal regions of the world. Although ideal phenological

datasets may not always be available, there are numerous types of alternative observations that, when combined, may offer powerful substitutes (Sparks 2007, Dickinson et al. 2010). In Chapter 2, I investigate the possibilities of combining conventional and non-conventional sources of avian phenological data for the Australian continent. I build on previous methods developed by Crick et al. (2003) and Joys and Crick (2004) and calculate first egg-laying dates from many different sources of data. Using these data, I assess the accuracy of phenology calculated from different sources and determine spatial variation in avian phenology across the Australian continent. To the best of my knowledge, this is the first attempt to bring together historical museum egg collections, bird banding records, data from nest record schemes, and citizen science databases to calculate phenology of birds across Australia. The methods developed have implications for determining avian reproduction phenology in regions of the world where conventional time-series are not available, and also to provide comprehensive analyses in those parts where multiple sources are available and can be combined.

Worldwide biodiversity is being profoundly affected by climate change (Crick et al. 1997, Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Carey 2009, Chambers et al. 2010, Chen et al. 2011, Chambers et al. 2013, Thackeray et al., 2016). Understanding the effects of climate change on biodiversity is the single greatest challenge facing ecologists, yet we do not fully know the climatic conditions that govern breeding in many regions. In Chapter 3, I investigate opportunistic breeding in birds, and test long-held views on when birds breed in response to an unpredictable climate. By combining the egg-laying dates, calculated in Chapter 2, with daily climatologies of minimum temperature, maximum temperature and precipitation, I show that climatic conditions shape opportunistic breeding. This research offers a globally significant advance in our understanding of bird phenology and climate, essential for conservation planning in an era of global change.

It is well established that climatic oscillations affect the timing of reproduction in birds, but species responses to climate change are typically treated as linear processes where we look for changes in the long-term without assessing inter-annual variation. We know over the very long-term how climate cycles change rates of extinctions amongst species (i.e. glacial maxima, (Wanner et al. 2008)) and in the short-term how

populations can have extreme variability in sequential years (see McCain *et al.*, 2016), but decadal climatic cycles and the associated species responses are relatively poorly studied, particularly for land birds in the Southern Hemisphere. Underestimating the effect of inter-decadal climatic variation on natural fluctuations in species abundance and phenology is likely to decrease the accuracy of detected responses to climate change (McCain *et al.* 2016). In Chapter 4 I aim to quantify variation in opportunistic breeding during the three phases of the El Niño Southern Oscillation (ENSO; La Niña, El Niño, Neutral). I assess variation in egg-laying dates and calculate breeding phenology for 64 species of birds in the temperate region and 15 species in the arid region of Australia. I found that rainfall associated with La Niña can have dramatic effects on breeding phenology and likely recruitment, but the dry conditions of El Niño may not have the dramatic impacts that are commonly assumed.

Variation in temperature and precipitation are extreme across the Australian continent. Birds should have traits and behaviours that make them better adapted to survive in particular regions (i.e. the very moist conditions of the wet tropics or the hot, arid conditions of the desert). In Chapter 5 I test this idea using a comparative analysis to assess variation in nest type and egg shape of 310 passerine species across the Australian continent. The interaction between an egg and its environment likely drives selection that will shape eggs across evolutionary time. Understanding geographic variation in nest type and egg elongation may provide insight as to which species are better suited to overcome the potential challenges faced under extreme weather events, particularly heat waves. I found that eggs are most spherical in open nests in the hottest environments, and most elongate in domed nests in wetter, shady environments. This suggests that climatic conditions played a key role in evolution of passerine egg shape.

Chapter 6 is a general discussion summarising that links our results to current avian conservation measures in Australia. I also present ideas about how this research can be used in conservation.

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## Chapter 2

# Characterizing opportunistic breeding at a continental scale using all available sources of phenological data: An assessment of 337 species across the Australian continent

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## Chapter Two Vignette

Understanding the timing of reproduction phenology is of critical importance for studying the effects of climate change on avian species the world over. The lack of reliable long-term baseline data are challenges in many regions of the globe, particularly in the Southern Hemisphere (Hughes 2003). The long-term data that does exist is typically specific to a particular location and has a taxonomic bias towards passerines. Although ideal phenological datasets may not always be available, there are numerous types of alternative observations that, when combined, may offer powerful substitutes (Sparks 2007, Dickinson et al. 2010). In this chapter, I aim to find creative and robust alternatives to understanding and calculating phenology in data deficient areas of the world, specifically, Australia, and for a larger taxonomic sample of species.

The work presented here is, to the best of my knowledge, the first attempt to bring together historical museum egg collections, bird banding records, data from nest record schemes, and citizen science databases to calculate phenology. The methods I have developed to work with to calculate measures of reproduction phenology will be of interest to climate change adaptation planners, conservation biologists, big-data specialists, ornithologists, and behavioural ecologists. This dataset and the methods developed here underpin the breeding observations and measures of phenology used in Chapter 3 and Chapter 4.

The supplementary material for this chapter is available from  
<https://doi.org/10.6084/m9.figshare.5413189.v4>

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Pages 25-36 of this thesis have been removed as they contain published material. Please refer to the following citation for details of the article contained in these pages.

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## Supplemental Material

Table S1 is available from: <https://doi.org/10.6084/m9.figshare.5413189.v4>

### ***Names of institutions and persons associated with the collection or maintenance of breeding observations***

Australian breeding bird occurrence records were collated from Australian Museum, Australian National Wildlife Collection, BirdLife Australia's ATLAS and Nest Record Schemes, eBird, Museum and Art Gallery of the Northern Territory, Museum Victoria, OZCAM (Online Zoological Collections of Australian Museums), Queen Victoria Museum and Art Gallery, Queensland Museum, South Australian Museum, Tasmanian Museum and Art Gallery, Western Australian Museum and ABBBS (Australia Bird and Bat Banding Scheme). Individual and organizations who contributed the ABBBS data are CW Meredith, Dr Grant, E Wyndham, GK Disher, H Bakker, H Sutherland, HE Brenton, HS Curtis, JD Martindale, JR Wheeler, LW Moran, M Cohn, M Smyth, Mrs Templeton, Mr SNP Ali, NW Longmore, R Cooper, RJ Broad, RJ Thomas, RK Westcott, RWJ Pidgeon, RWJ Warnock, T Norostrom, TH Guthrie, WGD Middleton, Mr R Aitken, Ms R Alderman, Mr FJ Alexander, Mr SWW Alford, Mr P Allan, Mr RP Allen, Mr TH Alley, Dr SJ Ambrose, Mr G Ambrose, Mr R Anderson, Mr HF Archer, Mr NW Arnold, Ms H Aston, Mr T Aumann, Mr CN Austin, Mr GB Baker, Dr DJ Baker-Gabb, Mr DA Ball, Dr M Bamford, Mr KA Barker, Mr DE Barnes, Mr GJ Barrett, Mr WF Barrett, Mr LH Barrow, Mrs IM Bateman, Mr H Battam, Mr CI Baxter, Mr G Beal, Dr C Beckmann, Mr SR Beggs, Ms MI Beilharz, Mr GD Bell, Mr H Bell, Mr C Bennett, Dr ML Berg, Mr RJ Bilney, Mr CM Bishop, Mr CA Bissell, Mr EF Boehm, Mr CRJ Boland, Mr PF Bolger, Mr AR Bougher, Mrs BFJ Bowen, Ms GM Bowker, Mr AN Boyle, Ms JB Bradley, Mr HA Bradley, Dr LW Braithwaite, Mr AT Brennan, Prof JLE Gay Brereton, Mr JG Brickhill, Ms SV Briggs, Ms L Broadhurst, Mr MG Brooker, Mr NP Brothers, Mr RE Brown, Mr RF Brown, Mr RJ Brown, Dr AH Burbidge, Mr L Burgess, Mr NW Burnett, Dr TC Burton, Rev CG Burt, Mr J Bywater, Dr BM Cale, Dr GR Cam, Mrs A Cam, Mr M Cameron, Mr RG Cameron, Mr CB Campion, AC Cameron, Dr C Cannon, Mr M Carins, Dr R Carrick, Mr RK Carruthers, Mr BS Carter, Mr NT Carter, Mr BG Chaffey, Dr K Chan, Mr FRH Chapman, Mr GS



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## Chapter 3

# Climatic conditions that inhibit and promote egg-laying in opportunistically breeding birds

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## Chapter Three Vignette

This chapter brings fresh data and analysis to long-established but imperfectly tested, ideas about what governs opportunistic breeding in birds. I combine approximately 146,000 egg-laying observations of 327 species, gathered in Chapter 2, with daily climatologies of minimum temperature, maximum temperature and precipitation. I use these data to address several long-standing hypothesis and questions raised in chapter 2 about climatic constraints and triggers of avian breeding. Specifically, I show how the observed and average climatic breeding niche differs systematically across five biomes and shape opportunistic breeding. The results show that bird's breed when observed daily temperature, precipitation, or both are distinctly different than the two-year average conditions around breeding events. This is the first cross-biome quantification of this phenomenon. Additionally, breeding responses are plastic along aridity and temperature gradients *within* species which breed across multiple biomes. Breeding in hot, arid regions is constrained by hot temperatures, and the lagged effect of previous rainfall is not as ubiquitous as commonly assumed. These results offer an exciting, data-driven resolution to questions about avian phenology essential for climate change adaptation planning. This chapter offers a globally significant advance in our understanding of bird phenology and climate, essential for conservation planning in an era of global change.

## Abstract

Globally a significant proportion of birds breed flexibly, taking advantage of intermittent resource pulses to provision offspring. Quantification of climatic conditions that govern flexible and opportunistic breeding is essential for understanding reproductive phenology, and adaptive responses to a changing climate. We bring fresh data and analysis to long-established but imperfectly tested, ideas about what governs opportunistic breeding in birds. We combine ~146,000 breeding observations (first egg-laying dates) of 327 species with gridded climatologies of daily minimum temperature, daily maximum temperature and daily precipitation in two complementary analyses which characterise breeding *among* bird species sharing a biome (solving a common set of environmental conditions), and *within* bird species occurring across a north to south temperature gradient or an east to west aridity gradient (solving variation in environmental conditions). We found that breeding is non-random in relation to climate. Within biomes, most species breed when observed temperature, precipitation, or both were distinctly different than the two-year average conditions. Additionally, there is both intra- and inter-specific variation in the climatic conditions under which species lay eggs across aridity and temperature gradients. Breeding in hot and arid regions is in part driven by the lagged effect of previous rainfall. However, hot temperatures are the primary constraint. Flexible and opportunistic breeding is shaped by climatic conditions, which drive vegetation productivity and food resources and limited by physiological stress from extreme temperature or rainfall.

**Key-words:** breeding phenology, climatic constraints, egg-laying, opportunistic breeding, phenology

## Introduction

Climate conditions are the primary driver of vegetation productivity globally (Cramer *et al.*, 1999) and therefore underpin the provision of food resources for birds. Variation in vegetation types and productivity are driven by precipitation and temperature as well as soil characteristics and floristic histories. Previous studies have shown that temperature and rainfall can act as surrogates for vegetation productivity, which is difficult to measure directly (Churkina *et al.*, 1999; Cramer *et al.*, 1999). Water availability limits vegetation growth on 40% of the earth's land surface while temperature limits it on 33%, and temperature and water availability can be co-limiting (Nemani *et al.*, 2003). Vegetation productivity directly affects organisms at higher trophic levels by governing the availability of food resources. For birds, this effect can be direct, through the provision of leaf, seed or fruit resources, or indirect by altering the availability of prey items, which feed on vegetation (e.g. invertebrates, small mammals).

Many birds time breeding opportunistically to coincide with the time of year when conditions are most suitable, with selection favouring individuals that produce young when survival is optimal (Cockrem, 1995). Food abundance can inhibit, drive, or maintain breeding activity (Zann *et al.*, 1995; Visser *et al.*, 1998; Both, 2010a) and, therefore, determine reproductive success (Visser *et al.*, 2015)). The timing of food resources is highly predictable in some well-studied temperate regions (Lack, 1950; Visser *et al.*, 1998; Both, 2010b). For example, in the northern hemisphere temperate region, day lengthening and increases of spring temperature cue important phenological shifts in plants (Garner & Allard, 1923) and invertebrates (Buse *et al.*, 1999) leading to relatively predictable increases in food resources. By contrast, food resource availability fluctuates markedly in areas where plant phenology responds to less predictable cues, such as sporadic rainfall in deserts (Blendinger & Ojeda, 2001; Morton *et al.*, 2011). In these less predictable systems, birds still maintain peak periods where breeding is most intense (Zann *et al.*, 1995; Stouffer *et al.*, 2013; Englert Duursma *et al.*, 2017), but the climatic cues and constraints on breeding are poorly characterised.

Relationships between climate and the timing of breeding in birds have been inferred from a select group of single-species studies or limited to the northern hemisphere temperate zone, and typically only relate breeding to spring temperatures (Cockrem, 1995; Crick *et al.*, 1997; Visser *et al.*, 1998, 2015). However, better prediction

of the phenological responses of birds to climate change requires a synthesis of breeding behaviour in relation to rainfall and temperature across large numbers of species and over multiple vegetation and climatic zones.

In this study, we combine 146,009 observations of birds breeding (first egg-laying dates; FEDs) across 327 Australian species with daily observations of minimum temperature, maximum temperature and precipitation at each breeding location. We use this dataset to quantify and compare the difference in temperature and precipitation during each breeding event relative to ‘average’ conditions (i.e. conditions during the one-year period either side of a breeding event) for bird species found in each of Australia’s five biomes. This analysis compares breeding among bird species sharing a biome (and, therefore, solving a common set of environmental challenges). To complement this analysis, we assess breeding flexibility within single bird species which occur across the continental north to the south temperature gradient (n = 19 species) and east to the west aridity gradient (n = 53 species), therefore, solving variation in environmental conditions.

Many Australian birds respond opportunistically or with seasonal flexibility to food resources (Franklin, 2001; Williams & Middleton, 2008; Morton *et al.*, 2011) and the timing and length of breeding differs across biomes (i.e. shortest breeding periods in temperate biomes; longest in tropical biomes (Englert Duursma *et al.* 2017)). The timing of breeding also differs markedly from other regions of the world, being more than twice as long in a region of the Australian temperate zone compared to the United Kingdom (Englert Duursma *et al.*, 2017). Australia consists of five biomes (desert, grassland, subtropical, temperate and tropical; based on a national modified Köppen classification system (Stern *et al.*, 2000; Bureau of Meteorology, 2006), where the equatorial and tropical regions were combined, because of the small amount of data in the equatorial region. The desert, grassland, and temperate biomes have greater seasonal variation in temperature than the tropical biomes, while the tropical and subtropical biomes have predictable seasonal variation in rainfall (Fig 1). Assuming temperature and precipitation act as a proxy for food resource availability (Gross Primary Productivity (GPP); kg C/m<sup>2</sup>) and environmental suitability for the raising of young we hypothesise as follows:

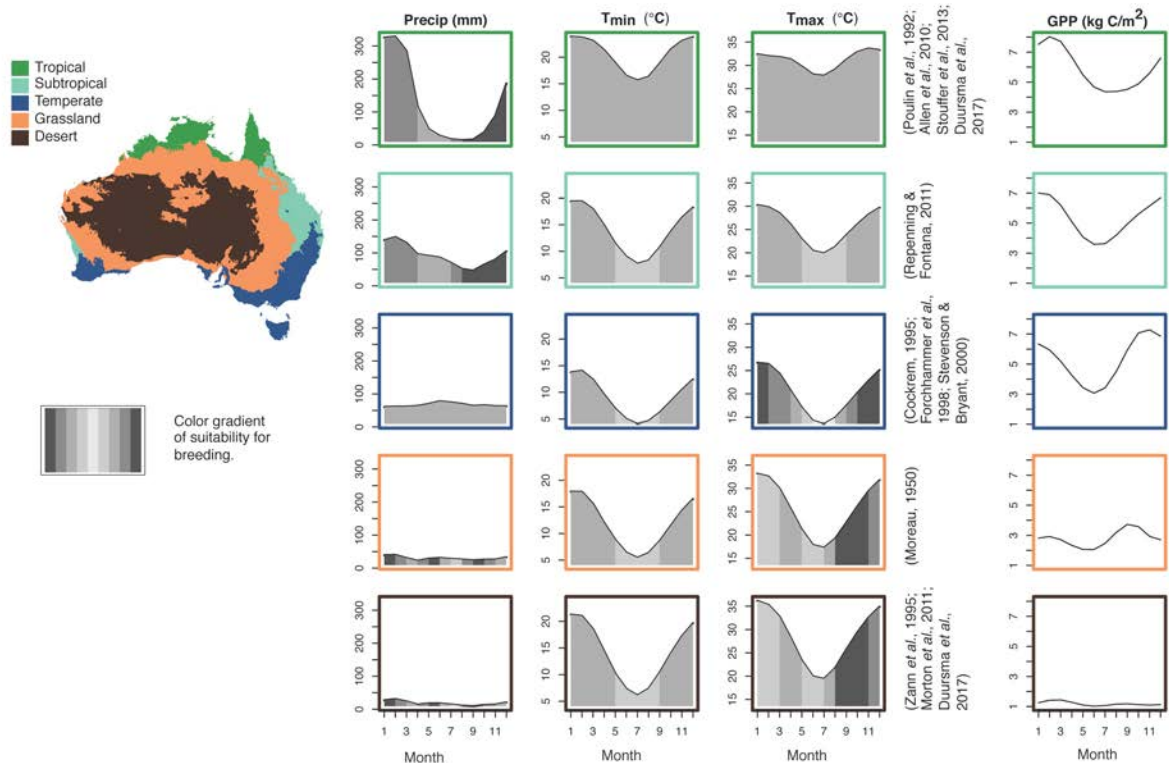
- (1) *Opportunistic breeding is triggered by distinct suites of climatic conditions in different biomes.* For instance, in desert and grassland biomes breeding of



some species is coupled to total rainfall and the resulting flush in vegetation (Moreau, 1950; Zann *et al.*, 1995), but many species are more persistent (Morton *et al.*, 2011). This contrasts to temperate biomes where breeding is more seasonal and cold temperatures constrain breeding due to reduced fitness from lower quality eggs when it is cold (Stevenson & Bryant, 2000) and in years where winters are warm, egg-laying occurs earlier in the year (Forchhammer *et al.*, 1998). We use the biomes of Australia to test for these differences in the drivers of avian breeding. We expect climate to drive (be positively associated with) breeding through its influence on food availability, food quality, while also constraining breeding (be negatively associated with) due to extreme climatic conditions that reduce the survival of parents, young and embryos. Figure 1 presents a conceptual framework for how we expect breeding to respond to climate and subsequent vegetation productivity (GPP). In the temperate biome of Australia (dark blue in Fig. 1), we expect cold temperatures, and the associated decrease in food resources, to constrain the timing of breeding for many of the species. We expect breeding in desert and grassland biomes to be limited by precipitation (brown and orange respectively in Fig. 1). We also expect breeding in these biomes to be constrained by extreme summer temperatures (Englert Duursma *et al.* 2017), thus realised climate niches associated with breeding should be less than yearly average maximum temperatures. Although breeding is less seasonal in tropical biomes, several studies have shown that more individuals breed during the end of the dry and beginning of the wet seasons, but the number of species breeding is relatively constant throughout the year (Stouffer *et al.*, 2013; Englert Duursma *et al.*, 2017). Other studies have found breeding peaks in response to sporadic rainfall during the rainy season (Poulin *et al.*, 1992; Hau, 2001) and in subtropical regions breeding may increase in response to changes in spring temperatures (Repenning & Fontana, 2011). We expect species breeding in the tropical and subtropical biomes (green and turquoise respectively, in Fig. 1) to have a mixed response to rainfall. Further, in the subtropics, cool winter temperatures may constrain breeding for some species.

(2) Rainfall has a lag effect on the productivity of vegetation (Noy-Meir, 1973), which will be important for determining food availability for successful bird breeding, particularly in desert and grassland biomes. We tested this hypothesis by looking for associations between rainfall and breeding events in five 30-day periods starting at 1, 31, 61, 91 and 121 days before egg-laying dates in the desert and grassland biomes. In desert and grassland biomes of Australia, rainfall events vary on decadal-scales resulting in irregular pulses of vegetation growth separated by periods of drought and annual and interannual rainfall events are typically small in magnitude (Morton et al., 2011). Variation in rainfall is largely caused by anomalies in sea-surface pressures and sea-level pressures from El Niño-Southern Oscillation and the inter-decadal Pacific Oscillation. In response to this variation many species in Australia are opportunistic or nomadic, especially in the desert region, and this helps species to respond intermittent food resource (Morton et al., 2011). In a comparison across Australian's biomes, it was noted that many orders of birds in the desert region had earlier egg-laying phenology than in any other biome (Englert Duursma et al. 2017), and although Australian desert breeding birds are commonly suggested as being some of the most opportunistic species, the birds in the desert biome seemed to exhibit the least plasticity in relation to temperatures in the summer months and this may be more important than lagged rainfall.

Testing our conceptual framework of breeding opportunism for 327 species across biomes we find that egg-laying is non-random in relation to the climatic conditions which govern vegetation productivity, namely temperature (minima and maxima) and precipitation (during breeding and lagged). This pattern is consistent across species sharing a biome, and in single species which occur in multiple biomes along environmental gradients.



**Figure 1.** Conceptual model of the relationship between climate and the intensity of avian breeding across five biomes (tropical, subtropical, temperate, grassland, desert). Map show a modified version of Australia's biomes where the tropical and equatorial regions have been combined (*modified from Stern et al. 2000, BOM 2006*) and plots show the long-term averages of monthly mean maximum temperature ( $T_{\max}$ ), monthly mean minimum temperature ( $T_{\min}$ ), and monthly total precipitation at the locations within the biomes where breeding was observed. The gray scale in plots represents the hypothesized relationship between the intensity of breeding and the climate variable from the literature for each biome (references shown). Climate data comes from the Australian Water Availability Project (Jones et al. 2009) via <http://www.bom.gov.au/jsp/awap/>, and GPP is MODIS derived using the DIFFUSE algorithm with three-veg-type parameterisation (Donohue et al. 2014), available from <http://www.auscover.org.au/purl/modis-gpp-diffuse-model>.

## Methods

### **Observations**

Breeding occurrence records (latitude and longitudinal coordinates and date of breeding observation) were collated from conventional records of avian breeding (Birdlife Australia's Atlas (Barrett *et al.*, 2003) and Nest Record Scheme), and non-conventional sources (historical museum egg collection, Australian Bird and Bat Banding Scheme and eBird (eBird 2015)). We excluded those species whose breeding habitat is restricted to coastal islets, beaches and mangroves according to Garnett *et al.*, (2015), because the environmental conditions these species are exposed to (tides, waves from boats, etc.) are likely to be different than inland species. Observations were divided into four types: *multi-visit* (occurrence records of a nest that was visited multiple times and for each visit the breeding stage was recorded, such as eggs, egg hatch, or young, *egg(s)* (single observation of eggs), *young* (single observation of young), and *undefined* (observation that states breeding was occurring but no information of breeding stage). Preference was given to observations that were *multi-visit*, *young*, and *eggs*. For species that had at least 100 of these observations in a biome, we excluded *undefined* observations because of their lower accuracy in defining breeding stage (Englert Duursma et al. 2017). If a species did not have a combined total of 100 *multi-visit*, *young*, and *eggs observations*, we included the *undefined* observations. The dates of breeding observations were back-calculated to first egg-laying dates (FEDs) following the methods provided in Englert Duursma et al. (2017). Briefly, differing by the observation types, the date of each breeding occurrence record was back-calculated to the FED by subtracting one or more species-specific life-history periods: period of lay (number of days it takes to lay an average clutch), length of incubation, and fledging period (Englert Duursma et al. 2017). For example, to find a FED of an occurrence record of an *egg*, we averaged FEDs back-calculated when we assume i) all eggs are laid but incubation has not begun. Thus we subtract the period of lay from the observation date, and ii) incubation is complete but eggs have not hatched, thus we subtract both the length of incubation and the period of lay.

Occurrence records were limited to those occurring after 1912 to match the temporal extent of available climate data. Only one occurrence at a specific location on a specific date was retained to reduce the effect of variation in sampling intensity due to

sampling method (i.e. sampling along a transect verses sampling over many hours using a mist net). Species were limited to those with a minimum of 50 breeding observations in at least one of Australia's biomes (based on a national modified Köppen classification system (Stern et al. 2000, BOM 2006), where the equatorial and tropical regions were combined). This resulted 146,009 observations of 327 species in 16 orders (temperate biome: 251 species in total with 102 of those species including *undefined* breeding observations; grassland biome: 180 species, 81 including *undefined* breeding observations; desert biome: 83 species, 64 including *undefined* breeding observations; subtropical biome: 139 species, 112 including *undefined* breeding observations, tropical biome: 46 species, 39 including *undefined* breeding observations. A complete list of institutes and persons who either collected these data or are custodians of the observations, is available in Appendix S1 in Supporting Information.

