

REVIEW

Shifting time: recent changes to the phenology of Australian species

Linda J. Beaumont^{1,*}, Teagan Hartenthaler¹, Marie R. Keatley², Lynda E. Chambers³

¹Department of Biological Sciences, Macquarie University, NSW 2109, Australia

²Department of Forest and Ecosystem Science, University of Melbourne, Creswick, Vic 3363, Australia

³Bureau of Meteorology, GPO Box 1289, Melbourne, Vic 3001, Australia

ABSTRACT: Phenology is the study of the timing of recurrent biological events and their biotic and abiotic drivers. There is considerable evidence, mostly from temperate regions of the Northern Hemisphere, of recent changes to phenological trends, likely to be in response to anthropogenic climate disruption. Here, we assess recent evidence of climate-related phenological shifts among Australian species, across environments ranging from alpine to semi-arid. While detailed knowledge of the phenology of many Australian species has a rich history among indigenous cultures, long-term recording of phenology has focused mostly on birds and plants, particularly agricultural crops, with few records for other taxa. Combined, datasets demonstrate that over recent decades there has been a strong trend towards advanced spring phenology associated with increases in temperature. However, precipitation also plays a key role in driving trends among numerous species, particularly where the onset of the phenophase is now occurring later in the season. In general, our understanding of changes to phenology is superficial: more complicated issues, such as identifying constraints to species responses, thermal sensitivity across life-cycle stages, non-climatic drivers of phenological trends, and disruptions to interacting species, remain poorly explored. Carefully designed studies, along with renewed interest in establishing observation networks supplemented with citizen science programs, can address some of these knowledge gaps.

KEY WORDS: Agriculture · Australia · Breeding · Citizen science · Climate change · Flowering · Migration · Phenology

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1. INTRODUCTION

Phenology is the term given to the study of the timing of recurrent biological events (such as flowering, migration and breeding of birds, emergence of insects) and their biotic and abiotic drivers (Leith 1974). Recent changes in phenological trends provide significant evidence of the 'fingerprint' of anthropogenic climate change on biota (Rosenzweig et al. 2008, Chambers et al. 2013, Poloczanska et al. 2013), with the signal apparent across diverse taxa (vertebrates, arthropods, plants, fungi and phytoplankton) and phenophases (migration, breeding, flowering,

fruiting and senescence), on all continents and in most oceans.

1.1. Australia: a unique continent

Australia is three-quarters of the size of Europe (7.7 million vs. 10.2 million km²), but with 97% fewer people (23 million vs. 739 million); it is the world's driest and flattest continent, contains the oldest soils, and has been isolated from other landmasses for ~55 million yr (Coleman 1980). Australia spans the latitudes 9–44° S and longitudes 112–154° E, and

*Corresponding author: linda.beaumont@mq.edu.au

contains a wide range of climate zones: arid and semi-arid ecosystems characterise two-thirds of the continent, while also present are tropical, subtropical, temperate and alpine regions (though alpine regions cover <1% of the landmass).

Australia's climate is heavily influenced by the El Niño–Southern Oscillation (ENSO), as well as being affected by monsoons in the north and polar influences to the south (for a more complete description of climate influences on Australia see www.bom.gov.au/climate/about/). This results in a highly variable climate. While some regions may experience relatively reliable seasonal rainfall and temperature, in other areas rainfall is less predictable, both in terms of frequency and quantity. The unique characteristics of Australia have resulted in the evolution of an amazing diversity of endemic species, including 94% of amphibians, 93% of reptiles, 87% of mammals and 93% of flowering plants (Chapman 2009).

In line with global trends, Australia's climate has changed over the last century. Annual mean temperature has increased 0.94°C (1911–2010) (Fawcett et al. 2012), with subtropical inland regions warming at a faster rate than elsewhere. Significant drying has occurred across southern Australia since the 1960s, particularly in the south-west (Hope et al. 2010), where change is likely due to a combination of natural variability, anthropogenic climate change and land-use change (Timbal et al. 2006). In contrast, rainfall has increased in north-west Australia (Jones et al. 2009). Associated with these climate disruptions are recent shifts in species distributions, physiology and morphology, as well as life-cycle timing (e.g. see Umina et al. 2005, Gardner et al. 2009, Chambers et al. 2014b, Cabrelli et al. 2015).

Here, we provide a brief history of phenological studies in Australia, and discuss recent phenological trends, and their drivers, across Australian terrestrial and marine systems, reported since the year 2000 (Table 1). To identify the latter, we searched Web of Science for publications from the year 2000 onwards that contained the search words 'climate' and 'Australia' and 'phenology' (or 'migration', 'breeding', 'flowering', 'maturity', 'horticulture'). We read the abstract of each paper matching these search criteria to identify studies that assessed phenological trends of Australian species for a time period exceeding 10 yr. We focused on events that have a predictable cycle, rather than 'boom or bust' events driven by spatial and temporal variability in precipitation. Finally, we scanned the reference list of each paper to identify additional studies that the Web of Science may not have indexed.