### ***Climate data***

Three climate variables were the focus of our study: minimum temperature ( $T_{\min}$ , °C), maximum temperature ( $T_{\max}$ , °C) and precipitation (mm) and data for each was accessed from Australian Water Availability Project (Jones *et al.*, 2009) via <http://www.bom.gov.au/jsp/awap/> at a 0.05° x 0.05° resolution. Climate data was used to compare the observed climatic niche to the average climate conditions at the time of breeding. The observed climatic niche during breeding was calculated for each occurrence record using daily AWAP data and was defined as the 30-day mean of daily  $T_{\min}$  and  $T_{\max}$ , and 30-day total precipitation, where the 30-day period was centred on the FED. The average climatic niche was similarly calculated using monthly AWAP data. However, the period of observation was defined as the two-year mean of  $T_{\min}$ ,  $T_{\max}$ , and monthly precipitation. The two-year averages were centred on the months of the FEDs and included the 12 prior months, observation month, and 11 subsequent months. This average climate niche approximates the typical conditions that a bird may potentially breed in over a biologically relevant period.

To assess if species respond opportunistically to rainfall in the months prior to breeding – the hypothesised 'lag effect' – in the hot, arid biomes of Australia (i.e., desert and grassland) we calculated five 30-day total precipitation periods. That is, for each occurrence record, using the daily AWAP data, we found 30-day total precipitation for

time intervals starting at 1, 31, 61, 91 and 121 days prior to the FED. Hereafter these intervals are referred to as 1-month, 2-month, 3-month, 4-month, and 5-months lagged precipitation.

A table of species occurrence records, the associated biome and climatic averages are available in Appendix S2 in Supporting Information via <https://doi.org/10.6084/m9.figshare.5413189.v4>.

## **Analyses**

All analyses and visualisations were carried out using R 3.3.3 (R Core Team 2017) using base packages, *data.table* (Bivand & Lewin-Koh, 2017), *raster* (Hijmans, 2016), *lme4* (Bates *et al.*, 2015), and *multcomp* (Hothorn *et al.*, 2008). Results of statistical analyses were considered significant at an alpha level of 0.05.

To assess if distinct suites of climatic conditions in different biomes trigger opportunistic breeding, we used species-level and biome-level paired *t*-tests. For each species, we performed three paired *t*-tests to compare the occurrence records observed 30-day  $T_{\min}$ ,  $T_{\max}$ , and precipitation to the two-year average  $T_{\min}$ ,  $T_{\max}$ , and precipitation. This allowed us to determine if the observed climate, at the times and locations a species was breeding, was significantly different than the average climate, at those same locations. To determine if in each biome, species breed when the realized climatic conditions were different than the average, we used biome-level paired *t*-tests of the species' means of observed  $T_{\min}$ ,  $T_{\max}$ , and precipitation two-year average means.

To establish if rainfall has a lag effect on the timing of reproduction in desert and grassland biomes, we used paired *t*-tests to determine if there were significant differences in the two-year average precipitation and lagged precipitation. We tested lagged precipitation at 1-month, 2-month, 3-month, 4-month, and 5-months prior to breeding to determine at what period the difference between average precipitation and lagged precipitation was the greatest. The 3-month lagged precipitation had the greatest difference and is the only time period used in additional analyses where lagged precipitation is of interest.

To assess if species breed under different climatic conditions across the north to the south temperature gradient (temperate, semi-tropical, and tropical biomes) and the east to the west aridity gradient (temperate, grassland, and desert biomes), we

performed linear mixed effects analyses, using *lme4* (Bates *et al.*, 2015). For the temperature gradient, we performed three analyses; the climate variable was 30-day  $T_{\max}$ , 30-day  $T_{\min}$  or precipitation. The aridity gradient analyses followed the same procedure, but 3-month lagged precipitation was included as an additional climate variable. ANOVA was calculated using Analysis of Deviance Table (Type II Wald F tests using Kenward-Roger approximation for degrees-of-freedom) and Tukey's pairwise comparisons in the *multcomp* package (Hothorn *et al.*, 2008) were used to determine if differences between biomes were significant. In all models, the climate variable and biome were fixed effects and species was a random effect, and we assumed the intercepts were different for each species.

## Results

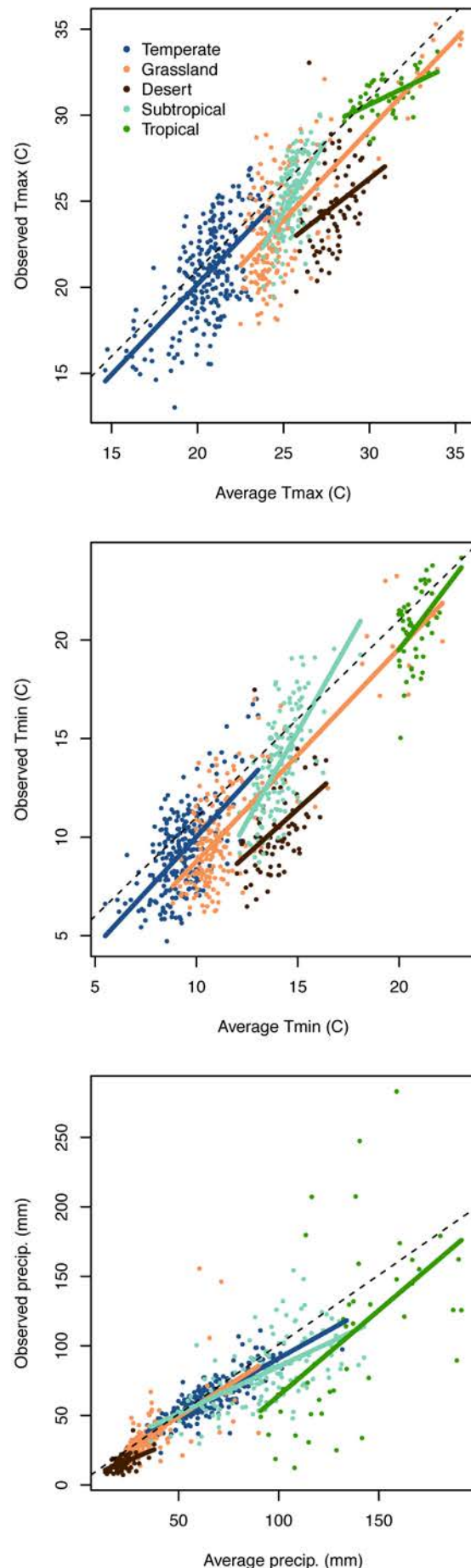
### ***Observed versus average climate in relation to egg-laying across species***

The relationship between the realised and 2-year average climate at the locations where breeding occurred varied considerably between biomes (Fig. 2). Biome-level paired *t*-tests show that species in the arid biomes (desert and grassland) breed when conditions are significantly cooler than the two-year averages. In the desert, 84% of all species ( $n = 75$ ) laid eggs when  $T_{\max}$  was significantly cooler than the two-year average. The observed  $T_{\max}$  was 3.9 °C (SD = 1.9°C) cooler for these species. Similarly, 57% of grassland species ( $n = 180$ ) laid eggs when  $T_{\max}$  was 2.8°C (SD = 1.4°C) cooler than the two-year average. The species-level results for  $T_{\min}$  were very similar; with 87% of species in the desert and 61% of species in the grassland breeding at significantly lower temperatures than expected based on the 2-year average. The remaining biomes did not have statistically significant differences between observed and 2-year average temperatures (Table 1). For species-level results see Appendix S3 in Supporting Information.

Observed precipitation niches during breeding were significantly drier than average precipitation conditions in four of the five biomes studied. In the subtropical and tropical biomes, the mean observed precipitation, across all species ( $n = 139$  and  $n = 46$ , respectively), was less than average (12% and 20%, respectively, Table 1), and ~50% of species laid eggs when rainfall was significantly less, although ~10% of species laid eggs when rainfall was significantly greater than average. The remaining species did

not have significant differences between observed and average precipitation (Fig 2, Appendix S3). In the temperate and desert biomes observed precipitation niches were drier than the 2-year average (2.5 mm and 6.3 mm drier, respectively, Table 1). Among the temperate species, 25% of species had significantly lower observed precipitation and 15% had greater. While in the desert biome, 66% of species laid eggs when observed precipitation was drier than average and only one species bred when it was wetter.





**Figure 2.** Observed and average mean maximum temperature ( $T_{\max}$ ), mean minimum temperature ( $T_{\min}$ ), and mean precipitation (precip) for species breeding in Australia's five biomes. Observed climate is the 30-day climatic condition centred on the first date of egg-laying (first egg date; FED) at locations where breeding occurred. Average climate is the mean of conditions over two-years centred on the month of the FED. Each point represents one species, and lines show the linear relationship between observed and average climate. The dashed black line is the 1:1 relationship between observed and average climate.

**Table 1.** Results from biome-level paired *t*-tests comparing observed and average climate conditions during avian breeding across 327 Australian bird species in five biomes. Observed climate is the average (temperature) or total (precipitation) 30-day climate conditions centred on the first date of egg-laying (first egg date; FED) at locations where breeding occurred. Average climate is the mean of conditions over two-years centred on the month of the FED. Climate variables examined are: mean maximum temperature ( $T_{\max}$ ), mean minimum temperature ( $T_{\min}$ ), and total precipitation (precip). Observed and average climate conditions are reported as the mean  $\pm$  standard deviation.

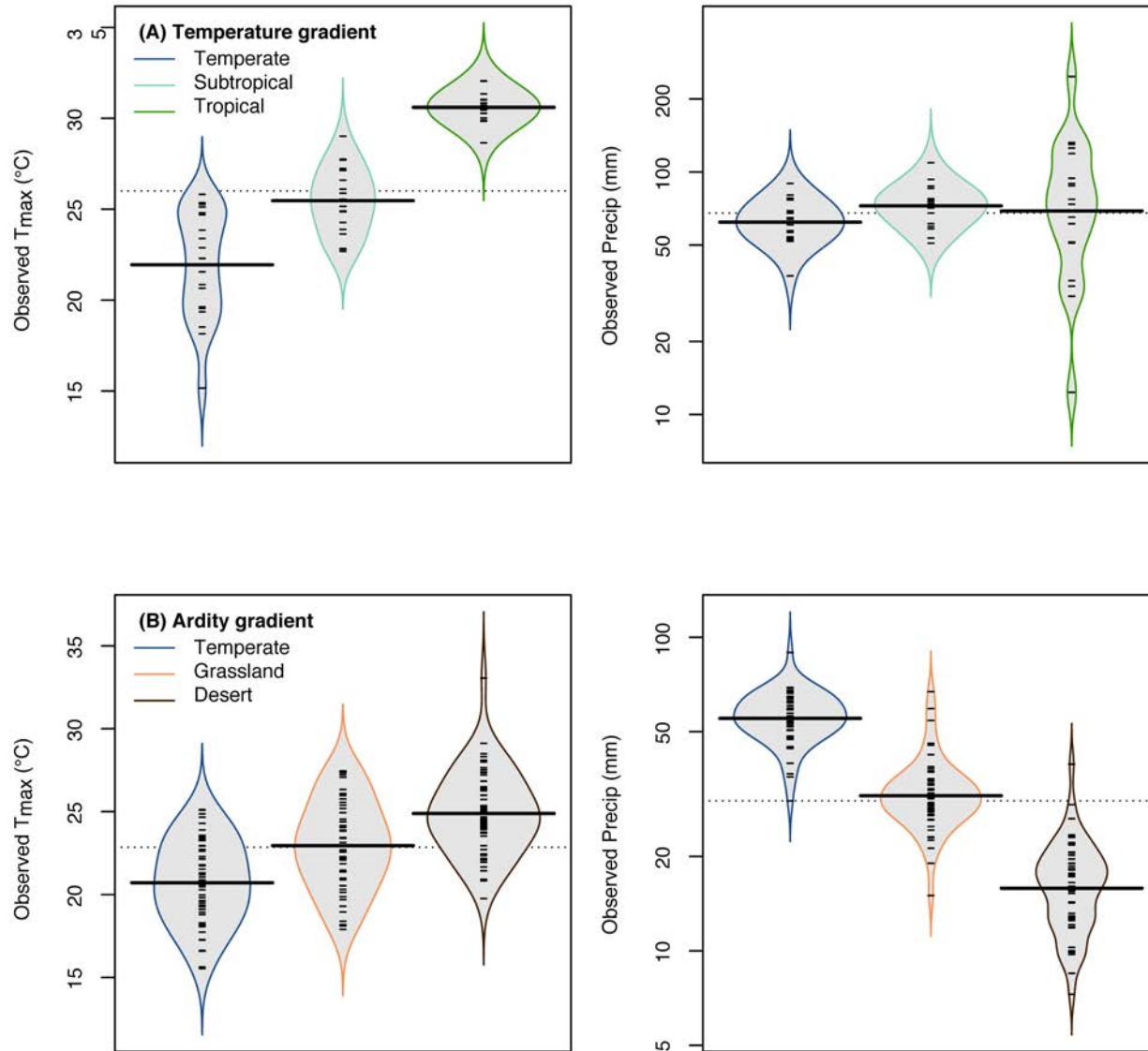
Biome	Observed climate	Average climate	<i>t</i> statement
$T_{\max}$ (°C)			
Temperate	20.8 $\pm$ 2.8	20.6 $\pm$ 1.7	$t(250) = 1.6$ , $p = 0.12$
Grassland	24.0 $\pm$ 3.5	25.1 $\pm$ 2.5	$t(179) = -6.2$ , $p < 0.001$
Desert	24.7 $\pm$ 2.4	27.9 $\pm$ 1.1	$t(75) = -12.2$ , $p < 0.001$
Subtropical	25.3 $\pm$ 2.1	25.5 $\pm$ 0.7	$t(138) = -1.7$ , $p = 0.09$
Tropical	31.0 $\pm$ 1.1	30.9 $\pm$ 1.4	$t(45) = 1.0$ , $p = 0.34$
$T_{\min}$ (°C)			
Temperate	9.3 $\pm$ 2.1	9.3 $\pm$ 1.2	$t(250) = -0.6$ , $p = 0.54$
Grassland	10.5 $\pm$ 3.2	11.6 $\pm$ 2.4	$t(179) = -7.5$ , $p < 0.001$
Desert	10.5 $\pm$ 2.2	14.0 $\pm$ 1.0	$t(75) = -15.6$ , $p < 0.001$
Subtropical	13.7 $\pm$ 2.5	14.1 $\pm$ 1.0	$t(138) = -2.2$ , $p < 0.05$
Tropical	20.6 $\pm$ 1.9	20.8 $\pm$ 0.7	$t(45) = -0.8$ , $p = 0.45$
Precip (mm)			
Temperate	64.3 $\pm$ 14.7	66.7 $\pm$ 15.3	$t(250) = -4.4$ , $p < 0.001$
Grassland	34.2 $\pm$ 16.2	33.8 $\pm$ 10.5	$t(179) = 0.5$ , $p = 0.70$
Desert	15.9 $\pm$ 5.3	21.9 $\pm$ 4.4	$t(75) = -10.6$ , $p < 0.001$
Subtropical	80.6 $\pm$ 23.8	93.1 $\pm$ 21.4	$t(138) = -7.4$ , $p < 0.001$
Tropical	107.5 $\pm$ 61.9	135.3 $\pm$ 27.4	$t(45) = -3.6$ , $p < 0.001$

### ***Intraspecific variation across biomes***

Species that breed in multiple locations across the north to the south temperature gradient (the tropical, subtropical, and temperate biomes) do so at significantly different temperatures [ $F(2, 36) = 141.25, p < 0.001$ ]. The results for  $T_{\max}$  and  $T_{\min}$  were similar; therefore we only report the results of  $T_{\max}$ . The warmest temperatures were observed in the tropical biome and coolest in the temperate biome (Figure 3a). There was no significant difference in precipitation during breeding across the gradient [ $F(2, 36) = 2.0375, p = 0.14$ ] (Figure 3a).

The east to west aridity gradient includes the temperate, grassland and desert biomes and the observed 30-day precipitation was significantly different in all biomes [ $F(2, 104) = 320.91, p < 0.001$ ] with the driest conditions in the desert (Figure 3b). Three-month lagged precipitation was also significantly different, with the temperate biome being wetter, while the desert and grassland biomes did not significantly differ from each other [ $F(2, 104) = 148.23, p < 0.001$ ]. There was also a significant difference in temperature across the three biomes [ $F(2, 104) = 85.869, p < 0.001$ ], with the desert being the warmest at the times species were laying eggs.

**Figure 3.** Distribution profile of observed mean maximum temperature (Tmax; °C) and precipitation (precip; mm) at the time of breeding (first-egg date; FED) for species occurring along (A) the north to the south temperature gradient, and (B) the east to the west aridity gradient in Australia. The width of the violin is proportional to the density of breeding at a given temperature or amount of precipitation. The dotted line is the mean across all biomes; long horizontal lines show the mean of all species in a biome; short horizontal lines represent the average of each species.



### ***Lagged precipitation***

Based on the biome-level paired *t*-tests, at least half the birds in the arid regions of Australia breed in response to lagged rainfall. In the desert and grassland, there was

significantly greater lagged precipitation than average precipitation at all 30-day time-periods (Table 2), except 1-month prior to egg-laying in the desert when across all species lagged precipitation was 2.8 mm less than the 2-year average. The relationship between lagged precipitation and the timing of breeding peaks around 3-months prior to the FEDs. For this period in the desert, 51% of species experienced significant greater 3-month lagged precipitation than the 2-year average, and for these species, it was 14.7mm more. Likewise, in the grassland biome, 63% of species had significantly greater precipitation 3-month prior to egg-laying, being an average of 13mm more (Table 2, Appendix S3). Although 51% of the species in the desert (63% in the grassland) breed when lagged rainfall was significantly greater, 6% (1.5% in the grassland) of the FEDs across these species were recorded when there was a near absence of any precipitation (<10mm) during the entire 3 month period prior to the FED. Additionally, half the species in the desert (49%) and 37% of species in the grassland don't seem to respond to lagged rainfall.

**Table 2.** Results from biome-level paired *t*-tests comparing breeding behaviour in response to lagged and average precipitation across 76 Australian bird species in the desert biome and 180 species in the grassland biome. Lagged precipitation is the summed total of 30-days of precipitation, where month 1 corresponds to days 1 through 30 before the first-egg date (FED), month 2 is for days 31 to 60 before the FED, and so on. Lagged precipitation values are reported as the mean  $\pm$  standard deviation. Average precipitation is the mean of 30-day total precipitation over two-years centred on the month of the FED. We report the number of species breeding at significantly greater lagged precipitation (*n* species), relative to average precipitation (desert =  $21.9 \pm 4.4$ ; grassland =  $33.8 \pm 10.5$ ), and the percentage difference in lagged precipitation when compared to the average precipitation. Significance was tested using species-level paired *t*-tests.

Month	<i>n</i> (species)	Lagged precipitation (mm)	Difference (%)	<i>t</i> -statement
Desert				
1	4	19.2 $\pm$ 6.8	12.3	<i>t</i> (75) = -3.9, <i>p</i> < 0.001
2	24	26.5 $\pm$ 10.8	-21.0	<i>t</i> (75) = 4.6, <i>p</i> < 0.001
3	39	30.3 $\pm$ 12.5	-38.4	<i>t</i> (75) = 7.1, <i>p</i> < 0.001
4	31	27.8 $\pm$ 11.5	-26.9	<i>t</i> (75) = 6.0, <i>p</i> < 0.001
5	22	26.3 $\pm$ 11.2	-20.1	<i>t</i> (75) = 4.4, <i>p</i> < 0.001

Grassland				
1	70	37.9 ± 19.5	-12.1	$t(179) = 3.8, p < 0.001$
2	109	41.9 ± 23	-24.0	$t(179) = 7.1, p < 0.001$
3	115	42.2 ± 24.8	-24.9	$t(179) = 6.6, p < 0.001$
4	94	39.9 ± 21.6	-18.0	$t(179) = 5.5, p < 0.001$
5	55	37.1 ± 17	-9.8	$t(179) = 3.7, p < 0.001$

## Discussion

We believe this is the first large-scale, multi-biome work that investigates how temperature and precipitation drive and constrains avian breeding. We found that (i) in five different biomes, the majority of species breed when either temperature, precipitation, or both were distinctly different than the average climatic conditions, (ii) species that breed across large climatic gradients are adapted to localized climate and use different suites of climatic conditions, and (iii) although lagged rainfall does emerge as an important driver of breeding in hot and arid regions, hot summer temperatures may constrain breeding to a greater degree (Table 1, Figure 2). These three findings suggest that majority of bird species in all biomes breed under distinct suites of climatic conditions when food resources are most abundant, and the physiological stress from extreme temperature or rainfall is low.

Determining the exact drivers and constraints of opportunistic breeding over an ecologically and climatically diverse land-mass is a complex task due to the diversity of species and their many life histories, breeding, and feeding strategies. Opportunistic breeders respond to a variety of environmental factors to time breeding (Cockrem, 1995; Hahn & MacDougall-Shackleton, 2008), and in regions with low seasonality of climate, using multiple factors can increase the ability of a species to breed successfully (Hau *et al.*, 2004). Much of what we know about seasonal breeding is derived from temperate regions with ornithologists from North America and Europe applying their knowledge of seasonal food resources and peaks in breeding to other biomes (Stouffer *et al.*, 2013). Although all biomes in Australia are less seasonal than the temperate biome of the Northern Hemisphere (Englert Duursma *et al.* 2017) and in all biomes egg-laying was observed in every month, most species still had either temperature or precipitation driving or apparently constraining their breeding activity.

In the hot and arid biomes of Australia, we found that breeding in most species is associated with seasonal temperatures in addition to lagged rainfall, but there was no indication that breeding was solely a response to seasonal variation in rainfall. This contrasts to the assumptions of many previous studies that have suggested rainfall was the ultimate driver of breeding in deserts (Zann *et al.*, 1995; Burbidge & Fuller, 2007), although even within these studies it was noted that breeding did not occur after every rainfall event. It is worth noting that of all the biomes in this study, the desert biome has the greatest seasonal fluctuation of temperature (Fig. 1). Our findings suggest that seasonally modulated maximum temperatures in the hot and arid regions constrained breeding to a greater degree than highly variable precipitation. Other studies of desert breeding birds have come to the same conclusion but focus on a small number of species (Barrientos *et al.*, 2007; Cunningham *et al.*, 2013).

Some species laid eggs when the climatic conditions were quite different than the majority of species observed within the same biome (Fig. 2). Much of this variation can be explained through preferred food resources and behavioural differences. For instance, in the tropical and subtropical biomes the vast majority of species breed when rainfall was below average, but 15 species breed when conditions were significantly wetter than expected based on the 2-year averages of precipitation (Fig. 2). These species occurred across six orders, with eight of the species being waterbirds and 11 of the species feeding on invertebrates for at least some of their diet (Garnett *et al.*, 2015). In tropical regions characterised by wet and dry seasons many freshwater, estuarine, marine and terrestrial invertebrates increase in abundance during the wet seasons (Poulin *et al.*, 1992; Williams & Middleton, 2008). Likewise, during breeding and the raising of offspring, many bird species increase the amount of invertebrates consumed (Poulin *et al.*, 1992). Typically flowers and fruits, in the wet/dry tropics, are greatest during the late dry and early wet periods (Poulin *et al.*, 1992), and this corresponds to the period where the greatest numbers of individuals are laying eggs (Stouffer *et al.* 2013, Englert Duursma *et al.* 2017). In the desert biome, the hoary-headed grebe (*Poliiocephalus poliocephalus*), breeds when the observed temperatures are well above the 2-year average in contrast to the majority of other species in this biome (Fig. 2). Historically this species did not breed in the arid interior of Australia, but it now breeds in

artificial water bodies indicating that human modification of the landscape can broaden the breeding niche of species.

Breeding phenology of species in the desert and grassland biomes of Australia are earlier than those in other biomes and it been hypothesized that this may have evolved to limit exposure to summer maximum temperature's (Englert Duursma et al. 2017). Our analysis of  $T_{\min}$  and  $T_{\max}$  support this hypothesis, with more than 80% of the species in the desert and 50% in the grassland breeding when temperatures were cooler than expected. Preventing exposure to extreme temperatures is critical for embryonic development, perhaps more so than constancy of temperatures. For most passerine species the upper thermal limit of core egg temperatures is between 43°C and 44°C and prolonged exposure high ambient temperatures being lethal (Webb 1987, DuRant et al. 2013) or greatly reducing hatchability (Stoleson and Beissinger 1999). In desert regions, eggs can reach their thermal limits rapidly when exposed to direct sunlight (Carey 2002) and when eggs are exposed to very warm temperatures, 'ambient' incubation can occur, reducing incubation time and decreasing hatch synchrony (Griffith et al. 2016). It is worth noting that even in some areas of the temperate biome daily maximum temperatures in the summer can be well over 40°C (Bureau of Meteorology 2009, Jones et al. 2009).

Adverse physiological effects of high temperatures on adults and offspring may compromise breeding during hot summer months. High temperatures have been related to reductions in adult health and reduced chick growth (Cunningham et al. 2013, Cunningham et al. 2014). Adverse effects on sperm quality have also been demonstrated in response to experimental, ecologically relevant heat exposure (Hurley et al., 2018). It is well noted that climate influences the demography and recruitment of avian populations (Crick, 2004; Sandvik et al., 2008; Brawn et al., 2017; McCauley et al., 2017), with several studies finding that this relationship is strongest for the first broods of the year (Järvinen, 1996; Winkel & Hudde, 1997; Møller, 2002). There is a growing body of evidence that extremes in climate influence the long-term survival and fitness of Australian birds to greater degrees than average climatic conditions (McKechnie et al., 2012).

In the tropical and subtropical biomes, egg-laying events for about half of the species occurred when rainfall was significantly less than average. This indicates that, at least for half the species in these regions, high levels of rainfall are associated with



reduced fitness. In tropical regions, which have a seasonally dry period, flowering, fruiting and flushing of leaves typically occur at the start of the wet season (Poulin et al. 1992, Schaik et al. 1993), and for many species, this would be a peak in food resources. Additionally, excessive moisture in the nest environment during the wet season can substantially reduce successful hatching of eggs due to inadequate gas exchange (Walsberg and Schmidt 1992).

In conclusion, the distinct suites of climatic conditions under which most species breed (Appendix S3), exemplifies how climate can influence the timing of breeding through food resources abundance as well as through the likely reduced survival of adults, juveniles and embryos under both extreme temperature and rainfall. This is likely to profoundly affect many aspects of physiology, behaviour, and life-histories of Australian birds. Here we have demonstrated both inter- and intraspecific phenological variation to the climate in five biomes. Understanding variation in breeding behaviour in relation to temperature and rainfall in multiple biomes and across many allows us to predict phenological responses to climate change and extreme events better.

## **Data deposition**

The breeding bird occurrence records and climatic data used in this study were collated from a variety of online databases, institutes, and persons (for a complete list institutes and persons, please see Appendix S1). Although most of these data are freely available, redistribution is restricted by license. To make this study reproducible, we have made available a table of occurrence records with biome of occurrence and 30-day means of daily  $T_{\min}$  and  $T_{\max}$ , 30-day total precipitation, 30-day lagged precipitation at 5 monthly intervals, and the two-year means of  $T_{\min}$ ,  $T_{\max}$ , and monthly precipitation for the 146,009 observations used. These data are available in Appendix S2. We have removed the latitude and longitude coordinates to meet the conditions of our license with data providers. Data are available from: <https://doi.org/10.6084/m9.figshare.5413189.v4>

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## Supporting Information

### Appendix S1

#### ***Names of institutions and persons associated with the collection or maintenance of breeding observations***

Australian breeding bird occurrence records were collated from Australian Museum, Australian National Wildlife Collection, BirdLife Australia's ATLAS and Nest Record Schemes, eBird, Museum and Art Gallery of the Northern Territory, Museum Victoria, OZCAM (Online Zoological Collections of Australian Museums), Queen Victoria Museum and Art Gallery, Queensland Museum, South Australian Museum, Tasmanian Museum and Art Gallery, Western Australian Museum and ABBBS (Australia Bird and Bat Banding Scheme). Individual and organizations who contributed the ABBBS data are CW Meredith, Dr Grant, E Wyndham, GK Disher, H Bakker, H Sutherland, HE Brenton, HS Curtis, JD Martindale, JR Wheeler, LW Moran, M Cohn, M Smyth, Mrs Templeton, Mr SNP Ali, NW Longmore, R Cooper, RJ Broad, RJ Thomas, RK Westcott, RWJ Pidgeon, RWJ Warnock, T Norostrom, TH Guthrie, WGD Middleton, Mr R Aitken, Ms R Alderman, Mr FJ Alexander, Mr SWW Alford, Mr P Allan, Mr RP Allen, Mr TH Alley, Dr SJ Ambrose, Mr G Ambrose, Mr R Anderson, Mr HF Archer, Mr NW Arnold, Ms H Aston, Mr T Aumann, Mr CN Austin, Mr GB Baker, Dr DJ Baker-Gabb, Mr DA Ball, Dr M Bamford, Mr KA Barker, Mr DE Barnes, Mr GJ Barrett, Mr WF Barrett, Mr LH Barrow, Mrs IM Bateman, Mr H Battam, Mr CI Baxter, Mr G Beal, Dr C Beckmann, Mr SR Beggs, Ms MI Beilharz, Mr GD Bell, Mr H Bell, Mr C Bennett, Dr ML Berg, Mr RJ Bilney, Mr CM Bishop, Mr CA Bissell, Mr EF Boehm, Mr CRJ Boland, Mr PF Bolger, Mr AR Bougher, Mrs BFJ Bowen, Ms GM Bowker, Mr AN Boyle, Ms JB Bradley, Mr HA Bradley, Dr LW Braithwaite, Mr AT Brennan, Prof JLE Gay Brereton, Mr JG Brickhill, Ms SV Briggs, Ms L Broadhurst, Mr MG Brooker, Mr NP Brothers, Mr RE Brown, Mr RF Brown, Mr RJ Brown, Dr AH Burbidge, Mr L Burgess, Mr NW Burnett, Dr TC Burton, Rev CG Burt, Mr J Bywater, Dr BM Cale, Dr GR Cam, Mrs A Cam, Mr M Cameron, Mr RG Cameron, Mr CB Campion, AC Cameron, Dr C Cannon, Mr M Carins, Dr R Carrick, Mr RK Carruthers, Mr BS Carter, Mr NT Carter, Mr BG Chaffey, Dr K Chan, Mr FRH Chapman, Mr GS Chapman, Mr RE Chatto, Ms MH Christie, Mr BJ Chudleigh, Ms SK Churchill, Dr GP



Clancy, Mr GF Claridge, Mr GS Clark, Mr M Clayton, Dr DH Close, Prof A Cockburn, Mrs  
 SJ Comer, Mr P Congreve Snr, Mr V Cooper, Mr RE Corbould, Mr DM Cornish, Mr JE  
 Courtney, Mr ML Courtney, Mr PP Coventry, Mr RJ Cox, Mr F Crome, Mrs MM Crouther,  
 Prof JM Cullen, Mr L Cupper, Mr A D'Andria, Mr AF D'Ombrian, Ms Mr Daley, Mr AV  
 Danks, Dr P Dann, Mr AT Dart, Mr VD Davenport, Dr SM Davey, Mr DHG Davidson, Mr  
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 Dennis, Mr DGH Dent, Mr PA Disher, Mr HJ Disney, The Antarctic Division, Dr VA  
 Doerr, Dr RH Donaghey, Dr DF Dorward, Mr GW Douglas, Dr DD Dow, Mr WMCK  
 Dowling, Ms HA Doyle, Mr FW Doyle, Mr PO Doyle, Mr R Draffan, Dr PV Driscoll, Mr PB  
 Du Guesclin, Dr JN Dunlop, Dr GM Dunnet, Dr M Dyer, Mr JN Dymond, Dr EHM Ealey,  
 Mr RJ Edge, Mr KH Egan, Mr MDB Eldridge, Mr RG Elks, Mr NN Ellis, Mr RA Elvish, Mr  
 WB Emison, Mr JA Estbergs, Mr RC Evans, Mrs DEM Evans, Mr JN Eveleigh, Mr ID  
 Falkenberg, Mr NJ Favaloro, Mr PJ Fell, Mr J Fennell, Mr LWC Filewood, Mr JH Fisher,  
 Mr KA Fisher, Dr MR Fleming, Mr AWJ Fletcher, Mr TI Fletcher, Mrs D Foley, Ms L  
 Fontanini, Dr HA Ford, Dr JR Ford, Mr W Ford, Mr N Forde, Mr JC Fordyce, Mr  
 BrianForeman, Mrs PJ Foster, Mr MT Fox, Mr D Franklin, Dr DW Frith, Dr HJ Frith, Mr C  
 Frith, Mr GR Fry, Dr PJ Fullagar, Mr PJ Fuller, Dr JL Gardner, Prof ST Garnett, Mr JA  
 Gates, Mr DJ Geering, Mr RM Gibbs, Mr D Gibson, Mr CL Gill, Mr B Glover, Dr AW  
 Goldizen, Mr RC Good, Mr GP Goodyear, Mr MD Gottsch, Mr TJ Gourlay, Mr CN Gove,  
 Mr RJP Gower, Mr I Grant, Dr DJ Gravatt, Dr D Green, Dr K Green, Dr RH Green, Mr R  
 Gregory-Smith, Dr PJ Guay, Mr MO Gunn, Mr RE Gurney, Mr HA Guyatt, Dr AM Gwynn,  
 Mr LC Haines, Dr ML Hall, Mr B Hall, Mr C Hall, Mr JH Hall, Sgt GT Hanlon, Mr RH  
 Hardie, Mr JL Hardy, Mr JW Hardy, Mr RF Harmer, Mr JGK Harris, Mrs JH Harvey, Mr  
 JA Hassall, Dr CF Heathcote, Dr RG Heinsohn, Dr DG Henderson, Mr NL Hermes, Mr  
 FK Hersey, Mr AL Hertog, Mr PJ Higgins, Mr FAR Hill, Mr MP Hines, Mr WB Hitchcock,  
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 Holdsworth, Mr AJ Hole, Mr C Hollamby, Mr LM Holland, Dr DG Hollands, Mr JB Hood,  
 Mr I Hore-Lacy, Mr GM Horey, Mr W Horton, Mr ES Hoskin, Mrs K Hough, Dr JM  
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 Mr J Hyett, Mr JC Ipsen, Mr J Izzard, Mr P Jackson, Mr BR Jahnke, Ms A Jansen, Ms L  
 Jansen, Mr PR Johnson, Mr SE Jolly, A/Prof DN Jones, Mr FE Jones, Mr R Jones, Mr R  
 Jordan, , Mr WL Klau Oam, Dr JO Karubian, Mr K Keith, Mr JW Kellam, Dr BJ Kentish,

Mr RF Kenyon, Prof J Kikkawa, Mr J Klapste, Dr SM Kleindorfer, Mr NW Kurtz, Mr N Kwapena, Mr IG Lane, Mr JAK Lane, Mr SG Lane, Dr NE Langmore, Mr GL Lansell, Mr AFC Lashmar, Mr WG Lawler, Mrs G Laybourne-Smith, Ms S Legge, Mr AJ Leishman, Dr AH Lendon, Mr N Lenz, Ms JE Lewis, Mr AJ Ley, Mr J Liddy, A/Prof A Lill, Dr E Lindgren, Dr LC Llewellyn, Mr TG Loffler, Mr GJ Logan, Mr JL Long, Mr RG Lonnon, Mr R Lossin, Dr KW Lowe, Mr T Lowe, Mr D Macdonald, Mr DB Mack, Mr KJ Mack, Mr RD Mackay, Mr RG Mackenzie, Mr WDF Mackenzie, Dr MN Maddock, Dr MJ Magrath, Dr RD Magrath, Mr PN Maher, Prof WJ Maher, Dr RE Major, Mr EB Male, Mr S Marchant, Mr AJ Marsland, Mr G Marston, Mr JM Martin, Mr RJ Martin, Mr JS Martyn, Mr LTE Marvelde, Mr WE Matheson, Mr G Maurer, Dr KL Maute, Dr PR Mawson, Mr I McCallum, Mr S Mccosker, Ms M Mccoy, Mrs RE Mcculloch, Dr PG McDonald, Dr DC McFarland, AM McGarvie, Mr PDD McIntosh, Mr JL Mckean, Mr EJ Mckenzie, Dr NG Mckilligan, Mr JG McLaughlin, Mr EG McNabb, Mr JA McNamara, Mr MV Melvin, Mr PW Menkhorst, Dr ALA Middleton, Dr PJ Milburn, Mr LJ Millar, Mr GJ Millard, Mr Dr Milledge, Mr B Miller, Dr CDT Minton, Mr N Mooney, Mr LA Moore, Mrs GJ Moors, Mr B Morgan, Mr DG Morgan, Mr AK Morris, Mr A Morrison, Mr OPP Mueller, Dr RA Mulder, Mr D Munro, Mr MT Murn, Dr SA Murphy, Mr D Murray, Mr MD Murray, Dr OMG Newman, Ms JL Nicholls, Ms CA Nicholls Am, Dr LW Nicholson, Mr HJ Nicholson, Mr LA Nielson, Mr DJ Noonan, AY Norris, Mr L O'Connor, Mr J O'Kelly, Mr GR Park, Mrs MP Park, Dr CJ Parmenter, Ms V Parry, Dr JS Pate, Ms VJ Pattemore, Mrs JD Patterson, Mr CK Pawsey, Mr RJ Pearse, Mr GB Pearson, Mr DL Pepper-Edwards, Mr TW Pescott, Dr AM Peters, Dr D Peters, Mr M Pickett, Mr FG Pinchen, Mr RL Pink, Mr D Pinner, Mr T Poldmaa, Mr JM Poole, Mr DJA Portelli, Mr KJ Pound, Ms EK Pratt, Ms MV Preker, Mr JG Pridham, A/Prof SG Pruett-Jones, Dr SR Pryke, Mr D Purchase, Mr D Putland, Dr GH Pyke, Ms MK Rathburn, Mr J Rawlins, Dr JL Read, Prof HF Recher, Dr NCH Reid, Mr AJ Reid, Mr DR Reid, Mr R Reid, Mrs PN Reilly, Mr DS Reimer, Mr JW Reside, Mr C Rich, Mr DC Richards, Mr GE Richards, Dr MG Ridpath, Mr DJ Ripper, Dr GG Robertson, Mr D Robinson, Mrs VA Robinson, Mr JL Rogan, Mr JH Rooke, Mr G Ross, Mr HM Ross, Mr M Rowe, Mr ICR Rowley, Ms JC Scarl, Mr NW Schrader, Mr DA Secomb, Dr DL Serventy, Mr DHC Seton, Dr TGD Shannon, Dr RC Shearer, Mr RJ Shick, Mr KF Silva, Mr KG Simpson, Dr RG Sinclair, Dr IJ Skira, Dr PJ Slater, Mr IJ Smales, Mr DI Smedley, Dr GC Smith, Dr GT Smith, Dr VW Smith, Mr JL Smith, Mr KW

Smith, Mr RJ Smith, Dr CN Smithers, Dr AK Smyth, Mr RJ Speechley, BA Speechley, Mr PJ Spurge, Mr AF Stewart, Mr DA Stewart, Mr A Stokes, Mr RH Stranger, BRM Strong, Mr PD Strong, Dr CA Surman, Mr AJG Sutton, Mr J Tagell, Dr MK Tarburton, Mr MK Tarburton, Dr ID Temby, Mr MT Templeton, Mr T Templeton, Mr RG Thoday, Mr DG Thomas, Mr EB Thomas, Mr GD Thomas, Mr HF Thomas, AT Thomason, Dr PJ Thomson, Dr CR Tidemann, Dr SC Tidemann, Mr RA Tilt, Dr A Tingay, Dr RT Todd, Mr PJ Tonelli, Mrs WA Trudgen, Mr RC Turnbull, Mrs LJ Turner, Mr BD Tynan, Mr GH Underwood, Mr SB Unthank, Mr FWC Van Gessel, Dr GF Van Tets, Mr WJ Vestjens, Mr NW Vincent, Dr WC Wakefield, Ms E Wakefield, Mr LE Wall, Mr SP Wallace, Mr JE Walsh, Mr RM Warneke, Mr MH Waterman Oam, Dr DM Watson, Ms I Watson, Mr NF Weatherill, Dr MS Webster, Dr JA Welbergen, Mr NB Wells, Dr MA Weston, Mr E Wheeler, Mr JS Whinray, Dr PJ Whitehead, Mr A Whitehead, Dr JA Wiens, Mr FB Wilkinson, Mr AC Williams, Mr DJ Williams, Mr L Willoughby, Mr JT Willows, Mr SJ Wilson, Mr T Wilson, Mr GB Winning, Dr JCZ Woinarski, Mr TO Wolfe, Mr KA Wood, Mr VJ Wood, Mrs R Woodell, Mrs SJ Wooller, Mr NR Wright, Mr VH Yeoman, Mr S Yorke, Dr RA Zann, The Bird Care And Conservation Society, The Taiwan Bird Banding Centre, Gippsland Lakes Ornithological Group, The Shorebird Study Group, The Broome Bird Observatory, The Eyre Bird Observatory Group, The Rotamah Island Observatory, The Dpipwe Orange-Bellied Parrot Management Group, The Taronga Zoo Rehab Program, The Western Australia Rehabilitation Group, The Wild Bird Rehabilitation Group, The Bird Migration Research Center, The Gluepot Reserve Study Group, The Australasian Wader Study Group, The Victorian Wader Study Group, The Western Australia Wader Study Group, The New South Wales Wader Study Group, and Tasmania Parks And Wildlife Service.

## **Appendix S2**

Table of 146,009 occurrence records which includes the biome, observed 30-day  $T_{\min}$ ,  $T_{\max}$ , and precipitation, and 2-year average  $T_{\min}$ ,  $T_{\max}$ , and precipitation. This table is available through <https://doi.org/10.6084/m9.figshare.5413189.v4>

## **Appendix S3**

Species level climatic averages and results from paired  $t$ -tests. This table is available through <https://doi.org/10.6084/m9.figshare.5413189.v4>

## Chapter 4

# Effects of El Niño Southern Oscillation on avian breeding phenology

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**KEYWORDS:** breeding phenology, climate change, climate oscillations, egg-laying, El-Niño Southern Oscillation, ENSO

## Chapter Four Vignette

Chapter four provides a globally significant advance in understanding the effect of El Niño Southern Oscillation on opportunistic avian breeding phenology. Using the methods and data from Chapter two, I further investigate how climate influences the timing of breeding to expand on Chapter three. In comparison to Chapter three, which investigated climatic conditions directly influencing breeding events, here I quantify the effects of cyclic climatic variation, specifically, El Niño Southern Oscillation (ENSO), on birds, which breed opportunistically to understand how inter-decadal climate fluctuations influence opportunistic breeding, this is essential for tracking the phenological responses of birds to climate change. I test a conceptual framework using approximately 80,000 egg-laying observations for 79 species. My results show how wet/mild La Niña positively affect avian breeding, yet dry El Niño conditions do not constrain breeding relative to the Neutral phase. I establish a seasonal effect of ENSO on bird reproduction; early breeding species have the largest positive response to La Niña. My findings are an exciting advance in understanding bird phenology, which is highly relevant to predicting species response to climate change.

## Abstract

### **Aim**

Climate oscillations are known to influence the reproductive phenology of birds that breed seasonally. Here, we quantify the effects of cyclic climatic variation, specifically, El Niño Southern Oscillation (ENSO), on birds, which breed opportunistically. We aim to overcome the lack of long-term data for terrestrial birds in the Southern Hemisphere to understand how inter-decadal climate fluctuations influence opportunistic breeding, this is essential for tracking the phenological responses of birds to climate change.

### **Location**

Temperate and arid regions of Australia.

### **Methods**

We assessed variation in egg-laying (start, peak, conclusion, length) during the three phases of ENSO (El Niño, La Niña and Neutral) for 64 temperate and 15 arid region species using ~80,000 observations of breeding over 116 years. Linear mixed-effect models and analysis of variance were used to (i) determine if, on average within each region, first egg-laying dates differed significantly among species between ENSO phases, and (ii) assess how La Niña and El Niño episodes influence egg-laying in birds which breed early or later in the year.

### **Results**

During La Niña phases, which are characterised by mild/wet conditions, most bird species in both temperate and arid regions exhibited longer egg-laying periods relative to Neutral phases. This effect was strongly seasonal in the temperate region; species breeding in early in the year experienced the greatest increase egg-laying period during La Niña phases. Importantly, we found no evidence of differences in average egg-laying dates during Neutral and El Niño phases in temperate species. This finding suggests that dry conditions associated with El Niño may not influence the aspects of breeding phenology studied.

### **Main Conclusions**

In both arid and temperate regions, increased rainfall associated with La Niña ENSO phases influences avian breeding phenology and likely recruitment, however, dry El Niño phases may not have the dramatic impacts on breeding that are commonly assumed.

## Introduction

Large-scale climate oscillations such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation influence year to year variation in avian breeding phenology (Forchhammer et al., 1998; Wilson & Arcese, 2003; Gibbs, 2007; Jaksic & Fariña, 2010), breeding intensity (Vilina et al., 2002; Wilson & Arcese, 2003; Gibbs, 2007; Gibbs et al., 2011) and migration phenology (*reviewed in* (Gordo, 2007; Beaumont et al., 2015)). It is well known that long-term climatic cycles influence extinction rates amongst species (i.e. during growth and retreat of glaciers (Wanner et al., 2008)) and short-term variability in climate extremes affects phenology and population numbers in sequential years (McCain et al., 2016). By contrast, species breeding responses to decadal climatic cycles are relatively poorly studied, particularly for land birds in the Southern Hemisphere. Although there have been several studies of variation in breeding phenology in relation to ENSO in land birds of Australia (Gibbs, 2007; Chambers et al., 2008a; Gibbs et al., 2011), they are typically characterised by low sample sizes and focus on just a relatively few species. This is largely due to the lack of long-term time-series data rather than any likely absence of an effect of contemporary climate change on species in the southern hemisphere (Hughes, 2003) and is in contrast to a number of very long-term datasets that are available in the northern hemisphere (Clutton-Brock & Sheldon, 2010).

The lack of long-term phenological data (for example, more than 30 years worth of observations) for terrestrial birds in the Southern Hemisphere is a major challenge to be overcome in developing an understanding of species' responses to a changing climate. An objective of this study was to overcome these challenges by using a combination of conventional and non-conventional sources of avian breeding observations to document variation in avian breeding phenology in relation to the three phases of ENSO, versus a more traditional approach involving time series analysis.

ENSO affects a combination of climatic parameters, including ambient temperature, precipitation and wind (Trenberth, 1990; Fiedler, 2002; Nemani et al., 2003) and is a global source of decadal climate variation affecting both marine and terrestrial ecosystems. Three distinct phases of ENSO are recognised (El Niño, La Niña, and the Neutral state) and their effects vary widely across regions. For instance, altered rainfall patterns are common in eastern and northern Australia, India and parts of the



Americas during ENSO cycles (Nicholls, 1991; Chiew et al., 1998). During the El Niño phase sea surface temperatures increase, resulting in heavier than average rainfall in areas of the Americas (Shimizu et al., 2017), including the arctic region (Trenberth, 1990) and drier conditions in Australasia. In the central Pacific and East Asia, extreme La Niña phases cause anticyclones with fine, calm weather (Wang et al., 2000). The Neutral state is when neither El Niño nor La Niña are occurring and conditions are moderate.

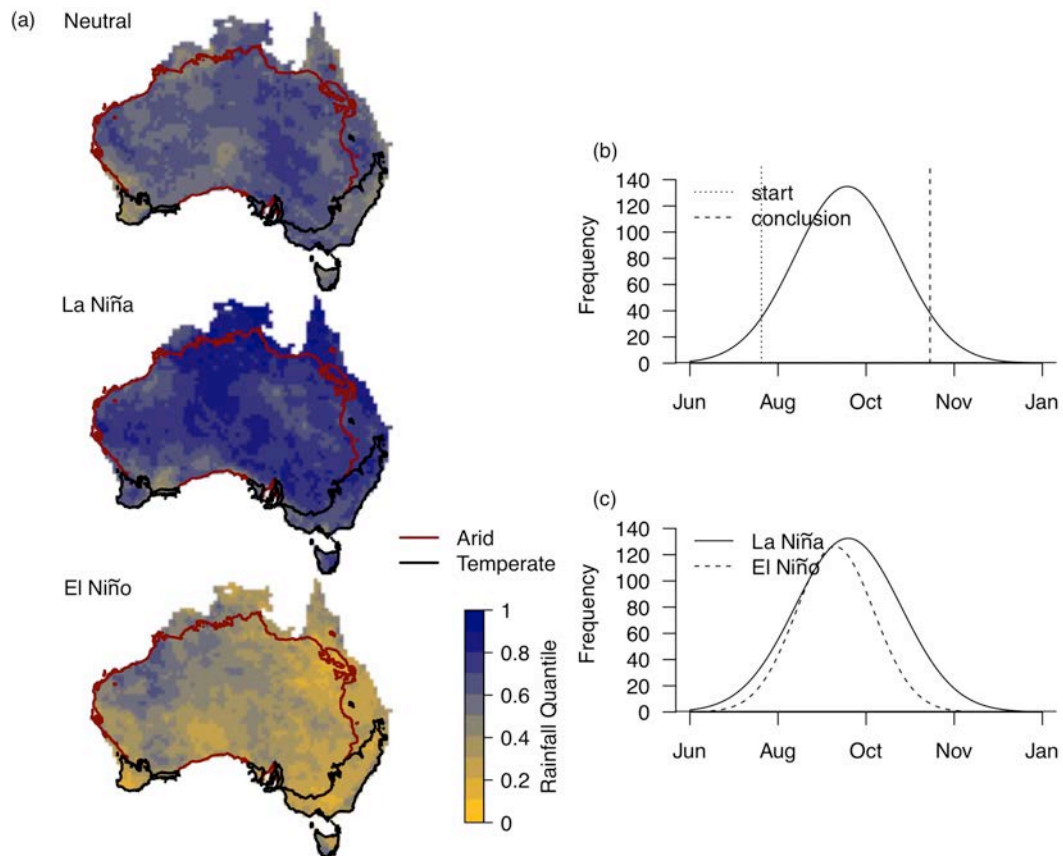
In Australia, ENSO amplifies inter-annual climate variation and alters vegetation productivity, which underpins the provision of food resources for birds. Birds typically breed when food resources are most abundant (Cockrem, 1995; Dunn & Winkler, 2010) and breeding activity can be driven, maintained or inhibited by food abundance (Zann et al., 1995; Visser et al., 1998; Both, 2010). The likelihood of wet/mild climate conditions occurring during the breeding season increases during the La Niña phase of ENSO (Fig. 1A). Conversely, the chance of dry/hot conditions increases during El Niño events (Nicholls, 1991; Suppiah & Hennessy, 1998). During El Niño events, a reduction in cloud cover usually results in increased maximum daily temperatures as well as the incidence of frost (i.e. frost is 20% more common in eastern and south-eastern Australia during El Niño ((Nicholls, 1991; Alexander & Hayman, 2008)). Variability in temperature and rainfall results in dramatic year-to-year changes in vegetation, and as a result, some areas of Australia do not have a long-term static vegetation state (Nicholls, 1991).