1.2. History of phenological studies in Australia

A detailed knowledge of the phenology of many Australian species has existed for countless centuries, interwoven with the indigenous culture of the land and passed from generation to generation via oral pathways and traditional practices. Some of this knowledge has been captured in the form of seasonal calendars (Rose 2005, Prober et al. 2011, Keatley et al. 2013), a variety of which can be accessed through www.bom.gov.au/iwk.

The European history of phenological recording in Australia is much more recent. Although it is difficult to confirm precisely when systematic phenological monitoring commenced, it is unlikely to have occurred prior to 1856, when the Royal Society of Tasmania began recording the leafing, flowering and fruiting dates of a number of standard plants in the Hobart Botanic Gardens (Chambers & Keatley 2010, Keatley et al. 2013). Unfortunately, these observations ceased in 1885. Since then numerous phenological programs have come and gone, with some of the longer running ones being: flowering dates of west Australian orchids (1928–1949; Erickson 1950), bird arrival dates in Western Australia (1934–1949; Sedgwick 1947, 1949, 1950) and eucalypt flowering dates in Victoria and South Australia (Boomsma 1972, Keatley et al. 2002). However, several long-term phenological studies are still ongoing, and include records for managed systems such as horticultural species (e.g. those used by Webb et al. 2012, Darbyshire et al. 2013), for birds (e.g. Birdlife International nest record scheme www.birdlife.org.au/projects/atlas-and-birddata/nest-record-scheme) and the arrival of migratory animals and flowering of plants in alpine regions (Green 2010).

As with other regions of the world, the most common type of phenological data in Australia are those recording the flowering of plants or migration of birds (see Table 1). There are also high-quality datasets on wine-grapes (Petrie & Sadras 2008, Webb et al. 2011, 2012). Less common are datasets for other vertebrates (particularly terrestrial mammals) and invertebrates, including butterflies (Table 1).

2. PHENOLOGY

2.1. Plant phenology

To date, the earliest substantive phenological records located in Australia are for crops (Chambers & Keatley 2010, Keatley et al. 2013): indeed, one of the

Table 1. Recent phenological studies of Australian terrestrial and marine organisms. Few studies have data for every year; thus, we have given the number of years the dataset spanned. dd^{-1} : days decade⁻¹; ACT: Australian Capital Territory; Mult: multiple taxa; other abbreviations, see Fig. 1 legend

Taxa	State	N species	Phenophase	Pattern	Dataset span (yr)	Reference
Plant						
Mult	NSW, Vic, ACT	20	Flowering	Generally, earlier flowering during warmer years	57	Gallagher et al. (2009)
Mult	NSW	2	Flowering	Earlier flowering, associated with snow melt	30	Green (2010)
Mult	Vic	101	Flowering	Eight species showed advances in flowering, associated with warming	87–153	Rumpff et al. (2010)
Mult	Vic	65	Flowering	Five species flowering significantly earlier, 3 significantly later	24	Keatley & Hudson (2012)
Pear	SA	1	Flowering	Advance of 7 d per 1°C increase in minimum temperature	44	MacGillivray (2013)
Orchid	SA	3	Flowering	Advance of 3.5 d per 1°C warming; 2.2 d per 100 mm rainfall	110	MacGillivray (2013)
Eucalypt	Vic	5	Flowering	1°C warming related to earlier flowering (~14 d) for 2 species and delayed flowering (11–15 d) for 3 species	36–39	Rawal et al. (2014)
Grass	Vic		Daily pollen count	Atmospheric pollen counts highly correlated with rainfall	17	de Morton et al. (2011)
Horticulture						
Grapes	SA	3 varieties	Maturity and harvest	Earlier maturity (5–31 dd^{-1}), associated with temperature		Petrie & Sadras (2008)
Grapes	Vic, SA, WA	Multiple varieties	Maturity and harvest	Advance of ~8 dd^{-1} , associated mostly with higher temperatures	17–115	Webb et al. (2011)
Grapes	Vic, SA	8 varieties	Maturity and harvest	Advance of 0.6–15.7 dd^{-1} , associated with warming, declines in soil moisture and changes in management practices	65	Webb et al. (2012)
Cherries	Vic	1	Arrival to markets	Earlier arrival to markets	173	M. R. Keatley (unpubl.)
Pome	Vic, SA	8 varieties	Green tip and full bloom	Significant advance for green tip, but not full bloom, expected advances of 4.1–7.7 dd^{-1} with 1°C warming	24–43	Darbyshire et al. (2013)
Bird						
Lapwing	Continental	1	Breeding	Variable across regions; earlier breeding associated with rainfall in central Australia and minimum temperature in Tasmania	21–44	Chambers et al. (2008a)
Honeyeater	Vic	1	Breeding	Earlier laying over time, associated with reduced rainfall and mild warming	17	Chambers et al. (2008b)
Penguin	Vic	1	Breeding (egg laying)	Laying date advances 17.6 d per 1°C increase in March sea-surface temperature	40	Cullen et al. (2009), Dann & Chambers (2013)
Seabirds	WA	3	Breeding	Delayed breeding over time, associated with more frequent El Niño events and higher sea-surface temperature	20	Surman & Nicholson (2009), Surman et al. (2012)
Mult	Continental	16	Breeding	General trend of earlier breeding in SE and delayed breeding in SW, strongly influenced by rainfall	>30	Gibbs et al. (2011)
Penguin	WA	1	Breeding (laying date)	Stronger current, warmer sea-surface temperature extends egg-laying period	20	Cannell et al. (2012)

(Table continues on next page)

Table 1. (continued)

Taxa	State	N species	Phenophase	Pattern	Dataset span (yr)	Reference
Seabirds	WA	2	Breeding (egg laying)	Opposite patterns between the 2 species: for one breeding occurs earlier under La Niña conditions while for the other it is delayed	26	Dunlop & Surman (2012)
Seabirds	Continental	6	Breeding	General trend of delayed breeding	14–43	Chambers et al. (2014b)
Cockatoo	WA	1	Breeding	Timing of egg laying tightly coupled with autumn rainfall; earlier during periods of high rainfall	42	Saunders et al. (2013)
Mult	Vic	1	Moult	Moult date advances 7.4 d per 1°C increase in October sea-surface temperature	43	Chambers et al. (2014b)
Mult	WA	8	Migration	General trend towards earlier arrival	20	Chambers et al. (2005)
Mult	NSW, Vic, SA	24	Migration	General trend of earlier arrival (3.5 dd ⁻¹), delayed departure (5.1 dd ⁻¹). Increased length of breeding season	17–45	Beaumont et al. (2006)
Mult	WA	20	Migration, length of season	Advances in spring arrival, delays in autumn or winter arrival. Trends influenced mostly by precipitation, less so by temperature	27	Chambers (2008)
Mult	Vic	22	Migration, peak abundance	Shifts among 7 species; 68% of movements associated with climate	21	Chambers (2010)
Mult	Vic, Tas	7	Migration, breeding	Variable trends across species; timing associated with local daily maximum or minimum temperature	14–47	Chambers & Keatley (2010)
Passerine	NSW	2	Migration	Earlier arrival, associated with snow melt or temperature	30	Green (2010)
Mult	NSW	16	Migration	Earlier arrival of 4.4 dd ⁻¹ , relationship with minimum temperature	31	Smith & Smith (2012)
Mult	Continental	52	Migration	Variable across regions; general advance in spring arrival dates; greater advances in arrival and departure in SE; many species strongly influenced by rainfall	14–38	Chambers et al. (2014b)
Mammal						
Sea lion	SA	1	Breeding	Longer interval between breeding seasons may be linked to warmer oceans	22	Goldsworthy et al. (2009)
Reptile						
Lizard	SA	1	Breeding (pairing)	~8 wk advance, associated with warmer, drier winters	15	Bull & Burzacott (2002)
Lizard	ACT	1	Breeding (timing of ovipositioning)	Advance in timing of ovipositioning and decrease in incubation length, associated with warming	10	Telemeco et al. (2009)
Lizard	Tas	1	Breeding (date of birth)	Higher local temperature advances offspring date of birth	9	Cadby et al. (2010)
Insect						
Moth	NSW	1	Migration	Delayed arrival to alpine sites	30	Green (2010)
Butterfly	Continental	20	Emergence	Contrasting patterns in emergence (6 significantly earlier, 6 significantly later)	~60	McClellan (2011)
Butterfly	Vic	1	Emergence	Emergence date advanced 1.5 dd ⁻¹ due to higher temperature	65	Kearney et al. (2010)

few data series encompassing early records (from 1895) to the present is for wine-grapes (Webb et al. 2011). That these data exist for crops is unsurprising given their economic value and that phenology has a significant influence in determining the adaptation of a crop to its environment (Mitchell et al. 1996, Sadras & Monzon 2006).