Due to extreme variation in weather patterns caused by ENSO globally, we do not expect universal avian breeding responses to ENSO phases, but some responses to climate should be general in nature. For example, mild, warm, wet conditions at the beginning of the breeding season result in earlier breeding in Australia (Gibbs, 2007; Chambers et al., 2008a, 2008b), the northern hemisphere (Forchhammer et al., 1998; Wilson & Arcese, 2003) and South America (Vilina et al., 2002). Additionally, these studies report increases in breeding intensity (i.e. more individuals breeding at a given time or an increased number of fledglings per female), although this may not always lead to population growth (Wilson & Arcese, 2003). Jaksic & Fariña (Jaksic & Fariña, 2010) showed that during wet phases of ENSO nesting failure and chick mortality may result from nest flooding, while during dry phases depletion of food resources reduced breeding success. In granivorous and insectivorous land birds, increases in primary

productivity during the wet phases of ENSO increased their abundance, however, in some carnivorous species there is a delayed response, which coincided with increases in mammal populations (Jaksic & Fariña, 2010).

Here we assess changes in avian breeding phenology in relation to climate variability caused by ENSO in Australia over the period 1900 to 2016. We assess 64 species of birds occurring across 11 orders in the temperate region and 15 species in 6 orders occurring in the arid region (desert and grassland biomes combined). Species examined include land birds and inland water birds, which meet a minimum requirement of 100 unique observations (date, and location), during each of the three phases of ENSO: El Niño, La Niña or Neutral. Using these groups, we evaluate variation in breeding phenology (start, conclusion, and length of breeding period), and model relationships between the timing of egg-laying and decadal climate oscillations. We hypothesise that the intensity and duration of avian breeding will be optimized to occur when food resources are most abundant and physiological stress (due to extremely hot conditions) is low. Thus, there should be significant differences in breeding duration during El Niño and La Niña. The Neutral phase of ENSO is assessed as a comparative measure; this phase is largely ignored in studies that assess species responses to ENSO phases (Jaksic & Fariña, 2010). We predict that during the La Niña phase, which is typically characterised as having wet/mild conditions as apposed to the dry conditions of El Niño (Fig. 1A) that the:

- (1) start of the egg-laying period (Fig. 1B) should begin earlier than during the dry/hot El Niño phase (Fig. 1C);
- (2) length of the egg-laying period (number of days between start and conclusion of egg-laying period, Fig. 1B) will be longer than those during El Niño (Fig 1C), with stronger results for species that breed primarily in early in the breeding season;
- (3) peak and conclusion of the egg-laying period (Fig. 1B) will be later in the year (Fig. 1C), because of increased vegetation productivity and associated food resources.



**Figure 1.** Variation in rainfall during the three phases of ENSO and the hypothesised effect of variation in rainfall during El Niño and La Niña events on avian breeding phenology. Rainfall deciles (A) show the ranking of the amount rainfall during the winter and spring months within each 50km x 50km grid cell compared to the average for the period 1900 – 2016. A mean rainfall decile of range 10 indicates that the grid cell has average rainfall values higher than 90% of other observations. Conversely, a decile value of 1 indicates the grid cell falls in the bottom 10% of observations. Rainfall data comes from the Australian Water Availability Project (Jones et al., 2009) via <http://www.bom.gov.au/jsp/awap/>. (B) The start, conclusion, and length of the egg-laying period (i.e. 5<sup>th</sup>, 95<sup>th</sup> percentiles of first-egg dates (FEDs), and the number of days between the 5<sup>th</sup> and 95<sup>th</sup> percentiles, respectively) were calculated for individual species in each ENSO phase. We hypothesised (C) that, on average, egg-laying would last longer, begin earlier, and peak and conclude later in La Niña events relative to El Niño events.

## Methods

### *Climate and environmental data*

The Australian Government Bureau of Meteorology (<http://www.bom.gov.au/>) defines historical El Niño and La Niña events and records the Southern Oscillation Index (SOI) for Australia. We used these to characterise as many breeding years as possible, since 1900, into one of three phases of ENSO; El Niño, La Niña and Neutral. A breeding year was defined as the period between July-June (of the following year), rather than January-December because winter months have the lowest incidence of bird breeding in the Australian temperate and arid regions (Englert Duursma et al., 2017). For this study, a La Niña or El Niño breeding year is defined as those years where these ENSO phases are sustained for at least 7 months ( $n = 26$  La Niña years, and  $n = 22$  El Niño years). A Neutral breeding year is defined as when the SOI is above -8 and below 8 (Bureau of Meteorology, 2012) and no La Niña or El Niño events occur for at least 10 of the months ( $n = 46$  Neutral years). SOI values were downloaded from [www.bom.gov.au/climate/enso/soi\\_monthly.txt](http://www.bom.gov.au/climate/enso/soi_monthly.txt) (July 25<sup>th</sup>, 2017). Years that had a high degree of variability and could not be confidently classified as ENSO phases were excluded ( $n = 23$  years). See Appendix S1 in Supporting Information for a table of breeding years and the associated ENSO phase.

We assessed breeding patterns across two regions: temperate and arid. Region boundaries were based on a national modified Köppen classification system (Stern et al., 2000; Bureau of Meteorology, 2006) where the desert and grassland biomes were combined to define the arid region.

We used elevation, latitude of observation, and distance to coast to assess variation in breeding dates due to breeding location. Elevation and latitude are known to affect the breeding dates of Australian birds (Gibbs et al., 2011) and ENSO does not affect coastal regions to the same extent as inland regions (Figure 1). Gridded data from a digital elevation model of Australia and the distance to a generalized coastline of Australia were obtained from ANUClimate 1.0 (Hutchinson et al., 2014; Hutchinson & Xu, 2014) via <http://dap.nci.org.au>, and made available by the Ecosystem Modelling and Scaling Infrastructure (eMAST, <http://www.emast.org.au>). The resolution of these data are  $0.01^\circ \times 0.01^\circ$ .

## **Observations**

All species used in the analyses met a minimum requirement of having  $\geq 100$  breeding observations during each of the three ENSO phases (i.e. we assessed the same species in all phases). Breeding observations (latitude, longitude, date) were combined from conventional sources of avian breeding (i.e. Birdlife Australia's Atlas (Barrett et al., 2003) and Nest Record Scheme), and non-conventional sources (i.e. historical museum egg collections, Australian Bird and Bat Banding Scheme, and eBird (eBird, 2015)) following the methods used in (Englert Duursma et al., 2017). Breeding records were limited to those occurring after 1900 to match the temporal range of climate data for characterizing El Niño, La Niña, and Neutral years. Duplicate observations (the exact same location, date and species) were removed to reduce the effect of variation in sampling intensity due to sampling method.

Following the methods and using trait data published in (Englert Duursma et al., 2017), observations were divided into four types: *multi-visit* (records where a nest was visited multiple times and at each visit the breeding stage was recorded (i.e. egg, egg hatch, or young)), *egg(s)* (single observation of eggs), *young* (single observation of young), and *undefined* (observation of breeding but no information of breeding stage). Briefly, the date of each breeding occurrence record was back-calculated to the first egg-laying dates (FEDs) by subtracting one or more species-specific life-history periods: period of lay (number of days taken to lay an average clutch), length of incubation, and fledging period. The exact back-calculation methods differed by the observation type. For example, to find a FED of an *egg*, we assume two possibilities, i) all egg-laying is complete but incubation has not begun, thus we subtract the period of lay from the observation date, and ii) incubation is complete but eggs have not hatched, thus we subtract both the length of incubation and the period of lay. We then averaged these two possible FEDs, to get one final date.

Preference was given to observations that were *multi-visit*, *young*, and *eggs* and for species that had at least 100 of these observations in each ENSO phase (temperate region,  $n = 25$ ; arid region,  $n = 9$ ) we excluded *undefined* observations because of their lower accuracy in defining breeding stage (Englert Duursma et al., 2017). If a species did not have a combined total of 100 *multi-visit*, *young*, and *eggs* observations, we included the *undefined* observations (temperate region,  $n = 39$ ; arid region,  $n = 6$ ). This

resulted in a total of 69,288 breeding observations across 64 species in the temperate region and 11,042 breeding observations across 15 species in the arid region, with a mean of 1,017 observations ( $\pm 561$ ) per species. A complete list of institutes and persons who either collected the data, or are custodians of the observations, is available in Appendix S2 in Supporting Information.

### ***Egg-laying phenology***

To calculate egg-laying phenology for each ENSO phase, we used the package *circular* (Agostinelli & Lund, 2013) in R version 3.3.3 (R Core Team, 2017). For each phase, we assessed three parameters: start, conclusion and length of egg-laying period. These parameters correspond with the 5<sup>th</sup>, 95<sup>th</sup>, and number of days between the 5<sup>th</sup> and 95<sup>th</sup> percentiles, respectively, during El Niño, La Niña and Neutral phases. Circular statistics with a median-unbiased quantile estimator (Hyndman & Fan, 1996) were used to account for breeding over the turn of a year.

### ***Statistical analysis***

All analyses were carried out in R version 3.3.3 (R Core Team, 2017). In addition to base functions we used the packages *raster* (Hijmans, 2016), *maptools* (Bivand & Lewin-Koh, 2017) *circular* (Agostinelli & Lund, 2013), *data.table* (Dowle & Srinivasan, 2017) and *visreg* (Breheny & Burchett, 2016) for data extraction, manipulation, and visualization. Statistical tests were considered significant at an alpha-level of  $p = 0.05$  and results are reported as mean  $\pm$  the standard deviation unless otherwise noted. Analyses were performed independently for the temperate and arid regions.

Analysis of variance (ANOVA) was used to compare the effect of ENSO phase on FEDs. For species that breed over the turn of the year, FEDs were modified so they were continuous (e.g. a FED for the first of January becomes day 366, second of January becomes day 367, and so on). We fit a linear mixed-effect model to determine if FEDs differed significantly across the three phases: El Niño, La Niña or Neutral, using the function *lmer* in the R package *lme4* (Bates et al., 2015). Species, taxonomic order and a binary variable indicating if a species included *undefined* breeding observations were random effects with differing intercepts. The binary variable was included to account for potential bias in observational data quality. Taxonomic order was included to

account for the potential effect of shared ancestry. The model included elevation, distance to coast and latitude of the observation, as fixed factors. Elevation and distance to coast were  $\log_{10}$  transformed to approximate normality. ANOVA was calculated using Analysis of Deviance Table (Type II with Satterthwaite approximation for degrees of freedom) using the R package *lmerTest* (Kuznetsova et al., 2016). Tukey's pairwise comparisons were performed using the *multcomp* package (Hothorn et al., 2008) to assess differences among the ENSO phases.

Based on our hypothesis we expected species that breed primarily early in the breeding season would show a greater response to La Niña and El Niño because their effects are strongest at this time. Relationships between changes in the length of the egg-laying period between the different phases and the time of year that breeding concluded during the Neutral phase were examined using a linear mixed-effect model with taxonomic order as a random effect. Percentage change in the length of the egg-laying periods for each species was calculated between all three phases (e.g. El Niño to Neutral, La Niña to Neutral, and El Niño to La Niña) and these phase comparisons (one data-point per species phase comparison) were included as a categorical variable represented in the model as an interaction.

## Results

### ***Variation in breeding in the temperate region***

ENSO phase influences the timing of avian egg-laying in Australia's temperate region, but with a large amount of variation across species. Mean FEDs across the 64 species were significantly different depending on ENSO phase [ $F(2, 62402) = 23.87, p < 0.001$ ]. Based on the linear mixed-effect model the least squares mean FED during the Neutral phase was 286.7 (SE = 3.9, Table 1). The least squares mean FED (peak of egg-laying period) was latest during the La Niña phase ( $p < 0.001$ ), being 2.4 days later (SE = 0.3 day) when compared to the Neutral phase and 1.7 days later (SE = 0.4 day) when compared to the El Niño phase. This supports our hypothesis that peak of the egg-laying period during La Niña will be later in the year, because of increased vegetation productivity and associated food resources. However, there was no significant difference in FEDs between El Niño and Neutral phases ( $p = 0.23$ ). During La Niña phases, 56% of

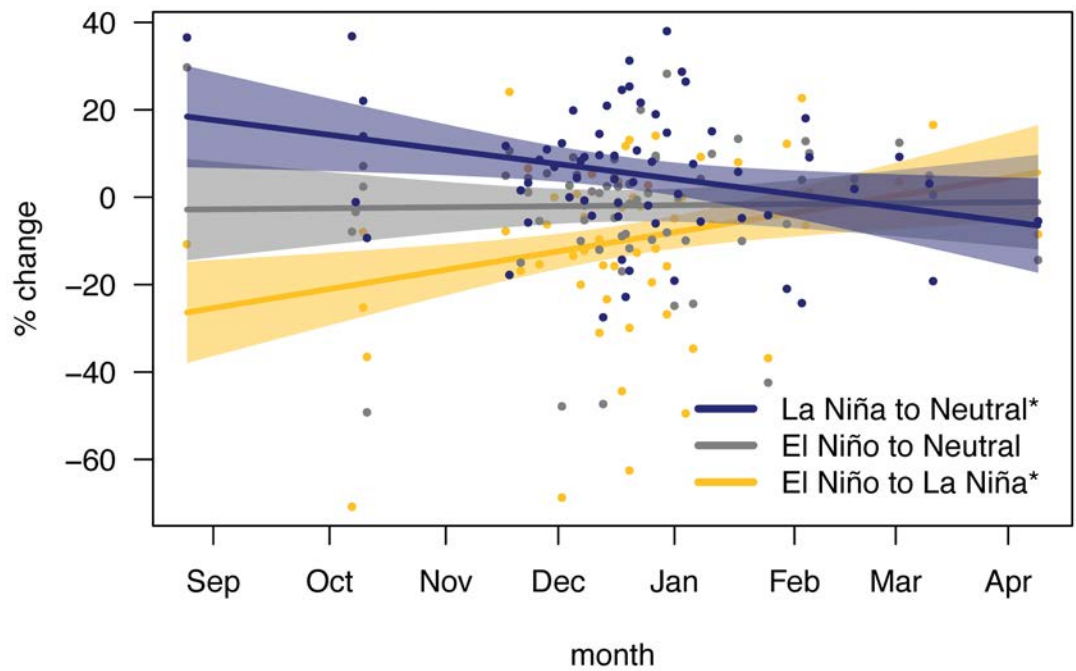
species had earlier starts to the egg-laying period, 61% species had longer egg-laying periods, and 62% of species had later conclusions of breeding activity relative to during the El Niño phase (for averages dates across all species see Table 1) offering some support to our hypothesis that during La Nina the start of the egg-laying period should begin earlier, the length should be longer and the conclusion should be later. Similar results were found for comparisons of breeding phenology between La Niña and Neutral phases (see Appendix S3 in Supporting Information for species level results).

**Table 1.** Average phenology and egg-laying periods for 64 species of birds in the temperate region and 15 species in the arid region. The start and conclusion of egg-laying period (i.e. 5th, 95<sup>th</sup> percentiles of all first-egg dates, respectively), and least squares mean FED (peak) are given as the day of the year. The egg-laying period is the number of days between the 5th and 95th percentiles. Values are given as the mean across all the species in a region  $\pm$  the standard deviation in days, unless otherwise noted. For species level results, please see Appendix S3 via <https://doi.org/10.6084/m9.figshare.5413189.v4>

	Start	Conclusion	Egg-laying period	Mean FED ( $\pm$ SE)
Temperate				
La Niña	218 $\pm$ 42	10 $\pm$ 42	156 $\pm$ 43	289.1 $\pm$ 3.9
El Niño	222 $\pm$ 39	3 $\pm$ 41	146 $\pm$ 47	287.4 $\pm$ 3.9
Neutral	222 $\pm$ 39	4 $\pm$ 39	147 $\pm$ 46	286.7 $\pm$ 3.9
Arid				
La Niña	163 $\pm$ 49	342 $\pm$ 51	179 $\pm$ 63	254.6 $\pm$ 13.7
El Niño	175 $\pm$ 51	344 $\pm$ 51	170 $\pm$ 68	255.2 $\pm$ 13.7
Neutral	182 $\pm$ 40	345 $\pm$ 50	163 $\pm$ 68	258.1 $\pm$ 13.7

The ENSO phase also effected the length of the egg-laying period for temperate species that finish egg-laying earlier in the year [ $F(2, 175) = 5.62$ ,  $p < 0.01$ ],  $R^2 = 0.29$ . That is, for species that conclude breeding early in the year, La Niña had a positive influence on the length of the breeding period (Fig 2).





**Figure 2.** Relationship between percentage change in the egg-laying periods between the three phases of El Niño Southern Oscillation and the time of the year that egg-laying concludes during the Neutral phase in the Temperate region. \* denotes significant relationships.

### ***Variation in breeding in the arid region***

In the arid region the ENSO phase affected the timing of avian egg-laying [ $F(2, 9952) = 8.73, p < 0.001$ ] across the 15 species assessed. Based linear mixed-effect model the least squares mean FED during the Neutral phase was 258.1 (SE = 13.7, Table 1). The least squares mean FED was 3.5 days (SE = 0.9 day) earlier during the La Niña phase when compared to the Neutral phase ( $p < 0.001$ ), and 3.0 days earlier (SE = 1.1 day) during El Niño phase when compared to Neutral phase ( $p < 0.05$ ). There was no significant difference between FEDs in El Niño and La Niña phases ( $p = 0.71$ ). Although there was no significant difference between FEDs in El Niño and La Niña, during La Niña 67% of species had earlier starts to the egg-laying period (86% when compared to Neutral), 60% species had longer egg-laying periods (80% when compared to Neutral), and 40% had later a later conclusion to breeding activity (53% when compared to Neutral). See Appendix 3 for species level results.

In the arid region there was no seasonal effect of ENSO phase on the length of the egg-laying period (i.e. species breeding early in the year having greater differences in the length of the egg-laying period depending on ENSO phase) [ $F(1, 39) = 1.67$ ,  $p = 0.20$ ].

## Discussion

La Niña events, which are characterised by mild/wet conditions, have a positive impact on avian breeding phenology in the Australian temperate and arid regions. For example, 64% of species in the temperate region and 80% of species in the arid region had longer breeding periods during La Niña when compared to the Neutral phase. In the temperate region there is a strong seasonal effect, with species that breed early in the year under the Neutral phase, showing the greatest increase in the length of the breeding period (Fig 2). In the temperate region, egg-laying dates during El Niño are not significantly different from those during the Neutral phase. This suggests that dry conditions which characterise El Niño phases (Fig. 1), may not constrain breeding phenology more than typical winter/spring dry season conditions during Neutral phases (Fig. 1). In the arid region, earlier and longer breeding seasons on average during La Niña and El Niño, when compared to the Neutral phase, may indicate a complex relationship between phenology and climate. Warmer spring daytime temperatures during El Niño, increased rainfall during La Niña, and the ability of mobile species to opportunistically move and breed with localized rainfall in dry periods may confound true differences between these phases. For example a species might breed uniformly over a large area during La Nina and only in a few select locations during El Niño. If they breed for the same amount of time, then measures of phenology would be the same, although the amount of breeding and breeding locations are actually quite different. Future studies should identify methods to distinguish these breeding patterns.

While there are numerous studies that have explored species responses to El Niño, and La Niña phases, fewer studies have captured baseline conditions during the Neutral phase (Jaksic & Fariña, 2010). Here, we demonstrate the importance of this omission by comparing Neutral breeding phenology and intensity to El Niño and La Niña phases. If we focus on only La Niña and El Niño years in Australia since 1900, this study would have assessed only 41% of all years of available breeding data. If we further

limited our analysis to the strongest events (12 years in La Niña and 12 in El Niño, (<http://www.bom.gov.au/>) 79% of years would have been ignored. Further, we would have identified significant differences in breeding when comparing El Niño and La Niña but we would have missed the important finding that egg-laying dates do not significantly differ between El Niño and Neutral phases in the temperate region.

The high degree of variation in breeding responses to decadal climate variation we found echoes previous findings from both the southern and northern hemispheres. However, this study is the first to examine patterns across suites of species sharing a biome, offering a novel comparative understanding of bird breeding, providing more general results. In the northern hemisphere variation in breeding has been noted in response to the North Atlantic Oscillation (Ahola et al., 2004; Sandvik et al., 2008). For example species have been shown both positive and negative responses to the degree of snow in winter ((Forchhammer et al., 1998), variation in the size of the first clutch (Møller, 2002), and changes to the timing and success of breeding (Ahola et al., 2004; Sandvik et al., 2008). In Australia several studies have shown that breeding intensity increases during the wet mild years of La Niña but the timing of breeding is not consistently related to the Southern Oscillation Index (Chambers & Keatley, 2010; Gibbs et al., 2011; Beaumont et al., 2015). These studies have been limited to single species or a low number of species (n=16). It is also worth noting SOI values can be both high and low without La Niña or El Niño events occurring. In this study we have found quite a lot of variation in the response across species (i.e. affected to different degrees with some species not be affected at all). Importantly, our study has looked at a reasonable number of species and our results indicate a general effect. Uniquely in our study we identified a seasonal effect (e.g. species that breed early in the year are affected to a greater degree than those who breed later) that helps to explain why some species are affected and others are not.

Importantly, we show that the impacts of climate and associated change in primary productivity on avian breeding phenology during El Niño and Neutral phases of ENSO may be similar. That is, we found no significant differences in egg-laying dates in the temperate region during El Niño and Neutral phases and in the arid region there was a high degree of variation in species breeding time to ENSO phase. For example, 60% species have longer breeding periods and 40% shorter during El Niño, when compared

to the Neutral phase. These findings may be modified by the effect of unmeasured variables such as breeding intensity and number of breeding attempts. It is worth noting that in much the temperate region the spring months are the typically the driest months of the year (Jones et al., 2009).

Australian birds exhibit a high degree of opportunism and breed in response to localised rainfall patterns (Davies, 1977; Zann et al., 1995; Gibbs et al., 2011), although there is some evidence that hot temperatures constrain breeding times in the desert (Englert Duursma et al., In review). Birds can be very mobile and if conditions are not suitable they either won't breed at all in a particular year (Williams & Middleton, 2008; Morton et al., 2011), or perhaps are more likely to move into a different area where conditions are better. Additionally, the effects of the ENSO phases do not have the same influence over the whole continent (Fig. 1). These breeding characteristics presumably explain some of the similarity of mean egg-laying dates we found during El Niño and La Niña in the arid region. With species during the El Niño and Neutral phases responding to local variation in rainfall to a greater degree, therefore having many short bouts of breeding over an extended period, resulting in a long breeding period but with low intensity and breeding success. This extreme opportunism likely explains the extensive breeding periods we observed for both the New Holland honeyeater (*Phylidonyris novaehollandiae*, temperate region) and the Zebra Finch (*Taeniopygia guttata*, arid region), two of Australia's iconic opportunistic breeding birds (Appendix S3).

Whilst seasonal trends in breeding were observed in the temperate region there was no indication of a seasonal trend in changes to breeding period lengths in the arid regions (e.g. species that breed primarily in the spring benefit from the wet conditions of La Niña more than those that breed later in the breeding year). This supports previous findings that in the desert, the timing of breeding is more constrained by temperature than it is motivated by rainfall (Englert Duursma et al., In review). During the summer months (Dec – Feb), in the arid region, daily maximum temperatures average between 33°C and 39°C and can exceed 45°C (Jones et al., 2009). The upper thermal limit of passerine egg temperatures is between 43°C and 44°C and with prolonged exposure high ambient temperatures being lethal (Webb, 1987; Stoleson & Beissinger, 1999; DuRant et al., 2013). Therefore, breeding during hot summer months may be detrimental through physiological heat stress, reducing the survival of parents, young and embryos.

Many adult birds are more tolerant of cold temperatures than they are of extremely high ones (Goldstein, 1984; Maddocks & Geiser, 1999).

### ***Implications for the conservation of bird populations***

It is well noted that climate influences the demography and recruitment of avian populations (Crick, 2004; Sandvik et al., 2008; Brawn et al., 2017; McCauley et al., 2017), with several studies finding that this relationship is strongest for the first broods of the year (Järvinen, 1996; Winkel & Hudde, 1997; Møller, 2002). Morton *et al.* (Morton et al., 2011) explored the pulse dynamics of Australia where heavy periodic rainfalls characterise landscapes and episodic growth of perennial plants and affects birds. Australian birds are globally distinct in their levels of opportunism and nomadism, with 30% of Australian desert birds displaying opportunistic breeding, and more than 50 species of waterbirds breeding irregularly in response to periodic flooding (Kingsford et al., 1999; Morton et al., 2011).

Periods of population increase offer crucial opportunities for targeted conservation efforts (Short et al., 1997; Marsh & Trenham, 2001; Letnic & Dickman, 2010). Natural increases in population numbers coupled with decreased fire risk and (often) the deliberate reduction of competing or invasive predators can improve species persistence (Garnett et al., 2013). Whilst our study does not explicitly test for changes in species recruitment and abundance during different phases, the average number of observations per breeding year of El Niño and Neutral, were 40% and 36% less than during La Niña years. Given that the datasets we have used was captured across a range of non-systematic methods, with collection effort presumably random with respect to ENSO phase, we believe that the number of observations collected across the different phases provides some indication of breeding intensity. If that is true, then it appears that birds were breeding at greater intensity, with a higher number of reproductive attempts during the mild/wet La Niña phase. This interpretation is consistent with the findings of Gibbs *et al.* (Gibbs et al., 2011), who reported the intensity of breeding in birds increased during the favourable La Niña phase. This means that the La Niña phase of the ENSO provides an excellent opportunity for conservation efforts for terrestrial species in Australia. During La Niña conditions, breeding seasons will last for longer and productivity is likely

to be higher, meaning that any effort focused on assisting reproduction will deliver greater yields in such conditions, than during Neutral or El Niña conditions.

There is a growing body of evidence that extremes in climate influence the long-term survival and fitness of Australian birds to greater extents than average climatic conditions (McKechnie et al., 2012). Given the strong positive response to La Niña we observed, it seems likely that the drier conditions that are predicted in association with anthropogenic climate change will have large negative effects on species breeding and recruitment.

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## **Data Accessibility Statement**

Data and code used in this study is available upon request.

## **Biosketch**

The authors are based at the Department of Biological Sciences, Macquarie University. Their collaboration brings together expertise in spatial ecology and avian biology to explore how climate shape the life history and behaviour of Australia's native bird species.

## Supporting Information

### Appendix S1

Table S1.1 - La Niña, El Niño and Neutral breeding years from 1900 to 2016. A breeding year is 12 months and extends from July through to June. The years reported are for the first month of the breeding year. El Niño and La Niña events are defined by the Australian Government Bureau of Meteorology (<http://www.bom.gov.au/>). A La Niña or El Niño breeding year occurs when the relevant ENSO phase is sustained for at least 7 months ( $n = 26$ , and  $n = 22$ , respectively). A Neutral breeding year is when the Southern Oscillation Index (SOI) is above -8 and below 8 and no La Niña or El Niño events were occur for at least 10 of the months ( $n = 46$ ). SOI values were downloaded from [www.bom.gov.au/climate/enso/soi\\_monthly.txt](http://www.bom.gov.au/climate/enso/soi_monthly.txt) (July 25<sup>th</sup>, 2017). Years that have a high degree of variability and do not meet the condition for any of the ENSO phases are excluded ( $n = 23$ ).

La Niña breeding years	El Niño breeding years	Neutral breeding years
1903 1909 1916 1917	1901 1905 1911 1913	1912 1915 1920 1921
1924 1928 1938 1942	1914 1919 1925 1940	1922 1926 1927 1929
1949 1950 1954 1955	1941 1951 1963 1965	1930 1931 1932 1933
1956 1970 1971 1973	1969 1977 1982 1987	1934 1935 1936 1937
1974 1975 1988 1998	1991 1994 1997 2002	1943 1944 1945 1947
1999 2000 2007	2009 2015	1948 1952 1958 1959
		1960 1961 1962 1966
		1967 1968 1976 1978
		1979 1980 1981 1983
		1984 1985 1986 1989
		1995 2003 2004 2005
		2012 2013

## Appendix S2

The breeding bird occurrence records were collated from the following institutions and organizations: Australian Museum, Australian National Wildlife Collection, BirdLife Australia's ATLAS and Nest Record Schemes, eBird, Museum and Art Gallery of the Northern Territory, Museum Victoria, OZCAM (Online Zoological Collections of Australian Museums), Queen Victoria Museum and Art Gallery, Queensland Museum, South Australian Museum, Tasmanian Museum and Art Gallery, Western Australian Museum and ABBBS (Australia Bird and Bat Banding Scheme). Individual and organizations who contributed the ABBBS data are CW Meredith, Dr Grant, E Wyndham, GK Disher, H Bakker, H Sutherland, HE Brenton, HS Curtis, JD Martindale, JR Wheeler, LW Moran, M Cohn, M Smyth, Mrs Templeton, Mr SNP Ali, NW Longmore, R Cooper, RJ Broad, RJ Thomas, RK Westcott, RWJ Pidgeon, RWJ Warnock, T Norostrom, TH Guthrie, WGD Middleton, Mr R Aitken, Ms R Alderman, Mr FJ Alexander, Mr SWW Alford, Mr P Allan, Mr RP Allen, Mr TH Alley, Dr SJ Ambrose, Mr G Ambrose, Mr R Anderson, Mr HF Archer, Mr NW Arnold, Ms H Aston, Mr T Aumann, Mr CN Austin, Mr GB Baker, Dr DJ Baker-Gabb, Mr DA Ball, Dr M Bamford, Mr KA Barker, Mr DE Barnes, Mr GJ Barrett, Mr WF Barrett, Mr LH Barrow, Mrs IM Bateman, Mr H Battam, Mr CI Baxter, Mr G Beal, Dr C Beckmann, Mr SR Beggs, Ms MI Beilharz, Mr GD Bell, Mr H Bell, Mr C Bennett, Dr ML Berg, Mr RJ Bilney, Mr CM Bishop, Mr CA Bissell, Mr EF Boehm, Mr CRJ Boland, Mr PF Bolger, Mr AR Bougher, Mrs BFJ Bowen, Ms GM Bowker, Mr AN Boyle, Ms JB Bradley, Mr HA Bradley, Dr LW Braithwaite, Mr AT Brennan, Prof JLE Gay Brereton, Mr JG Brickhill, Ms SV Briggs, Ms L Broadhurst, Mr MG Brooker, Mr NP Brothers, Mr RE Brown, Mr RF Brown, Mr RJ Brown, Dr AH Burbidge, Mr L Burgess, Mr NW Burnett, Dr TC Burton, Rev CG Burt, Mr J Bywater, Dr BM Cale, Dr GR Cam, Mrs A Cam, Mr M Cameron, Mr RG Cameron, Mr CB Campion, AC Cameron, Dr C Cannon, Mr M Carins, Dr R Carrick, Mr RK Carruthers, Mr BS Carter, Mr NT Carter, Mr BG Chaffey, Dr K Chan, Mr FRH Chapman, Mr GS Chapman, Mr RE Chatto, Ms MH Christie, Mr BJ Chudleigh, Ms SK Churchill, Dr GP Clancy, Mr GF Claridge, Mr GS Clark, Mr M Clayton, Dr DH Close, Prof A Cockburn, Mrs SJ Comer, Mr P Congreve Snr, Mr V Cooper, Mr RE Corbould, Mr DM Cornish, Mr JE Courtney, Mr ML Courtney, Mr PP Coventry, Mr RJ Cox, Mr F Crome, Mrs MM Crouther, Prof JM Cullen, Mr L Cupper, Mr A D'Andria, Mr AF D'Ombrian, Ms Mr Daley, Mr AV Danks, Dr P Dann,

Mr AT Dart, Mr VD Davenport, Dr SM Davey, Mr DHG Davidson, Mr PM Davidson, Dr SJJF Davies, Mr CPS De Rebeira, Dr SJS Debus, Mr J Dell, Mr TE Dennis, Mr DGH Dent, Mr PA Disher, Mr HJ Disney, The Antarctic Division, Dr VA Doerr, Dr RH Donaghey, Dr DF Dorward, Mr GW Douglas, Dr DD Dow, Mr WMCK Dowling, Ms HA Doyle, Mr FW Doyle, Mr PO Doyle, Mr R Draffan, Dr PV Driscoll, Mr PB Du Guesclin, Dr JN Dunlop, Dr GM Dunnet, Dr M Dyer, Mr JN Dymond, Dr EHM Ealey, Mr RJ Edge, Mr KH Egan, Mr MDB Eldridge, Mr RG Elks, Mr NN Ellis, Mr RA Elvish, Mr WB Emison, Mr JA Estbergs, Mr RC Evans, Mrs DEM Evans, Mr JN Eveleigh, Mr ID Falkenberg, Mr NJ Favaloro, Mr PJ Fell, Mr J Fennell, Mr LWC Filewood, Mr JH Fisher, Mr KA Fisher, Dr MR Fleming, Mr AWJ Fletcher, Mr TI Fletcher, Mrs D Foley, Ms L Fontanini, Dr HA Ford, Dr JR Ford, Mr W Ford, Mr N Forde, Mr JC Fordyce, Mr BrianForeman, Mrs PJ Foster, Mr MT Fox, Mr D Franklin, Dr DW Frith, Dr HJ Frith, Mr C Frith, Mr GR Fry, Dr PJ Fullagar, Mr PJ Fuller, Dr JL Gardner, Prof ST Garnett, Mr JA Gates, Mr DJ Geering, Mr RM Gibbs, Mr D Gibson, Mr CL Gill, Mr B Glover, Dr AW Goldizen, Mr RC Good, Mr GP Goodyear, Mr MD Gottsch, Mr TJ Gourlay, Mr CN Gove, Mr RJP Gower, Mr I Grant, Dr DJ Gravatt, Dr D Green, Dr K Green, Dr RH Green, Mr R Gregory-Smith, Dr PJ Guay, Mr MO Gunn, Mr RE Gurney, Mr HA Guyatt, Dr AM Gwynn, Mr LC Haines, Dr ML Hall, Mr B Hall, Mr C Hall, Mr JH Hall, Sgt GT Hanlon, Mr RH Hardie, Mr JL Hardy, Mr JW Hardy, Mr RF Harmer, Mr JGK Harris, Mrs JH Harvey, Mr JA Hassall, Dr CF Heathcote, Dr RG Heinsohn, Dr DG Henderson, Mr NL Hermes, Mr FK Hersey, Mr AL Hertog, Mr PJ Higgins, Mr FAR Hill, Mr MP Hines, Mr WB Hitchcock, Mr CY Ho, Mr JN Hobbs, Mr GJ Hocking, Mr CR Hodge, Mr DM Hodges, Mr MC Holdsworth, Mr AJ Hole, Mr C Hollamby, Mr LM Holland, Dr DG Hollands, Mr JB Hood, Mr I Hore-Lacy, Mr GM Horey, Mr W Horton, Mr ES Hoskin, Mrs K Hough, Dr JM Hughes, Mr TH Hughes, Dr CL Hull, Dr K Hulsman, Mr BR Hutchins, Mr BG Hutchison, Mr J Hyett, Mr JC Ipsen, Mr J Izzard, Mr P Jackson, Mr BR Jahnke, Ms A Jansen, Ms L Jansen, Mr PR Johnson, Mr SE Jolly, A/Prof DN Jones, Mr FE Jones, Mr R Jones, Mr R Jordan, , Mr WL Klau Oam, Dr JO Karubian, Mr K Keith, Mr JW Kellam, Dr BJ Kentish, Mr RF Kenyon, Prof J Kikkawa, Mr J Klapste, Dr SM Kleindorfer, Mr NW Kurtz, Mr N Kwapena, Mr IG Lane, Mr JAK Lane, Mr SG Lane, Dr NE Langmore, Mr GL Lansell, Mr AFC Lashmar, Mr WG Lawler, Mrs G Laybourne-Smith, Ms S Legge, Mr AJ Leishman, Dr AH Lendon, Mr N Lenz, Ms JE Lewis, Mr AJ Ley, Mr J Liddy, A/Prof A Lill, Dr E Lindgren, Dr LC Llewellyn, Mr TG



Loffler, Mr GJ Logan, Mr JL Long, Mr RG Lonnon, Mr R Lossin, Dr KW Lowe, Mr T  
 Lowe, Mr D Macdonald, Mr DB Mack, Mr KJ Mack, Mr RD Mackay, Mr RG Mackenzie,  
 Mr WDF Mackenzie, Dr MN Maddock, Dr MJ Magrath, Dr RD Magrath, Mr PN Maher,  
 Prof WJ Maher, Dr RE Major, Mr EB Male, Mr S Marchant, Mr AJ Marsland, Mr G  
 Marston, Mr JM Martin, Mr RJ Martin, Mr JS Martyn, Mr LTE Marvelde, Mr WE  
 Matheson, Mr G Maurer, Dr KL Maute, Dr PR Mawson, Mr I McCallum, Mr S Mccosker,  
 Ms M Mccoy, Mrs RE Mcculloch, Dr PG McDonald, Dr DC McFarland, AM Mcgarvie, Mr  
 PDD McIntosh, Mr JL Mckean, Mr EJ Mckenzie, Dr NG Mckilligan, Mr JG McLaughlin, Mr  
 EG McNabb, Mr JA McNamara, Mr MV Melvin, Mr PW Menkhorst, Dr ALA Middleton, Dr  
 PJ Milburn, Mr LJ Millar, Mr GJ Millard, Mr Dr Milledge, Mr B Miller, Dr CDT Minton, Mr  
 N Mooney, Mr LA Moore, Mrs GJ Moors, Mr B Morgan, Mr DG Morgan, Mr AK Morris,  
 Mr A Morrison, Mr OPP Mueller, Dr RA Mulder, Mr D Munro, Mr MT Murn, Dr SA  
 Murphy, Mr D Murray, Mr MD Murray, Dr OMG Newman, Ms JL Nicholls, Ms CA Nicholls  
 Am, Dr LW Nicholson, Mr HJ Nicholson, Mr LA Nielson, Mr DJ Noonan, AY Norris, Mr L  
 O'Connor, Mr J O'Kelly, Mr GR Park, Mrs MP Park, Dr CJ Parmenter, Ms V Parry, Dr JS  
 Pate, Ms VJ Pattemore, Mrs JD Patterson, Mr CK Pawsey, Mr RJ Pearse, Mr GB  
 Pearson, Mr DL Pepper-Edwards, Mr TW Pescott, Dr AM Peters, Dr D Peters, Mr M  
 Pickett, Mr FG Pinchen, Mr RL Pink, Mr D Pinner, Mr T Poldmaa, Mr JM Poole, Mr DJA  
 Portelli, Mr KJ Pound, Ms EK Pratt, Ms MV Preker, Mr JG Pridham, A/Prof SG Pruett-  
 Jones, Dr SR Pryke, Mr D Purchase, Mr D Putland, Dr GH Pyke, Ms MK Rathburn, Mr J  
 Rawlins, Dr JL Read, Prof HF Recher, Dr NCH Reid, Mr AJ Reid, Mr DR Reid, Mr R  
 Reid, Mrs PN Reilly, Mr DS Reimer, Mr JW Reside, Mr C Rich, Mr DC Richards, Mr GE  
 Richards, Dr MG Ridpath, Mr DJ Ripper, Dr GG Robertson, Mr D Robinson, Mrs VA  
 Robinson, Mr JL Rogan, Mr JH Rooke, Mr G Ross, Mr HM Ross, Mr M Rowe, Mr ICR  
 Rowley, Ms JC Scarl, Mr NW Schrader, Mr DA Secomb, Dr DL Serventy, Mr DHC Seton,  
 Dr TGD Shannon, Dr RC Shearer, Mr RJ Shick, Mr KF Silva, Mr KG Simpson, Dr RG  
 Sinclair, Dr IJ Skira, Dr PJ Slater, Mr IJ Smales, Mr DI Smedley, Dr GC Smith, Dr GT  
 Smith, Dr VW Smith, Mr JL Smith, Mr KW Smith, Mr RJ Smith, Dr CN Smithers, Dr AK  
 Smyth, Mr RJ Speechley, BA Speechley, Mr PJ Spurge, Mr AF Stewart, Mr DA Stewart,  
 Mr A Stokes, Mr RH Stranger, BRM Strong, Mr PD Strong, Dr CA Surman, Mr AJG  
 Sutton, Mr J Tagell, Dr MK Tarburton, Mr MK Tarburton, Dr ID Temby, Mr MT  
 Templeton, Mr T Templeton, Mr RG Thoday, Mr DG Thomas, Mr EB Thomas, Mr GD

Thomas, Mr HF Thomas, AT Thomason, Dr PJ Thomson, Dr CR Tidemann, Dr SC Tidemann, Mr RA Tilt, Dr A Tingay, Dr RT Todd, Mr PJ Tonelli, Mrs WA Trudgen, Mr RC Turnbull, Mrs LJ Turner, Mr BD Tynan, Mr GH Underwood, Mr SB Unthank, Mr FWC Van Gessel, Dr GF Van Tets, Mr WJ Vestjens, Mr NW Vincent, Dr WC Wakefield, Ms E Wakefield, Mr LE Wall, Mr SP Wallace, Mr JE Walsh, Mr RM Warneke, Mr MH Waterman Oam, Dr DM Watson, Ms I Watson, Mr NF Weatherill, Dr MS Webster, Dr JA Welbergen, Mr NB Wells, Dr MA Weston, Mr E Wheeler, Mr JS Whinray, Dr PJ Whitehead, Mr A Whitehead, Dr JA Wiens, Mr FB Wilkinson, Mr AC Williams, Mr DJ Williams, Mr L Willoughby, Mr JT Willows, Mr SJ Wilson, Mr T Wilson, Mr GB Winning, Dr JCZ Woinarski, Mr TO Wolfe, Mr KA Wood, Mr VJ Wood, Mrs R Woodell, Mrs SJ Wooller, Mr NR Wright, Mr VH Yeoman, Mr S Yorke, Dr RA Zann, The Bird Care And Conservation Society, The Taiwan Bird Banding Centre, Gippsland Lakes Ornithological Group, The Shorebird Study Group, The Broome Bird Observatory, The Eyre Bird Observatory Group, The Rotamah Island Observatory, The Dpipwe Orange-Bellied Parrot Management Group, The Taronga Zoo Rehab Program, The Western Australia Rehabilitation Group, The Wild Bird Rehabilitation Group, The Bird Migration Research Center, The Gluepot Reserve Study Group, The Australasian Wader Study Group, The Victorian Wader Study Group, The Western Australia Wader Study Group, The New South Wales Wader Study Group, and Tasmania Parks And Wildlife Service.

## Appendix S3

**Table S3.1** The start, peak, conclusion, and length of egg-laying for 64 species of birds in the temperate region and 15 species in the arid region of Australia. Dates are given as the numeric day of the year, where January 1 = 1, February 1 = 32, etc. Birds can breed over the turn of the year. The observation count is the number of unique first egg-lay dates per a species in a particular region during an El Niño Southern Oscillation phase. This table is available through <https://doi.org/10.6084/m9.figshare.5413189.v4>

## Chapter 5

# Variation in egg shape and nest structure modulates the effects of climate extremes

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## Chapter Five Vignette

In Chapter three we identified that temperature and precipitation drives and constrains avian breeding. Yet some species are not affected by extreme climatic conditions during the breeding period. In this chapter, we investigate how egg shape and nest type may mitigate the pressure of extreme climatic conditions. The evolution of the classic egg shape in birds remains enigmatic despite some recent high-profile attention. We present an analysis of egg shape in relation to extreme heat and aridity across 310 passerine bird species at a continental scale. We have identified landscape-level relationships between egg elongation, nest type, and key environmental parameters (leaf area index: a measure of the degree of potential shade, and vapour pressure deficit: a measure of aridity). Understanding how reproductive traits vary across climatic gradients is of critical importance, given that projections of future climate predict increases in the duration, intensity, and frequency of extreme temperatures and heatwaves globally. Importantly, predicting which species may cope with extreme conditions from easily measured traits provides a timely technique for assessing the vulnerability of species to climate change.

## **Abstract**

Why are avian eggs ovoid, while the eggs of most other vertebrates are symmetrical? The interaction between an egg and its environment likely drives selection that will shape eggs across evolutionary time. For example, eggs incubated in hot, arid regions face acute exposure to harsh climatic conditions relative to those in temperate zones, and this exposure will differ across nest types, with eggs in open nests being more exposed to direct solar radiation than those in enclosed nests. We examined the idea that the geographical distribution of both egg shapes and nest types should reflect selective pressures of key environmental parameters, such as ambient temperature and the drying capacity of air. We took a comparative approach using 310 passerine species, many of which are found in some of the most extreme climates on earth. We found that, across the Australian continent, egg elongation decreases and the proportion of species with domed nests increases in hotter and drier areas with sparse plant canopies. Eggs are most spherical in open nests in the hottest environments, and most elongate in domed nests in wetter, shady environments. Our findings suggest that climatic conditions played a key role in the evolution of passerine egg shape.

**Key-words** breeding birds, egg shape, nest microclimate, shell conductance, vapour pressure deficit, nest type

## Introduction

The classic ovoid egg shape of birds is one of the most familiar of all shapes, and yet it remains surprisingly poorly understood (Birkhead, 2016; Stoddard et al., 2017). The eggs of most other oviparous vertebrates are much more symmetrical and often more spherical (Stoddard et al., 2017). The extent of our ignorance about the adaptive significance of egg shape in birds was recently highlighted by Birkhead et al. (2017), who corrected a long-standing myth that the eggs of Common Guillemots (*Uria aalge*) are pear-shaped to prevent them from rolling off cliff ledges. Although this was an intuitively appealing idea, in fact, the guillemot's egg is not strikingly different in shape from the eggs of most other birds, and relatively few birds lay their eggs on cliff ledges, suggesting that some more widely applicable explanations remain to be found for the ubiquitous ovoid shape of birds' eggs (Birkhead, 2016; Birkhead et al., 2017).

In a recent comparative study 1400 bird species, Stoddard et al. (2017) identified a link between egg shape and the flight abilities of different species. Although this impressively broad analysis considered a range of biophysical, life history and ecological parameters, it did not consider the abiotic environment into which an egg is laid, which includes a wide range of factors that may be detrimental to the development of an embryo. For instance, eggs must remain within a relatively narrow temperature range (Turner, 2002), and a balance must be found between gaseous exchange and dehydration (Grant, 1982). Many avian species breed successfully under extreme climatic conditions, including hot and arid environments where extreme temperatures augment the drying capacity of the air. In addition, the paucity of vegetation in such habitats reduces the amount of shade available, increasing the potential for intense solar radiation to affect the egg and the embryo developing within.

The design of an egg should be optimised for the environmental conditions to which it is exposed (Deeming, 2002). For example, birds breeding in deserts, at high altitudes, or at high temperatures have a relatively lower shell conductance, limiting water loss while maintaining an adequate level of gaseous exchange of respiratory gases (Rahn & Paganelli, 1988; Carey, 2002). But there is a lower limit on eggshell conductance and permeability, given the need for effective exchange of oxygen and carbon dioxide between the embryo and the atmosphere. The shape of an egg also affects gaseous exchange, as well as the thermal dynamics of the egg and the surface

area exposed to solar radiation. For any given volume, a spherical egg has a lower surface area to volume ratio than does an ovoid egg (Hoyt, 1976). Therefore, if all else is equal, a spherical egg will gain and lose heat more slowly, lose less water, and have lower exposure to solar radiation than will a more elongate egg with the same volume. In the well-studied domestic chicken (*Gallus gallus domesticus*), for example, rounder eggs have thicker shells (Altuntaş & Şekeroğlu, 2008), but the relationships between elongation and shell conductance have not been well explored at a broader level (Deeming, 2002).

Nest humidity is known to affect water loss from eggs (Ar & Rahn, 1980; Rahn & Paganelli, 1990; Ar & Sidis, 2002), and for the majority of species humidity levels within eggs is greater than those in the nest (Mortola, 2009). The size, structure and composition of nests – along with the brood patch of incubating parents – all contribute to the microclimate around an egg, with differences in vapour pressure between egg and nest microclimate largely determining the degree of water loss. Experimental studies have shown that changes in nest humidity can reduce egg hatchability (Walsberg, 1983; Walsberg & Schmidt, 1992). The most obvious way in which a species can reduce or buffer exposure of the egg to the wider environment is through the design of the nest. Nests that are enclosed (e.g. those in cavities or burrows, or domed structures with roofs) should be beneficial in the maintenance of desirable humidity and temperature in hot and arid regions (Heenan, 2013). Deeming (Deeming, 2016) hypothesised that nests can function as incubators in which both temperature and humidity are maintained. Here, we assume that enclosed nests have the greatest potential to maintain optimal nest humidity and temperatures (Deeming, 2011). Further, enclosed nests provide shade in areas with little vegetation cover reducing the likelihood that incubating birds and eggs overheat when exposed to direct sunlight (Carey, 2002). Indeed, in the arid zone of Australia, experimental removal of the roof of Zebra Finch (*Taeniopygia guttata*) nests results in a significant increase in temperature in the nest cup, and orientating the nest entrance towards or away from direct sunlight also significantly affects internal temperatures (Griffith et al., 2016).

In the passerines (Passeriformes), nest form is largely phylogenetically conserved across taxa, with transitions between domed nests and open cup nests occurring relatively rarely during passerine evolutionary history (Price & Griffith 2017). On the

Australian continent, the geographic origin of the oscine passerines (Barker et al., 2004), 33.7% of passerine species build dome-shaped nests that have roofs, and phylogenetic analyses indicate that this is the ancestral form that has remained largely unchanged in some lineages for tens of millions of years (Price & Griffith 2017). Cavity nesting has evolved in relatively few Australian taxa (Price & Griffith 2017). Given this evolutionary inertia in nest form, it seems likely that as species have adapted to different environments, they have been more likely to adjust the shape of their eggs than make a significant shift in the form of their nest.

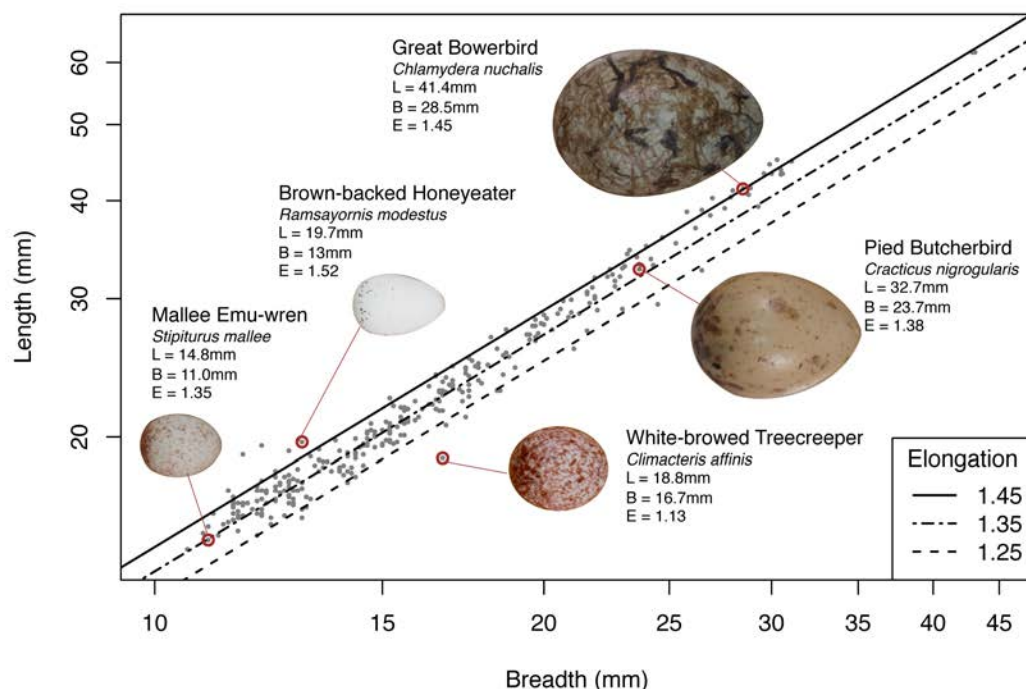
Given that gaseous exchange renders an egg vulnerable to water loss, we expect egg shapes that reduce the overall surface area to dominate where environmental conditions are hot, dry and sparsely vegetated to reduce water loss and decrease exposure to UV radiation. Furthermore, given that the three distinct nest types (in cavities, open cup and domed nests) provide different levels of protection against exposure to climatic conditions, we would expect the relationship between environmental conditions and egg shape to differ with nest structure.

We test these ideas at the continental scale across the assemblage of Australian passerines. Assessing traits, and geographic variation of traits across assemblages of species is a way to assess ecological strategies that optimize fitness under a set of environmental conditions. It has been demonstrated that geographic variation in functional traits can largely be explained by environmental factors (Liu et al. 2013; Foden et al., 2013). Australia provides an ideal opportunity to assess variation in bird traits and phenology because of its wide range of environmental conditions, distinct biogeography and because relative to other continents, it contains a large proportion of the Passerine families, being the host of the early evolutionary radiation of this important group that constitutes more than half of all avian species. Although a large portion of the country is covered by arid vegetation, there are also tropical, subtropical, and temperate biomes (Stern et al. 2000; Bureau of Meteorology, 2006).

This is the first comprehensive examination of how egg shape varies for a range of species (Fig. 1) in an explicit spatial context. We combine records of avian breeding locations (e.g. ATLAS records and nest record schemes) with data from museum egg-collections, bird-banding records, and citizen science initiatives (Englert Duursma et al., 2017) to determine the geographic extent of breeding for 310 species of passerine birds



occurring in 100 km x 100 km grid cells across Australia. This information is coupled with data on two key functional traits: egg elongation (the ratio of the egg length to breadth) and nest type (cup-shaped, dome-shape with roof, cavity). We examined how avian nest type and egg shape vary across the Australian continent in relation to two environmental variables important for understanding climatic stress: average vapour pressure deficit (VPD) and leaf area index (LAI). In particular, we focused on understanding strategies for successful breeding in hot and arid environments. In the arid zone of inland Australia, for example, where tree cover is typically sparse, we expect natural selection to have favoured traits beneficial for reducing water loss, maintaining eggs below critical upper-temperature limits, and decreasing exposure of the incubating birds and embryos to solar radiation.



**Figure 1.** The relationship between egg length (L) and breadth (B) for Australian passerine species. The diagonal lines show egg elongation (E, the ratio of the egg length to breadth) at values of 1.25, 1.35, and 1.45.

## Material and Methods

### ***Geographic Distributions***

The geographic breeding ranges for 310 native Australian mainland passerine species were compiled using occurrence observations (latitude and longitude coordinates) from Birdlife Australia's Atlas (Barrett et al., 2003) and Nest Record Scheme, historical museum egg collection records, Australian Bird and Bat Banding Scheme, Atlas of Living Australia (ALA, 2016), Global Diversity Information Facility (GBIF, 2016), and eBird (eBird, 2015). For a complete list of contributing institutes and persons, and detailed methodology of how data was cleaned, please see Supplementary Material. Breeding records used in this study, where the latitudinal and longitudinal coordinates are the centre-points of the 100 km x 100 km grid cells in Albers Equal Area Conic Projection, are available in Table S1.

### ***Trait Data***

We gathered information on egg elongation – the ratio of egg length to breadth – from three sources: (1) published values in the Australian Bird Data Version 1 (Garnett et al., 2015), (2) by directly measuring eggs at the Australian National Wildlife Collection (Canberra, Australia: <http://www.csiro.au>), and (3) using photos of eggs from the Online Zoological Collections of Australian Museums (<http://ozcam.ala.org.au>). Egg elongation was calculated for 308 of the species; the remaining two species, *Glycichaera fallax*, Salvadori, 1878 (Green-backed Honeyeater) and *Amytornis ballarae*, Condon, 1969 (Kalkadoon Grasswren), were dropped from the elongation analysis because we lacked information on egg length and breadth.

We classified nest type for 309 species as either cup-shaped, domed, or cavity using published sources (Price & Griffith, 2017). Green-backed Honeyeater lacked nest information and was dropped from the nest type analysis. Cup-shaped nests were defined as those with the upper portion exposed ( $n = 191$ ), while domed nests have the upper proportion enclosed with a constructed roof, including globular and pendulous nests with side entrances (Collias, 1997; del Hoyo et al., 2016) ( $n = 102$ ). Cavity nesters ( $n = 16$ ) include those nesting in burrows or hollows in locations such as

tree holes, rock cavities, or holes in the ground. The majority of cavity nesters occur in the families Climacteridae, and Pardalotidae. Two species made highly variable nests (*Mirafrja javanica* Horsfield, 1821 and *Cisticola juncidis*, Rafinesque, 1810) that are typically partly or fully roofed (Higgins, 1999; Higgins et al., 2006), which we classified these species as domed. See Table S2 for species level information via <https://doi.org/10.6084/m9.figshare.5413189.v4>.

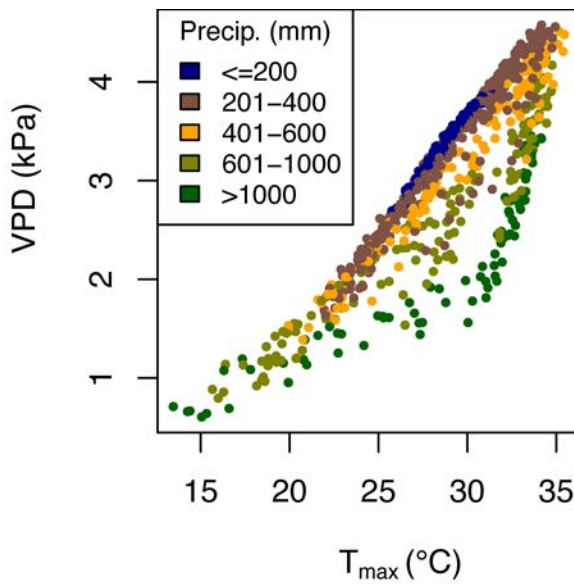
To assess variation of average egg elongation, we found the mean elongation for species with cup-shaped nests and species with domed nests for grid cell species assemblages (i.e. the species breeding in each 100 km x 100 km grid cell). Cavity nesting species had significantly rounder eggs than species with domed and cup-shaped nests and given there were only 16 species, we excluded them from the grid cell species assemblage's analyses. For each grid cell: we also found the proportion of the species assemblages with domed nests.

## ***Environmental Data***

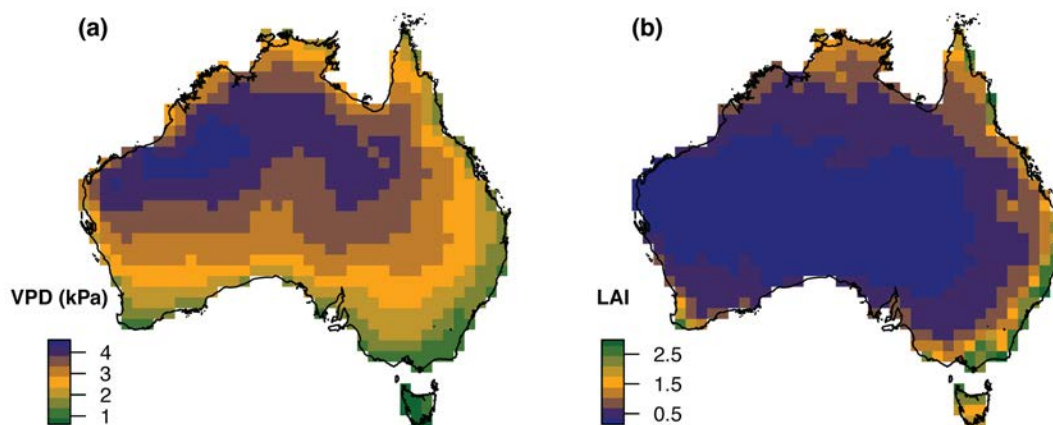
To assess the relationships between environmental conditions and functional traits, we calculated average daily maximum vapour pressure deficit (VPD) and average Leaf Area Index (LAI) for the Australian continent, at a 100 km x 100 km grid cell resolution. We defined VPD as the difference between the saturated vapour pressure at the daily maximum temperature ( $T_{\max}$ ) and daily vapour pressure (VP) at 3pm.  $T_{\max}$  and VP were downloaded from Australian Water Availability Project (Jones et al., 2009) via <http://www.bom.gov.au/jsp/awap/>. The *esat* function in the R library *plantecophys* (Duursma, 2015) was used to convert daily maximum temperature to saturated vapour pressure. Data were averaged across the period 1950 to 2016, projected to Albers Equal Area Conic Projection, and aggregated to 100 km x 100 km grid cells. VPD is potentially of critical importance in the maintenance of nest humidity and eggshell conductance. VPD is a function of the amount of water vapour in the air and ambient temperature (Jones, 1992). As temperatures increase so does VPD, since higher temperature air can hold more moisture (Fig. 2). If moisture is not available, however, the VPD, or the air's ability to dry increases. Conversely, low-temperature air cannot support much moisture, therefore preventing a large difference in vapour pressure and saturated vapour pressure. The Australian continent has a large range of average annual VPD (Fig. 3a), with moist temperate regions having values close to 0 kPa, and arid, warmer regions having values over 4 kPa.

LAI is the amount of green leaf area in relation to the ground area (Watson, 1947). Areas with higher values of LAI, such as the tropical region of Australia (Fig. 3b), have greater canopy cover protecting nests and eggs from UV radiation throughout the day. In open environments, with lower values of LAI, more direct sunlight reaches the ground, and nests are likely to be exposed to some direct solar radiation, although nest position can influence the amount of UV radiation a nest is exposed to, and even in very open environments a nest can be well shaded. LAI values used in this study were satellite-derived and indicated the number of leaf layers per unit ground. LAI measurements for 16-day intervals during the period February 2000 to 2016 were obtained via the TERN AusCover portal (<http://www.auscover.org.au>) and were produced from tiles originally downloaded from USGS (<https://lpdaac.usgs.gov>). Data

were averaged across the time period and aggregated to 100 km x 100 km resolution following the process above.



**Figure 2.** Relationship between mean ambient air temperature ( $T_{\max}$ ), mean vapour pressure deficit (VPD), and mean monthly total precipitation (Precip) for the Australian continent at 100 km x 100 km grid cell resolution. Data were downloaded from Australian Water Availability Project (Jones et al., 2009) via <http://www.bom.gov.au/jsp/awap/> and averaged across the time period 1950 to 2016.



**Figure 3.** Variation in (a) average annual vapour pressure deficit (VPD, kPa) and (b) average annual leaf area index (LAI) for the Australian continent. Maps show average values for 100 km x 100 km grid cells.

## **Analyses**

Three specific statistical analyses were performed to examine: (1) the relationship between egg elongation and nest type across species, (2) variation in grid cell averages of egg elongation in relation to VPD and LAI, and (3) variation in the proportion of species with domed nests in relation to VPD and LAI. All analyses were carried out in R 3.3.2 (R Core Team 2016), and relationships were considered significant at an alpha level of 0.05. Throughout, summary values are reported as means  $\pm$  SE.

ANOVA was used to test for differences in elongation among nest-types, with Type II Wald *F* tests and Kenward-Roger approximation for degrees-of-freedom using the *car* package (Fox & Weisberg, 2011) and Tukey's pairwise comparisons using the *multcomp* package (Hothorn et al., 2008). To test for bias in our model from shared ancestry, we performed the same analysis using a linear mixed-effects model, using *lme4* package (Bates et al., 2015), with nest-type as fixed effects and taxonomic family as a random effect. We found no meaningful difference in the results (see Supplementary material). Thus we only report the results from the ordinary least squares (OLS) regression.

We assessed the variation in (i) the proportion of species with domed nests and (ii) the mean egg elongation for grid cell assemblies of species in domed nests and species in cup-shaped nests, in relation to VPD and LAI. We used OLS regression and a simultaneous autoregressive model (SAR). In all regression models, we included an interaction between LAI and VPD.

Spatial autocorrelation of model residuals violates a key assumption of statistical analysis, i.e., independence of residuals and identical distribution (Dormann et al., 2007; Plant, 2012). Moran's *I* statistic was used to detect spatial autocorrelation in the model residuals (i.e., values with close spatial distribution are more similar than expected when compared to those that are of further distance apart) using the *ncf* package (Bjornstad, 2016). Where spatial autocorrelation was detected, we used a simultaneous autoregressive model (SAR) to add an autocorrected error term of spatial weights using the package *spdep* (Bivand et al., 2013; Bivand & Piras, 2015). A row standardized spatial weight matrix was calculated using a neighbourhood distance of 200 km. These parameters were selected because they returned the low values of Moran's *I* statistic

over the first 20 distance groups when coding schemes of binary and row standardised were tested, in preliminary analysis to calculate spatial weights using neighbourhood distances of 200 km, 300 km, 400 km, 500 km, 750 km, and 1000 km.

## Results

Across the Australian passerine species, egg shape varies markedly, from nearly spherical (1.13 for the White-browed Treecreeper (*Climacteris affinis*)) to highly elongated (1.62, much greater length than breadth, for the Dusky Gerygone (*Gerygone tenebrosa*)), with an overall mean elongation of  $1.37 \pm 0.00$  (Fig. 1, species level data available in Table S2 via <https://doi.org/10.6084/m9.figshare.5413189.v4>). Egg elongation ratios for the 308 species and for within grid cell species assemblages (i.e. the species breeding in each 100 km x 100 km grid cell) were normally distributed, although three species that had very elongated eggs fell outside of the normal distribution. Therefore, we performed separate analyses for (i) all species, and (ii) species with egg elongation values within three standard deviations of the mean. We found no meaningful difference between these two groups, so we only report results across all species.

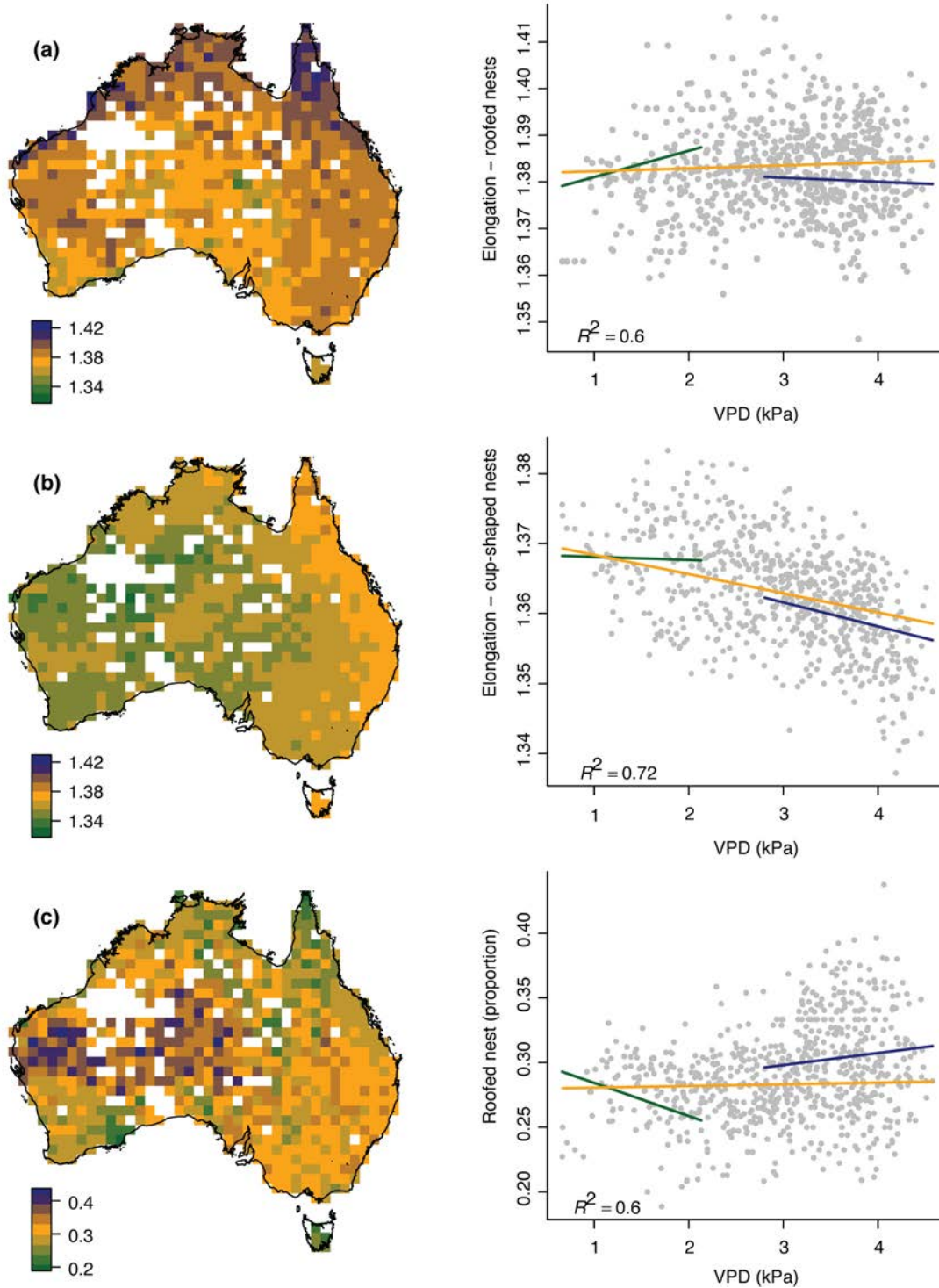
Nest type explained 6% of the variation in egg elongation across all species ([ $F(2, 305) = 10.59, p < 0.001$ ]). Cavity-nesting species had significantly less elongated eggs ( $p < 0.001, 1.30 \pm 0.02, n = 16$ ) than species that nest in cup-shaped and domed nests ( $1.37 \pm 0.02, n = 191; 1.37 \pm 0.02, n = 101$ , respectively); however, there was no significant difference in elongation between cup-shaped and domed species ( $p = 0.95$ ). See Table S2 for species level data including nest type via <https://doi.org/10.6084/m9.figshare.5413189.v4>.

Across the Australian continent, on average, avian eggs were less elongated and domed nests were more common in areas that are hot and dry (high VPD) and have sparse plant canopies (low LAI). Mean egg elongation for grid cell assemblages of species with domed nests ranged from 1.35 to 1.42 (mean:  $1.38 \pm 0.01$ , Fig. 4a) and for cup-shaped nests ranged from 1.33 to 1.38 (mean:  $1.36 \pm 0.01$ , Fig. 4b). Mean elongation for species with domed nests was greatest for the tropical biome of Australia (based on a national Köppen classification system (Stern et al. 2000, BOM 2006) where the equatorial and tropical regions were combined), with values greater than the 80%



quantile (1.390) predominately located there. Species with cup-nests had a different pattern, with mean elongation values above the 80% quantile (1.368) located across eastern Australia. For both nest types, the grid cells with the lowest values of mean elongation were predominately located in the desert and grassland biomes. Likewise, the proportion of species with domed nests was greatest in the hot and dry areas, with nearly all grid cells above the 80% quantile (0.317) located in the desert (Fig. 4c). The proportion of species with domed nests varied from 0.19 to 0.44 (mean:  $0.29 \pm 0.04$ ; Fig. 4c).

LAI and VPD explained a significant proportion of the variation in mean egg elongation and in the proportion of species with domed nests (Table 1). Based on the SAR models of these variables, as VPD increased and LAI decreased: (i) mean egg elongation for species in cup-shaped and in domed nests both declined (i.e. eggs became significantly rounder), and (ii) the proportion of species with domed nests increased (Fig. 4). However, for species with domed nests, mean elongation increased under conditions with moderate VPD and high LAI. These conditions can occur in the tropics during the dry season.



**Figure 4.** Variation in egg elongation and the proportion of species with domed nests for Australia's passerines. The maps depict the spatial variation in  $1^\circ \times 1^\circ$  grid cells of (a) mean egg elongation for species with domed nests, (b) mean egg elongation for species with cup-shaped nests, and (c) the proportion of species with domed nests. White grid cells either do not meet the required Completeness Index (i.e. the ratio of the observed

species richness to the estimated species richness) or had less than ten species with domed nests or less than ten species with cup-shaped nests. Plots show the relationship between mean grid cell values (response variables) and vapour pressure deficit (kPa). Coloured lines depict the predicted response from the simultaneous autoregressive models when LAI is at the mean (yellow line), below the 5<sup>th</sup> percentile (blue) above the 95<sup>th</sup> percentile (green line). Nagelkerkes pseudo R<sup>2</sup>s are given.

**Table 1** The importance of VPD, LAI, and their interaction for explaining variation in mean elongation for species with domed nests and for those with cup-shaped nests, and the proportion of species with domed nests. Elongation is the ratio of egg length to egg breadth. \* indicates a variable that contributed significantly to model ( $p < 0.05$ )

Model	Variable	Mean ( $\pm$ SE) SAR model coefficients
Elongation – Species with domed nests	VPD	1.382 $\pm$ 0.001
	LAI*	1.378 $\pm$ 0.002
	VPD:LAI*	1.388 $\pm$ 0.002
Elongation – Species with cup-shaped nests	VPD*	1.369 $\pm$ 0.001
	LAI	1.370 $\pm$ 0.001
	VPD:LAI	1.374 $\pm$ 0.001
Proportion of species with domed nests	VPD*	0.279 $\pm$ 0.004
	LAI*	0.288 $\pm$ 0.009
	VPD:LAI*	0.245 $\pm$ 0.006

## Discussion

To the best of our knowledge, this is the first continental study of functional avian traits in extreme environments. We found that in the hot, dry, and sparsely vegetated interior of Australia (high VPD, low LAI): (i) the proportion of species with domed nests was greater (Fig. 4c) and (ii) average egg elongation was lower than that found across the rest of Australia (Figs 5a and 5b). This variation in egg elongation and nest type in response to VPD and LAI indicates how, at the landscape level, strategies for reducing stress in hot and dry environments are favoured in bird assemblages.

We identify an association across bird assemblages between high abiotic stress (in deserts) and the occurrence of rounder eggs, particularly in open nests. The potential advantages of round eggs under hot and dry climatic conditions have not been well explored, and elongation and asymmetry have often been related to nest type, space occupied in a clutch, and the ability to roll (Hoyt, 1976; Mortola, 2009). Based on current research we hypothesise three potential benefits to rounder eggs in desert regions. First, it is likely that the shape of eggs is acting as a surrogate for traits that affect shell conductance. Shell conductance and pore density vary across an egg, with the blunt end of eggs having greater values (Rokitka & Rahn, 1987). Future research is needed to investigate whether there is a relationship between egg elongation, which is a trait readily available for many species, and shell conductance. Further, it would be useful to investigate if wide-spread species such *Colluricincla harmonica* have variation eggshell elongation that reflect our findings. This may influence the results found here. It is worth noting that intraspecific variation in egg shape is linked to shell thickness in poultry eggs, with rounder eggs having thicker shells (Altuntaş and Şekeroğlu, 2008). Thick eggshells have greater pore length and, according to Fick's law of diffusion, this decreases shell conductance. Decreased shell conductance in arid regions reduces the likelihood of excessive water loss, but in very moist hot areas this would not be advantageous because water loss is directly related to adequate exchange of oxygen and carbon dioxide through the eggshell (Rahn & Paganelli, 1988). Second, we hypothesise that the thermal inertia of elongated eggs is lower than that of round eggs (Turner, 2002); therefore, elongated eggs warm and cool more quickly than round eggs. Third, round eggs in cup-shaped nests in open environments have a lower proportion of surface area receiving radiation to total surface area ratio compared to eggs that are highly elongated

under the same conditions, as shown for different animal shapes (Morhardt, 2012). This reduces heat transfer from thermal radiation and exposure of the embryo to potentially harmful UV radiation (Maurer et al., 2015).

The methods and results presented here complement laboratory-based experiments on critical temperature thresholds and variable humidity for eggs and embryos. These experiments have been limited to looking at embryonic stress for a small number of species in field or laboratory-based settings (Webb, 1987; Walsberg & Schmidt, 1992). However, understanding variation in traits at large-scales, across many species, is important for practical activities such as estimating the potential impact of climate change (Williams et al., 2008; Dawson et al., 2011; Foden et al., 2013). Identifying traits that may be advantageous when species are breeding in extreme conditions, such as high temperatures with little precipitation, is crucial for providing a more holistic understanding of species responses to climatic drivers.

As proposed by Deeming (2016), the spatial variation in nest type that we see across Australia supports the idea that nests act as incubators where temperature, humidity, and respiratory gases (i.e. oxygen and carbon dioxide) are maintained within optimal conditions. In hot, dry, and open environments, domed nests: provide shade, benefiting both the incubating bird and embryos through reduced temperatures (Griffith et al., 2016); reduce the vapour pressure difference between the ambient air and the eggs (Deeming, 2011); and provide shelter from the wind (reviewed in Deeming, 2011). The connection between nest type and the regulation of humidity and temperature of eggs has been well established (Deeming, 2011, 2016; Mainwaring et al., 2014). Deeming (2016) recently proposed that multiple selective drivers have acted upon nest architecture and that there are two main functional properties of nests. The first function is for the conservation of heat and the second is to maintain the appropriate microclimate. In the desert and grassland regions of Australia, it seems likely that the primary function of nests is for the maintenance of suitable microclimates, particularly higher humidity and lower temperatures than the ambient air. Given the stability of nest structure over long periods of evolutionary time (Price & Griffith, 2017), we propose that dome-building species are better adapted to living in harsh arid environments and are therefore more likely to immigrate into those regions, rather than the alternative explanation that species modify their nest structures during or following immigration.

Our findings from hot and arid desert regions contrast markedly to those from tropical regions within Australia. Tropical regions typically have very high LAI, i.e. large areas of closed canopy forest. During the rainy season, VPD can be close to 0 kPa while during the dry season VPD can be quite high with average annual VPD around 2.5 kPa (Jones et al., 2009). Species that nest in very wet conditions (i.e. grebes, Gaviiformes) have many pores in their eggshells to allow for adequate water loss and gas exchange (Rahn & Paganelli, 1990). In areas with seasonally low levels of VPD, i.e. wet conditions, fewer passerine species make domed nests (~25 % of species, Fig. 4c), especially when compared explicitly to arid regions (~40 % of species). This is likely because domed nests may absorb excessive water, resulting in the nest humidity being high and adequate gas exchange inhibited, as shown in studies where nests were exposed to air saturated with moisture (Walsberg, 1983; Walsberg & Schmidt, 1992).

The need to meet adequate gas exchange may also explain why birds with domed nests in the tropics have, on average, the highest values for elongation (above the 80% quantile, Fig. 4a), which may facilitate gas exchange. The amount of water an egg loses during incubation is a combination of the water vapour pressure difference between the egg and its microclimate, egg size, incubation duration, and shell conductance (Walsberg, 1980; Rahn & Paganelli, 1988; Walsberg & Schmidt, 1992; Whittow, 1999; Deeming, 2011). Whilst birds do not actively control for water loss from eggs; they can influence water loss through nest site selection, nest type, nest material, nesting behaviour and the timing of breeding (Deeming & Ferguson, 1991; Ar & Sidis, 2002; Mortola, 2009). The appropriate loss of water from avian eggs during incubation is directly related to the successful development of embryos (Ar et al., 1991; Mortola, 2009), and for most species water loss accounts for 15% of the initial egg mass (Rahn & Paganelli, 1988).

## Conclusion

Our study suggests that nest type and egg elongation vary under large-scale changes in VPD and LAI, particularly under extreme values. This variation in nest type and egg elongation may provide insight as to which species may be better suited to overcome the potential challenges faced under extreme weather events, particularly heatwaves. This area of research would benefit from experimental studies aimed at investigating

intra-specific variation in nest-shape and egg elongation to further explore whether there are relationships within species among these factors, gas exchange rates, and embryonic temperatures.

## **Data Accessibility**

The data used in this manuscript are publically available (i.e., climatic data and occurrence observations). Observations were collated from a variety of online databases, institutes, and persons (for a complete list institutes and persons, please see the Supplementary Material). Although most of these data are freely available, redistribution is restricted by license. To make this study reproducible and to adhere to licensing agreements, we have made the gridded presence of breeding passerines in Australia at a 100 km x 100 km resolution (Appendix S1) and trait data (Appendix S2) available. These are available through <https://doi.org/10.6084/m9.figshare.5413189.v4>

## **Authors' Contributions**

DED, SCG, RVG conceived the designed the study. DED collated and vetted the observational and climatic data. JJP and SCG collected the nest type data. DED analysed the data. All authors contributed to the writing of the manuscript and gave final approval for the publication.

## **Competing Interests**

We declare to have no competing interests.

## **Ethics Statement**

This article uses data that is historical in nature and therefore ethics is not required.

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## Supplementary Material

### ***Institutes and persons that contributed data***

Australian breeding bird occurrence records were collated from Atlas of Living Australia, Australia Bird and Bat Banding Scheme (ABBBS), Australian Museum, Australian National Wildlife Collection, BirdLife Australia's ATLAS and Nest Record Schemes, eBird, Global Biodiversity Information Facility, Museum and Art Gallery of the Northern Territory, Museum Victoria, Online Zoological Collections of Australian Museums, Queen Victoria Museum and Art Gallery, Queensland Museum, South Australian Museum, Tasmanian Museum and Art Gallery, and Western Australian Museum. Organizations and individual that contributed the ABBBS data are The Antarctic Division, The Bird Care And Conservation Society, The Broome Bird Observatory, Gippsland Lake Ornithological Group, The Gluepot Reserve Study Group, The Western Australian Rehabilitation Group, The Wild Bird Rehabilitation Group, R Aitken, SWW Alford, NP Ali, P Allan, TH Alley, G Ambrose, SJ Ambrose, NW Arnold, H Aston, CN Austin, GB Baker, DJ Baker-Gabb, H Bakker, KA Barker, DE Barnes, IM Bateman, H Battam, G Beal, C Beckmann, H Bell, GD Bell, C Bennett, CM Bishop, CA Bissell, EF Boehm, PF Bolger, AR Bougher, BFJ Bowen, GM Bowker, AN Boyle, JB Bradley, HA Bradley, HE Brenton, RJ Broad, L Broadhurst, MG Brooker, RJ Brown, AH Burbidge, TC Burton, CG Burt, BM Cale, GR Cam, A Cam, AC Cameron, RG Cameron, CB Champion, M Carins, RK Carruthers, BS Carter, NT Carter, BG Chaffey, GS Chapman, FRH Chapman, BJ Chudleigh, GP Clancy, GF Claridge, GS Clark, M Clayton, A Cockburn, SJ Comer, P Congreve, R Cooper, V Cooper, RE Corbould, DM Cornish, JE Courtney, ML Courtney, PP Coventry, RJ Cox, MM Crouther, JM Cullen, HS Curtis, MR Daley, P Dann, VD Davenport, PM Davidson, SJJF Davies, CPS De Rebeira, SJS Debus, J Dell, DGH Dent, PA Disher, HJ Disney, VA Doerr, DF Dorward, DD Dow, WMCK Dowling, HA Doyle, FW Doyle, PO Doyle, R Draffan, JN Dunlop, RJ Edge, NN Ellis, WB Emison, RC Evans, NJ Favaloro, PJ Fell, J Fennell, LWC Filewood, JH Fisher, KA Fisher, MR Fleming, TI Fletcher, L Fontanini, HA Ford, JR Ford, N Forde, JC Fordyce, B Foreman, PJ Foster, MT Fox, D Franklin, C Frith, DW Frith, HJ Frith, JL Gardner, JA Gates, DJ Geering, RM Gibbs, D Gibson, B Glover, AW Goldizen, RC Good, MD Gottsch, CN Gove, RJP Gower, I Grant, MR Grant, RH Green, K Green, D Green, R Gregory-Smith, MO Gunn, RE Gurney, TH

Guthrie, AM Gwynn, LC Haines, C Hall, ML Hall, JH Hall, RH Hardie, JL Hardy, JW Hardy, JGK Harris, CF Heathcote, RG Heinsohn, NL Hermes, AL Hertog, PJ Higgins, MP Hines, WB Hitchcock, CY Ho, JN Hobbs, CR Hodge, DM Hodges, AJ Hole, C Hollamby, JB Hood, I Hore-Lacy, GM Horey, W Horton, ES Hoskin, K Hough, TH Hughes, BR Hutchins, J Hyett, JC Ipsen, J Izzard, A J Leishman, P Jackson, BR Jahnke, A Jansen, PR Johnson, FE Jones, DN Jones, R Jordan, JO Karubian, K Keith, JW Kellam, BJ Kentish, RF Kenyon, J Kikkawa, J Klapste, WL Klau Oam, SM Kleindorfer, SG Lane, NE Langmore, AFC Lashmar, G Laybourne-Smith, S Legge, N Lenz, JE Lewis, AJ Ley, J Liddy, A Lill, E Lindgren, LC Llewellyn, TG Loffler, GJ Logan, NW Longmore, RG Lonnon, KW Lowe, HF Macarthur, D Macdonald, KJ Mack, DB Mack, DB Mack, WDF Mackenzie, RG Mackenzie, MJ Magrath, RD Magrath, WJ Maher, PN Maher, RE Major, EB Male, S Marchant, AJ Marsland, G Marston, RJ Martin, JS Martyn, WE Matheson, KL Maute, I Mccallum, PG Mcdonald, PDD Mcintosh, JL Mckean, JA Mcnamara, MV Melvin, PW Menkhorst, CW Meredith, ALA Middleton, WGD Middleton, PJ Milburn, GJ Millard, DR Milledge, CDT Minton, GJ Moors, B Morgan, AK Morris, OPP Mueller, RA Mulder, MT Murn, SA Murphy, D Murray, MD Murray, JL Nicholls, HJ Nicholson, LA Nielson, T Norostrom, AY Norris, L O'Connor, MP Park, GR Park, CJ Parmenter, VJ Pattemore, JD Patterson, DL Pepper-Edwards, TW Pescott, D Peters, AM Peters, M Pickett, FG Pinchen, D Pinner, T Poldmaa, JM Poole, DJA Portelli, KJ Pound, EK Pratt, JG Pridham, SG Pruett-Jones, SR Pryke, D Putland, GH Pyke, MK Rathburn, J Rawlins, HF Recher, AJ Reid, R Reid, DR Reid, PN Reilly, JW Reside, C Rich, DC Richards, DJ Ripper, D Robinson, VA Robinson, JL Rogan, JH Rooke, HM Ross, M Rowe, ICR Rowley, NW Schrader, DA Secomb, DL Serventy, TGD Shannon, RC Shearer, KG Simpson, PJ Slater, IJ Smales, DI Smedley, RJ Smith, JL Smith, KW Smith, GT Smith, CN Smithers, M Smyth, AK Smyth, PJ Spurge, AF Stewart, DA Stewart, A Stokes, RH Stranger, BRM Strong, PD Strong, H Sutherland, J Tagell, MK Tarburton, MRS Templeton, MT Templeton, T Templeton, RG Thoday, EB Thomas, DG Thomas, HF Thomas, GD Thomas, PJ Thomson, SC Tidemann, RA Tilt, A Tingay, WA Trudgen, LJ Turner, FWC Van Gessel, NW Vincent, WC Wakefield, E Wakefield, LE Wall, JE Walsh, RM Warneke, RWJ Warnock, MH Waterman Oam, DM Watson, I Watson, NF Weatherill, MS Webster, JA Welbergen, E Wheeler, JR Wheeler, A Whitehead, AC Williams, DJ Williams, L Willoughby, JT Willows, SJ Wilson, GB

Winning, JCZ Woinarski, KA Wood, VJ Wood, R Woodell, SJ Wooller, NR Wright, E Wyndham, and RA Zann.

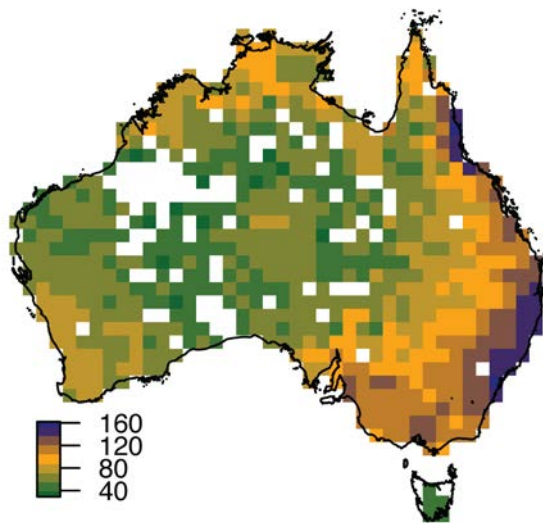
### ***Geographic Distributions***

Australian passerines were divided into two groups: sedentary ( $n = 292$ , taxa whose breeding range and year-round range are largely the same with only local dispersal by juveniles) and definitive ( $n = 18$ , taxa that have defined breeding ranges that differ from their year-round ranges) (Garnett et al., 2015). For sedentary species, we used all observations and for definitive species, we limited observations to those during breeding (e.g. nest, eggs, young, or defined as breeding). We increased the spatial accuracy of breeding ranges by removing observations that were farther than 200 km from BirdLife's species distribution polygons (BirdLife International and NatureServe, 2015) ( $n = 279$  species) and manually removing erroneous observations that were well outside of known ranges ( $n = 15$  species). To limit the duplication of observations at a given location, we reduced the spatial accuracy of records to 1 km, using Albers Equal Area Conic Projection, and kept only one observation of a species per 1 km x 1 km grid cell. This resulted in a total of 4,313,381 observations. The 310 passerine species were spread across 39 families, with the largest family, Meliphagidae (honeyeaters and chats), being represented by the most species ( $n = 73$  species). The number of occurrences per species ranged from 7 to 144533, with a mean of 14037 and median of 3174.

To assess the effect of spatial resolution on observed species richness (number of species with breeding observations in a grid cell), we compared observed and estimated species richness in grid cells of 50 km x 50 km and 100 km x 100 km (*sensu* Soberón et al., 2007). Species richness was estimated using a bias-corrected Chao estimation (Chao, 1987; Chiu et al., 2014) in R (R Core Team, 2016) using the package *vegan 2.3-4* (Oksanen et al., 2016). We compared species richness by calculating a Completeness Index (CI): the ratio of the observed species richness to the estimated species richness. The 50 km analysis performed poorly when assessing all passerine species, with 12.7% of grid cells having  $CI < 0.7$ , while at the 100 km resolution only 6.2% of grid cells had  $CI < 0.7$ . Thus, all assessments of geographic patterns in this study are carried out for 100 km x 100 km grid cells. We excluded grid cells from our



analysis when; (i) CI was less than 0.7, or (ii) there were fewer than ten species with cup-shaped nests and ten species with domed nests in a grid cell. After exclusions, a total of 713 grid cells were assessed. The number of grid cells occupied per species had a strong positive skew and ranged from 2 to 712 with a mean of 174 and median of 97. Species richness within 100 km x 100 km grid cells varied from 29 to 162 species, with a mean of 75 and a median of 69 (Fig. S1).



**Figure S1.** Variation in observed passerine species richness for breeding birds across the Australian continent. Observed species richness is for 100 km x 100 km grid cells. White grid cells either have less than ten species in domed or cup-shaped nests or do not meet the required Completeness Index (i.e. the ratio of the observed species richness to the estimated species richness).

#### ***Variation in egg elongation using a mixed-effect model***

Nest type explained 4% of the variation in egg elongation across all species ([F (2, 95.6) = 3.7,  $p < 0.05$ ]). Cavity-nesting species had significantly less elongated eggs ( $1.32 \pm 0.02$ ,  $n = 16$ ) than species that nest in cup-shaped and domed nests ( $1.37 \pm 0.02$ ,  $n = 191$ ;  $1.37 \pm 0.02$ ,  $n = 101$ , respectively). There was no significant difference between species nesting in cup-shaped and domed nests.

# Chapter 6

## General Discussion

In this thesis, I have investigated variation in breeding phenology and traits of Australian bird species and assessed how these are optimised across assemblages of species in relation to climatic and environmental variables. The results highlight the vast degree of variation in both phenology and traits between Australian avian species and across their assemblages. Much of this variation relates to the climatic conditions in which species breed, or are exposed to over the year. The work I present here is some of the first to examine patterns across suites of species sharing a biome, offering a novel comparative understanding of birds breeding and providing more general results.

The impact of climate change on the timing of reproduction has primarily been studied in highly seasonal locations, in particular, regions of the United Kingdom and North America (Crick *et al.* 1997; Crick & Sparks 1999; Dunn & Winkler 2010). This geographic bias stems from a long history of intensive phenological data collection. In the absence of this type of systematically collected observational data in other regions, creative solutions are urgently required to understand phenological patterns in relation to climate (Sparks 2007). In Chapter 2, I presented new methods for combining existing phenological observations of breeding from many different sources and assess bias, both spatial and temporal, caused by differences in collection methods. Importantly I found that phenological measures calculated for historical museum egg collections, observations of juvenile birds, and from nest records schemes agree remarkably well. This finding has wide-ranging implications for long-term population studies aimed at quantifying phenology, especially in regions of the world where systematically collected observational data are not available.

Seasonal breeding is present at all latitudes (Wyndham 1986; Sharp 1996; Stouffer, Johnson & Bierregaard 2013) and birds use climatic or environmental signals to cue and optimise breeding events (Lack 1950; Carey 2009). Changes in the timing of breeding in response to climate change are well documented in the Northern Hemisphere (*for example*, Crick *et al.* 1997, Crick and Sparks 1999, Dunn and Winkler

2010). In this region, most birds breed just once a year, and most variation is related to the onset of breeding, which may not reflect responses in other areas of the world where breeding seasonality is potentially different. In Australia, I found clear differences in the timing and length of egg-laying periods between biomes (Chapter 2). A likely driver is the distinct difference in climatic conditions in each biome and their effects on bird reproduction. In Chapter 3 I investigated how temperature and precipitation drive and constrain avian breeding in Australian biomes. The majority of species breed under distinct climatic conditions likely when food resources are most abundant, and the physiological stress from extreme temperature or rainfall is low. I further assessed effects of climate in Chapter 4, by determining avian breeding phenology during the three phases of El Niño Southern Oscillation (ENSO). La Niña events, which are characterised by mild/wet conditions, have a positive impact on avian breeding phenology in the Australian temperate and arid regions. In the temperate region, egg-laying dates during El Niño are not significantly different from those during the Neutral phase. This finding suggests that dry conditions which characterise El Niño, may not constrain breeding phenology more than typical winter/spring dry season conditions during Neutral phases, while the wet/mild conditions during La Niña provide an ideal opportunity to increase conservation measures and boost population levels.

In Chapter 5, I used a comparative approach to assess variation in functional traits in relation to climate. Measures of egg-shape and nest types for all Australian passerines were collated and combined with locations where each bird species breed to assess continental variation in these traits. In the sparsely vegetated interior of Australia, where conditions are hot and dry, the proportion of species with domed nests was greater, and average egg elongation was lower than that found across the rest of Australia. This variation in egg elongation and nest type in response to temperature, dryness, and shade from vegetation indicates how, at the landscape level, bird assemblages favour strategies for reducing climate stress. It is well known that the amount of water an egg loses during incubation is a combination of the water vapour pressure difference between the egg and its microclimate, egg size, incubation duration, and shell conductance (Walsberg 1980; Rahn & Paganelli 1988; Walsberg & Schmidt 1992; Whittow 1999; Deeming 2011). While birds do not actively control for water loss from eggs, they can influence water loss through nest site selection, nest type, nest

material, nesting behaviour and the timing of breeding (Deeming & Ferguson 1991; Ar & Sidis 2002; Mortola 2009). Further, it is likely that the shape of eggs further affects egg water loss and heat transfer. For instance, shell conductance and pore density vary across an egg, with the blunt end of eggs having greater values (Rokitka & Rahn 1987). Future research is needed to investigate whether there is a relationship between egg elongation, which is a trait readily available for many species, and key physiological variables. Knowing the physiological tolerance of these traits will enable an assessment of the sensitivity to extreme climatic events.

### ***Drivers of variation***

Australia is an ecologically and climatically diverse landmass with distinct bird species that have many life histories, breeding, and feeding strategies. These characteristics make it challenging to determining the exact drivers and constraints of opportunistic breeding. Opportunistic breeders respond to a variety of environmental factors (Cockrem 1995; Hahn & MacDougall-Shackleton 2008), and in regions with low seasonality of climate, using multiple factors can increase the ability of a species to breed successfully (Hau *et al.* 2004). These challenges are amplified by the year-to-year variation in avian breeding phenology caused by three phases of the ENSO. Large-scale climate oscillations influence year-to-year variation in avian breeding phenology (Forchhammer, Post & Stenseth 1998; Wilson & Arcese 2003; Gibbs 2007; Jaksic & Fariña 2010), breeding intensity (Vilina *et al.* 2002; Wilson & Arcese 2003; Gibbs 2007; Gibbs, Chambers & Bennett 2011) and migration phenology (*reviewed in* Gordo, 2007; Beaumont *et al.*, 2015). Australian birds are globally distinct in their opportunism and nomadism, with 30% of Australian desert birds displaying opportunistic breeding (Morton *et al.* 2011), and more than 50 species of waterbirds breeding irregularly in response to periodic flooding (Kingsford, Curtin & Porter 1999). Although Australian desert birds are distinct in their level of opportunism, they do have generalised breeding patterns, which the majority of species breeding in this region share. In Chapter 2, I found that desert breeding species laid eggs at significantly earlier dates than in other biomes. In Chapter 3 I found that in the arid regions (desert and grassland) 57- 84% of species breed when temperatures were cooler than average conditions, while 51-63% breed when rainfall 3-months before egg-laying was more than on average. These findings suggests that on

average breeding in the desert is constrained by temperature and stimulated by rainfall. In Chapter 4 I assessed changes in phenology due to variation in climate from ENSO phase. Species selected for assessment met a minimum requirement of at least 100 breeding observations in each of the three phases of ENSO. In the arid regions, the species with enough observations to meet the minimum requirement were all identified in Chapter 3 as breeding in response to lagged rainfall. This suggests that during El Niño events species that do not breed in response to lagged rainfall, are breeding at a very low rate, not breeding at all, or perhaps are more likely to move into a different area where conditions are better. It is worth noting that foregoing breeding during dry periods has been as reported by Morton *et al.* (2011) in the arid region and Williams & Middleton (2008) in the tropics.

In the results that I have presented in this thesis, some species have considerable variation in phenology or traits when compared to the averages values across all species. This variation is likely linked to species demography. It is well noted that variation in suites of traits is related to demographic differences (*reviewed in* Bennett & Owens 2002). For instance, clutch size has been linked to food availability (Lack 1968; Saether 1994; Sæther 1994). Further, it is well noted that climate influences changes in demography and recruitment of avian populations (Crick 2004; Sandvik, Coulson & Sæther 2008; McCauley *et al.* 2017; Brawn *et al.* 2017). In Chapter 3 I noted that in the tropical and subtropical biomes the vast majority of species ( $n = 46$  and  $n = 139$ , respectively) breed when rainfall is below average or average, but 15 species breed when conditions are significantly wetter than expected. The majority of these species (73%) feed on invertebrates for at least some of their diet (Garnett *et al.* 2015). In tropical regions invertebrates, which are a major source of protein for young birds, increase in abundance during the wet seasons (Poulin, Lefebvre & McNeil 1992; Williams & Middleton 2008). In Chapter 4 I point out that extreme opportunism of the New Holland honeyeater (*Phylidonyris novaehollandiae*, temperate region) and the Zebra Finch (*Taeniopygia guttata*, arid region), two of Australia's iconic opportunistic breeding birds, likely explains the long periods in which they can breed. In Chapter 5 I noted that cavity nesting species had significantly rounder eggs than species in domed or cupped nests. It would be useful for future studies to investigate further how variation in these traits related to temporal changes in demography and life history traits.

The effect of climate change on birds is determined by a species exposure to climate change drivers and its sensitivity (Williams *et al.* 2008; Garnett *et al.* 2013). Sensitivity is a species-specific trait or property that makes them more likely to be impacted by climate change. Based on the work of this thesis there are several traits that I believe will make species more susceptible to climate change and increased frequencies of extreme events. For instance, eggs from desert-breeding birds with open cup nests that are highly elongated may be more at risk of excessive water loss during extreme heat events than eggs in domed nests. In Passeriformes, nest form is largely phylogenetically conserved across taxa (Price & Griffith 2017), it seems unlikely that as species can make a significant shift in the form of their nest to reduce climate-related stress. Further, future changes in climate might amplify the effects of ENSO on species that primarily breed early in the year and experience substantial decreases in the length of the egg-laying period during El Niño and Neutral phases of ENSO when compared to the wet/mild La Niña phase. These species may have large changes in demography as the continent becomes hotter and dryer. Additionally, species that breed when either temperature or precipitation are very different from the average climatic conditions may lose their current breeding climate space in the future as the climate continues to change. The loss of climate space is especially worrying because in a recent assessment of Australian terrestrial birds it was found that 50% of species in tropical forests and temperate forests, grasslands, and savannahs have experienced a reduction in their suitable climate space over the last 60 years, resulting in range shifts (VanDerWal *et al.* 2013). Further, in an assessment of climate change impacts for terrestrial and inland waterbirds, it was found that 12.4% of species (n=122) are projected to be highly exposed to shifts in climate by 2085 (Garnett *et al.* 2013). As the impacts of climate change become stronger and extreme events more common, I anticipate that those species with the breeding phenologies and traits I have highlighted may be most likely to be impacted by climate change.

It is unlikely that a shift in phenology or a change in range due to climate change will affect most species so severely that they face immediate risk. Instead, most threats from climate change will be caused by detrimental changes in demography (Pearce-Higgins & Green 2014). My data used in Chapter 4 presents some evidence that changes in demography are likely if the Australian continent becomes drier. The

observation pool of breeding events during Neutral and El Niño phases was 36-40% less than during La Niña. This supports Gibbs *et al.* (2011) finding that breeding intensities were lower with low values of Southern Oscillation Index (low values indicate conditions are right for El Niño). Further, in Australian, substantial declines in species (42-62% depending on survey program) have been observed during severe droughts with about half the species having substantial increases in populations during a period of rainfall that followed the drought (Bennett *et al.*, 2014). These findings that it is likely that if drying across southern Australia continues (CSIRO & Bureau of Meteorology 2016) than demography will be affected in drastic ways that are not cyclic.

### ***Consequences for conservation***

Although much of the variation in species ranges and abundance arises from variation in climate and environments, human actions are the biggest threat to bird species and populations of birds. Human activities have destroyed native habitats and caused large-scale changes in the landscape across the Australian continent, putting numerous species at risk (Garnett *et al.* 2013). It has become apparent that reserve systems are not enough to maintain species under the threat of climate change, with declines in avian populations and low breeding success observed in reserves, woodland remnants, and cleared landscapes (Mac Nally *et al.*, 2009). The main anthropogenic threats to birds are from habitat loss, introduced predators, introduced species that compete for resources, and exploitation by humans. In Australia, the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) lists 22 species of birds as extinct, 16 species as critically endangered, 51 as endangered, and 66 as vulnerable. The species most at risk from climate change are habitat specialist, with low colonisations rates, who have already experienced the destruction of habitat and what remains is patchy. It is likely that these species are least likely to adapt and maintain critical population levels (Travis 2003). For most species, climate change will only enhance threats that already exist (Garnett *et al.* 2013).

In conclusion, this thesis demonstrates how phenology and functional traits are optimised across assemblages of species to deal with a range of climatic and environmental conditions. This variation may provide insight as to which species may be better suited to overcome the potential challenges faced under extreme weather events,

notably heatwaves and droughts. The methods and conceptual frameworks I present can be broadened into other areas of phenology to further investigate questions of avian life history. They can also be applied to regions of the world where ideal long-term datasets are not available. My findings are an exciting advance in understanding bird phenology and avian traits. They are highly relevant to predicting species response to climate change.

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## Appendix 1:

### Publication during candidature related to Ph.D.

*This Appendix is presented as the published journal article:*

Garnett ST, **Englert Duursma D**, Ehmke G, Guay PJ, Stewart A, Szabo JK, Weston MA, Bennett S, Crowley GM, Drynan D, Dutson G et al. (2015) Biological, ecological, conservation and legal information for all species and subspecies of Australian bird. *Scientific Data*, **2** 150061.

## Appendix 1 Vignette

During the first six months of my thesis, I spent the majority of my time collating species trait data and occurrence records. I assemble life history and functional trait data, for Australian bird species, using information available from books, such as the Handbooks of Australian New Zealand and Antarctic Birds (see Chapter 2 for more detail) and from other databases. In the process of collating data, I become aware of an extensive database that already existed and included information on biological, ecological, conservation and legal information for every species and subspecies of Australian bird. I was invited to contribute my data to the existing dataset, and as a co-author, I suggested publishing the data as a Nature Data Descriptor. The authors of this dataset had previously attempted to publish this in *Emu*, but the journal does not publish datasets. I played a significant role in getting these data published, by contributing not only several columns of data but also formatting and vetting the additional data. Due to this, I am an important co-author on the paper. Although I have included this Data Descriptor as an appendix, it is an important part of my thesis.

In the future, updates to the data will be published. These updates will include revisions and new columns of information as more data are collated, such as the nest types used in Chapter 5.

# SCIENTIFIC DATA

OPEN

## SUBJECT CATEGORIES

- » Conservation biology
- » Zoology
- » Biodiversity
- » Taxonomy

## Biological, ecological, conservation and legal information for all species and subspecies of Australian bird

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We introduce a dataset of biological, ecological, conservation and legal information for every species and subspecies of Australian bird, 2056 taxa or populations in total. Version 1 contains 230 fields grouped under the following headings: Taxonomy & nomenclature, Phylogeny, Australian population status, Conservation status, Legal status, Distribution, Morphology, Habitat, Food, Behaviour, Breeding, Mobility and Climate metrics. It is envisaged that the dataset will be updated periodically with new data for existing fields and the addition of new fields. The dataset has already had, and will continue to have applications in Australian and international ornithology, especially those that require standard information for a large number of taxa.

Design Type(s)	data integration objective • database creation objective
Measurement Type(s)	ornithology
Technology Type(s)	digital curation
Factor Type(s)	
Sample Characteristic(s)	Australia • <i>Struthio</i> • <i>Casuarius</i> • <i>Dromaius</i> • <i>Anseranas</i> • <i>Dendrocygna</i> • <i>Oxyura</i> • <i>Malacorhynchus</i> • <i>Cereopsis</i> • <i>Cygnus</i> • <i>Branta</i> • <i>Radjah</i> • <i>Tadorna</i> • <i>Aythya</i> • <i>Spatula</i> • <i>Mareca</i> • <i>Anas</i> • <i>Stictonetta</i> • <i>Biziura</i> • <i>Chenonetta</i> • <i>Nettapus</i> • ...

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### Background & Summary

Extensive datasets of faunal attributes play an important role in the analysis and understanding of biological systems and the conservation of biodiversity. For birds, they have been used, for example, to identify traits predictive of extinction risk<sup>1</sup>, to predict vulnerability to recent and impending climate change<sup>2,3</sup>, and to identify the correlates of invasion success<sup>4</sup>. Often these datasets are compiled *de novo* from primary sources for each application, leading to duplication of effort and repetition of the opportunity for error, as well as impeding replication of analyses.

To overcome these problems for Australian birds, we introduce a dataset (Data Citation 1) with associated metadata and reference list for free use by researchers and other interested persons. Ecological, biological and conservation information is provided for every species and subspecies recorded in Australia since European settlement, including vagrants and extinct taxa, with separate entries for Australian breeding and non-breeding populations of seabirds, taxa that have been officially but erroneously reported and introduced species that subsequently died out, 2,056 taxa or populations in total (Table 1). For the purpose of this database, Australia is defined to include the Australian mainland and continental islands, Australian territories (excluding the Australian Antarctic Territory) and the Australian Fishing Zone, which extends 200 nautical miles (370 km) off the coast of the above-named areas. Version 1 of the database contains 230 fields of data for each relevant taxon, grouped into 15 categories (Table 2). Of eight data types, the most frequent are binary, followed by numeric values and unranked categories other than binary (Table 3).

The Australian avifauna features high rates of endemism at species and higher taxonomic levels up to that of families, especially among the passerines. Over 60% of all terrestrial birds globally are passerines and Australia was the major early centre of their radiation<sup>5,6</sup>. Many Australian passerines are cooperative breeders such that the continent has a high incidence, and the highest proportional incidence, of

Taxon level	Core*	Extinct	Introduced	Vagrant	Total
species	725	12	27	151	915
subspecies	931	21	20	76	1048
population <sup>†</sup>	na <sup>‡</sup>	na	na	na	58
supplementary <sup>§</sup>	na	na	na	na	35
<b>Total row entries</b>	<b>1656</b>	<b>33</b>	<b>47</b>	<b>227</b>	<b>2056</b>

**Table 1.** Taxa presented in Australian Bird Data Version 1 (Data Citation 1). \*Core taxa are extant species and subspecies that occur regularly and naturally in Australia, i.e. that are not extinct, introduced or vagrant. <sup>†</sup>entries are provided separately for non-breeding (visiting) populations of seabirds where the species or subspecies also breeds in Australia. <sup>‡</sup>na = not applicable. <sup>§</sup>erroneous records and introduced taxa that have died out.

Field category (category no.)	No. of fields	Example field(s) (type of data)
Sequence (1)	2	Taxon sort (no.)
Taxonomy & nomenclature (2)	23	Genus name (name), Species (1/0/NA)*, Ultrataxon uniqueness (value)
Phylogeny (3)	3	Hackett coarse clade (category)
Australian population status (4)	12	Endemic (entirely in Australia) (1/0/NA), Endemic (breeding only) (1/0/NA)
Conservation status (5)	10	Global IUCN status 2015 (category)
Legal status (6)	16	EPBC status July 2015 (national, category), CAMBA (China Australia Migratory Bird Agreement, 1/not listed)
Distribution (7)	29	New South Wales (categories), Christmas Island (categories), Also in Papua New Guinea (categories)
Morphology (8)	19	Taxon average body mass (value), Brain volume (value)
Habitat (9)	48	Feeding habitat: Terrestrial: Arid shrubland (1/0/NA), Breeding habitat: Beaches and sand cays (1/0/NA)
Food (10)	11	Food: fruit (1/0/NAV/NA), Food: fish / invertebrates (marine) (1/0/NAV/NA)
Behaviour (11)	4	Mean flight initiation distance (value)
Breeding (12)	15	Nest location: Burrow (1/0/NA), Nest aggregation: Colonial (1/0/NAV/NA)
Mobility (13)	12	Nature of international movements (category), No. of banded birds recovered (value)
Climate metrics (14)	24	[climate change] Sensitivity index (value), Climate model factor - Annual mean temperature (%)
Administration (15)	2	BirdLife Australia Taxon ID (code)
<b>Total fields</b>	<b>230</b>	

**Table 2.** Categories of data fields provided in Australian Bird Data Version 1 (Data Citation 1). \*Binary fields with 'NA' = not applicable or not assessed; sometimes also with NAV = not available.



Field type	n fields	% of fields
Numeric value	62	27.0
Class value	2	0.9
Ranked category	21	9.1
Binary	97	42.2
Other unranked category	25	10.9
Name	11	4.8
Notes	8	3.5
Other*	4	1.7

**Table 3.** Types of data provided in 230 fields in Australian Bird Data Version 1 (Data Citation 1). \*taxonomic sequence numbers and administrative codes.

cooperative breeding species globally<sup>7</sup>. Australia was also likely to have been the major centre for early diversification of parrots<sup>6</sup> and remains rich in parrot and cockatoo species. Australian birds, therefore, have a role in global ornithology that is at once both unique and central.

We envisage that the dataset (Data Citation 1) will have a wide range of applications in Australian as well as international ornithology, with particular relevance to analyses which require standard information for a large number of taxa. It was initially developed in 1990 to support the first national assessment of the conservation status of all Australia's avian species and subspecies<sup>8</sup> and was then published as a 3.5 inch disk<sup>9</sup>. It was refined to support subsequent status assessments of extinction risk<sup>10,11</sup>, analyses of population trends in Australian birds<sup>12</sup> and analyses of the risk and potential management of climate change<sup>13,14</sup>. It was built concurrently with the *Handbook of Australian, New Zealand & Antarctic Birds* (HANZAB)<sup>15–21</sup> and subsequently cross-checked against it. Recent applications independent of its construction are as a source of standard body mass data for the calculation of relative brain size in 504 Australian bird species<sup>22</sup>, and an analysis of flight initiation (escape) distances of 250 species<sup>23</sup>.

We intend to provide progressive updates with expansion of its coverage. Management of the data, including oversight of taxonomy, format, eligibility and peer review of new columns, will be overseen by a committee answerable to the BirdLife Australia Research and Conservation Committee. The new version will specify any changes from previous versions. Co-authorship of future versions will be available to anyone contributing a full column of data with attribution of the data to original sources.

## Methods

Order names follow Jarvis *et al.*<sup>24</sup> and family and generic names follow Dickinson and Remsen<sup>25</sup> and Dickinson and Christidis<sup>26</sup>, thus following the most-recent synopsis of developments in the understanding of higher-level relationships among all bird taxa. To allow seamless international comparison of trends in conservation status, species definitions are those of BirdLife International<sup>27</sup> and BirdLife Australia, which are based on the use of 'divergence between undisputed sympatric species as a yardstick for assessing the taxonomic status of allopatric forms'<sup>28</sup>. Subspecies taxonomy and nomenclature largely follows HANZAB<sup>15–21</sup> unless this has been updated by recent research. Where this recent research includes genetic analyses, we adopt the 'precautionary view that, while genetic studies can detect differences between populations, some of which may not readily be apparent in the phenotype, a failure to detect variation may reflect incomplete sampling of the genome'<sup>11</sup>.

Data were variously sourced (copied), derived from or extracted from a wide variety of sources, or interpreted *de novo*, as documented for each field in the metadata (Data Citation 1, file 'Australian\_Bird\_Data\_Version\_1\_Metadata.csv'). In many cases, a primary source that provided data on core or common or breeding or native Australian taxa<sup>15–21</sup> was complemented with one or more secondary sources for taxa that are rare visitors, which do not breed in Australia, or have been introduced to it. Almost every field required some interpretation for a few taxa to align data from past with current taxonomies; this was mostly straightforward because most such changes involve elevation or reduction of geographically-discrete taxa between species and subspecies levels. However, many fields required greater levels of interpretation as discussed in the following paragraphs.

One issue is that source data were not necessarily systematic and so varied in quality between taxa. For example, source data on food types is variously quantitative, qualitative, or admixtures of these. In this case, data were converted to binary scores of 'non-trivial' usage for each of a number of categories of food type or feeding substrate. An analogous interpretative process of categorisation was used for many ecological fields such as feeding and breeding habitats. Where possible, such categories were sourced from external authorities, and in all cases are supported by detailed definitions in the metadata. For example, the at-times borderline distinction between *vagrant* and regular visitor to Australia was made with reference to the Convention on Migratory Species and the decisions of the BirdLife Australia's Rarities Committee, along with definitions to deal with cases such as when a small number of individuals arrived

together, bred but failed to establish a viable population. Feeding and Breeding habitats aggregate habitat types defined in a national classification system into 31 and 17 categories respectively judged relevant to birds. Notwithstanding, conversion of source data to these categories required considerable interpretation based on knowledge of habitats and Australian birds, and was undertaken by experienced senior ornithologists (mostly STG).

Body mass is a key biological attribute for which underlying source data are exceptionally disparate in quality and quantity and with varying levels of attribution to age, gender and subspecies. We have provided detailed source data (average, minimum, maximum) for males, females and unsexed birds, preferencing measurements for adults where this was available and documented, along with a field documenting our sources. These are used as a basis for calculation of three taxon summary fields (average, minimum, maximum) by methods documented in detail in our metadata (Data Citation 1, file 'Australian\_Bird\_Data\_Version\_1\_Metadata.csv').

Many sources provide data only for species, or only patchily for subspecies, so attribution of it to subspecies is problematic and limited. We have provided data for at least some, and often all subspecies in 142 (61.7%) of fields. It is provided for most fields relating to taxonomy, status and distribution. Among biological and ecological fields, subspecies data is more limited but includes some body mass, egg size and mobility fields, and all climate metric fields, the latter based on detailed mapping of subspecies undertaken in the course of that study<sup>14</sup>. An absence of data is coded as NA (not assessed) or NAV (not available). All data presented for subspecies explicitly relate to that subspecies (i.e. are not simply reiterated from the parent species).

A further and major source of interpretational challenge arises with ascribing usage as 'non-trivial'. This was essential in order to avoid attributions based on one-off or accidental records; for example, a seabird blown inland by storm winds cannot reasonably be considered to make use of the woodland habitat in which it finds itself. Preliminary test extractions by a second person demonstrated the often highly subjective nature of 'non-trivial', prompting revision of the metadata to further minimise it. 'Non-trivial' is defined for each data field in our metadata as more than 1% of quantitative records, and in anecdotal terms as (for example) including 'occasionally' but not 'very occasionally'.

Fields subject to high levels of interpretation based on 'non-trivial' usage and conversion of source data to defined categories are denoted in the *Source of data* field of the Metadata file with 'interpretation this database'. It is anticipated that most users will wish to use even the fields of greatest interpretational subjectivity as these interpretations have been made systematically by expert Australian ornithologists based on documented methods and referenced sources; indeed, the systematisation of such information across all Australian taxa is a key value of this database.

### Data Records

Data, metadata and references are presented in csv files, and as an alternative the three are combined as worksheets in an Excel file (all in Data Citation 1).

Data are presented in 'Australian\_Bird\_Data\_Version\_1.csv' as a row for each taxon and columns for data. Data headers start with a Column number for ready matching with the Metadata and conclude with a Category number (Table 2).

Metadata, with a row of information for each field in the data file, are provided in 'Australian\_Bird\_Data\_Version\_1\_Metadata.csv' under the following topic headings: Column number, Column header, Category number, Category, Definition, Taxa assessed, Field codes, Explanation of field factor codes, Source of data and Notes.

References are cited in the Data and Metadata files using the author-date system and listed in alphabetical order in 'Australian\_Bird\_Data\_Version\_1\_References.csv'.

The Excel file, 'Australian\_Bird\_Data\_Version\_1.xlsx', includes colour coding of some fields for ease of use but which do not provide additional information. It also includes formulae for calculation of taxonomic uniqueness and relative brain size which are not retained in csv files.

### Technical Validation

The database was extensively checked for structural anomalies such as inappropriate data types or field codes (all fields) and inconsistencies between related fields. We also conducted quality checks on a random sample of 100 taxa for each of seven groups of fields (Table 4). These took the form of extraction of data for these taxa from primary original sources blind to the current dataset and by a person different to the original extractor. Test extractions were compared to database entries and discrepancies attributed by a third person (the assessor, always DCF) to: a. database error; b. test error; or c. interpretational discrepancy. Because the original extractor frequently had access to additional sources of information (as documented in our Metadata), these assessments were then offered to the original extractor for comment, and some discrepancies attributed to a forth category, d. data from other sources, final decisions about which were always made by the assessor. We here report (Table 4) only finalised database errors and interpretational discrepancy rates.

Errors and interpretational discrepancies were confined to fields requiring moderate to high levels of interpretation and, in particular, decisions about triviality of use and attribution to categories where the source data did not employ categorisation or consistent categorisation across all taxa (Table 4). Some



Field category	Fields [description]	Nature of data	Level of interpretation	Test taxa	n fields checked	n species checked *	n cells checked	% error in database	% inter-pretational discrepancies	Source of interpretational discrepancies
Taxonomy & nomenclature	Species, Subspecies, Ultrataxon	binary	None	all	3	100	296	0	0	
Australian population status	Population description	16 categories	Moderate	species	1	100	100	0	0	
Australian population status	Core, Non-breeding population, Extinct, Introduced, Vagrant, Supplementary	binary	Slight	species	6	95	570	0	0	
Conservation status	Global IUCN status 2014	9 categories	None	species	1	99	99	0	0	
Distribution	[Occurrence on] Continental islands and Offshore islands only	binary/tertiary	Slight	all	3	95	285	0	0	
Habitat	[breeding habitats]	binary	Great	species	17	87	1479	1.1	2.1	misalignment of habitat categories between database and sources, and failure of source to discriminate between breeding and other habitat
Breeding	Nest aggregation: Solitary, Colonial, Parasitic	binary	Moderate	species	3	78	234	0.6	1.9	borderline cases between solitary and dispersed (loose) colonies

**Table 4.** Fields, data types, discrepancy rates and interpretational issues in quality check tests of Australian Bird Data Version 1 (Data Citation 1). \*this was often less than the 100 taxa randomly selected because the test extractor proved unable to identify suitable data from the key source.

discrepancies between database and test results also arose because the database reflected information additional to that in the key source.

#### Usage Notes

Issues with interpretation during data extraction are discussed above. In addition, an appreciation of the nature of systemic uncertainty is key to sound use of the data. Generically, uncertainties are either *epistemic* (associated with the state of our knowledge) or *linguistic* (associated with the terms and definitions employed)<sup>29</sup>. For example, body mass data reflect sampling issues including time-of-day, time-of-year, age, gender, regional variation and measurement error, all of which are epistemic uncertainties<sup>30</sup>. Similarly, flight-initiation distances may vary between areas with different prevailing exposure to human activity<sup>31</sup>. In contrast, the nature of habitat and food substrate categories is a *linguistic* problem both in definition and in imposing arbitrary boundaries on habitats that may intergrade.

Two taxonomic sorting fields are provided with subspecies in alphabetical order by scientific name. These follow alternate recent published representations of avian evolutionary relationships. The dataset may also readily be subsetted for any given analytical requirement using sort and filter options available in various database software packages. Filterable fields in the main database include, for example, Species, Core species, Extinct taxa, Vagrant taxa, Introduced taxa, Endemic taxa (either entirely or breeding only), and taxa occurring in particular sub-jurisdictions (states and territories) and territorial islands.

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### Data Citation

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### Author Contributions

S.T.G. led the project and was involved in all stages of data assembly, drafting of the manuscript and revision of the data set. D.E.D. assembled data on egg size and clade membership and participated in the quality check tests. G.E. assembled data related to threatened birds and climate impacts, reviewed assembled data, advised on nomenclatural and taxonomic changes and participated in the quality check tests. P.-J.G. assembled data on brain sizes and flight initiation distances. A.S. assembled data related to climate impacts. J.K.S. assembled data related to threatened birds, commented on the manuscript and reviewed assembled data. M.A.W. provided data on flight initiation distances and commented on the manuscript. S.B. assembled data related to threatened birds. G.M.C. assembled data related to threatened birds. D.D. provided all data on movements derived from the Australian Bird and Bat Banding Scheme. G.D. assembled data related to threatened birds. K.F. assembled data related to threatened birds. D.C.F. provided data on brain size, drafted the manuscript, reviewed assembled data, coordinated revision of the dataset and manuscript and participated in the quality check tests.

### Additional Information

**Competing financial interests:** The authors declare no competing financial interests.

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## Appendix 2

### List of publications during candidature unrelated to Ph.D.

Beaumont LJ, **Englert Duursma D** (2016) Impacts of Climate Change on the Distributions of Allergic Species. In: *Impacts of Climate Change on Allergens and Allergic Diseases* (ed Beggs PJ), pp. 29–49. Cambridge University Press.

Beaumont LJ, Graham E, **Englert Duursma D** et al. (2016) Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges? *Ecological Modelling*, **342**, 135–146.

Beaumont LJ, **Englert Duursma D**, Kemp DJ, Wilson PD, Evans JP (2017) Potential impacts of a future persistent El Niño or La Niña on three subspecies of Australian butterflies. *Biotropica*, **49**, 110–116.

Roger E, **Englert Duursma D**, Downey PO et al. (2015) A tool to assess potential for alien plant establishment and expansion under climate change. *Journal of Environmental Management*, **159**, 121–127.