Early records (e.g. finishing prior to 1990) are particularly valuable as they provide baseline data against which current phenological behaviour can be compared, and enable climatic drivers to be identified. For instance, Chambers & Keatley (2010) analysed data on flowering, fruiting and leafing phenology of 49 (mostly horticultural) species, recorded in Tasmania from 1864 to 1885. The authors found that 53% of species had at least 1 phenophase that appeared to be driven by rainfall and/or minimum temperature. Unfortunately, poor instrument siting, which occurred prior to 1880, meant that the maximum temperature record could not be examined.

Temperature has also been identified as a major influence in the timing of flowering in eucalypts (Rawal et al. 2014), although variation between species and locations may be substantial (House 1997). An examination of early Victorian Forest Commission records (1940–1970) found flowering to be related to temperature to a greater extent than rainfall, although the direction of influence (positive or negative) depended on the particular species (Keatley et al. 2002, Hudson et al. 2011). Monthly surveys from 1982 to 1992 of 20 *Eucalypt* species at sites on the east coast of Australia found relationships between high autumn (March–May) rainfall and prolific flowering in late spring, while low temperatures triggered flowering among 9 species (Law et al. 2000). In contrast, Rawal et al. (2014) found that for every 1°C increase in mean temperature, flowering of 2 dry sclerophyll *Eucalypt* species advanced 14.1–14.9 d, whereas it was delayed by 8.7–14.1 d for 2 wet sclerophyll *Eucalypt* species. Although not assessed, delayed flowering may be a response to chilling requirements and photoperiod length (Rawal et al. 2014). Thus, in response to 21st century climate change, flowering in *Eucalypt* species is expected to be individualistic, and general patterns may be difficult to predict (Law et al. 2000, Keatley et al. 2002).

A recent meta-analysis of Australian datasets demonstrated that plant phenology has advanced an average of 9.7 d decade⁻¹ (n = 390; 95% credible interval of 7.3–12.1 d decade⁻¹) (based on datasets published in Chambers et al. 2013) (Table 1, Fig. 1). Given the limited number of known long-term data-

sets, records mostly from lateral sources were used to assess these trends. For instance, Gallagher et al. (2009) analysed herbarium specimens collected between 1950 and 2007, and found that *Senecio pectinatus* had significantly advanced its first flowering date (6.9 d decade⁻¹). In contrast, although flowering dates of the herbs *Colobanthus affinis*, *Ewartia nubigena*, *Prasophyllum tadgellianum* and *Wahlenbergia ceracea* were associated with mean annual temperature, the timing of this phenophase did not change significantly (Gallagher et al. 2009). Supplementing herbarium records with his own and those of another researcher, Green (2010) found the flowering of 2 alpine herbs, *Psychrophila introloba* and *Chionogenias muelleriana*, to be correlated with the date of snow melt, which advanced significantly over the period 1954–2008 (2.8 d decade⁻¹). Similarly, in South Australia, peak flowering of the donkey orchid *Diuris orientis* shifted 1.67 d decade⁻¹ earlier from 1897 to 2005 (MacGillivray et al. 2010). The timing of first flowering of 4 species growing along the Victorian coastline (*Atriplex paludosa*, *Dendrophthoe vittellina*, *Lepidium foliosum* and *Logania ovate*) also advanced significantly, averaging 8.6 d decade⁻¹ from the mid-19th to the late 20th century (Rumpff et al. 2010) (Fig. 1). It was also noted that species flowering in spring or summer may be more sensitive to temperature changes compared with those flowering in winter (Rumpff et al. 2010).

Using 2 methods to examine a naturalist's records of flowering among 65 species in Victoria, Keatley & Hudson (2012) determined that first flowering had significantly advanced in 5 species (range: 6.4–32.6 d decade⁻¹, 1983–2006) and was delayed in 3 (range: 8.4–28.8 d decade⁻¹). For each species, the timing of flowering was associated with climate (temperature, rainfall, or a combination of both), with the phenological shifts primarily occurring between 1987 and 1998 (Keatley & Hudson 2012).

Whereas phenological phases are commonly estimated via visual observations, for grapes a biophysical measure based on sugar concentrations is used, enabling cross-site comparisons and attribution analyses of trends to be undertaken (Webb et al. 2012). Maturity and harvest of grapes demonstrate some of the strongest phenological advances across Australian taxa. For instance, among the major wine-growing regions in Victoria, South Australia and Western Australia, the date of designated maturity has advanced 0.6–31 d decade⁻¹ (5–31 d decade⁻¹, Petrie & Sadras (2008); 0.6–15.7 d decade⁻¹, Webb et al. (2012); Table 1). Webb et al. (2012) calculated that across these regions, advances of 4–11 d were attrib-

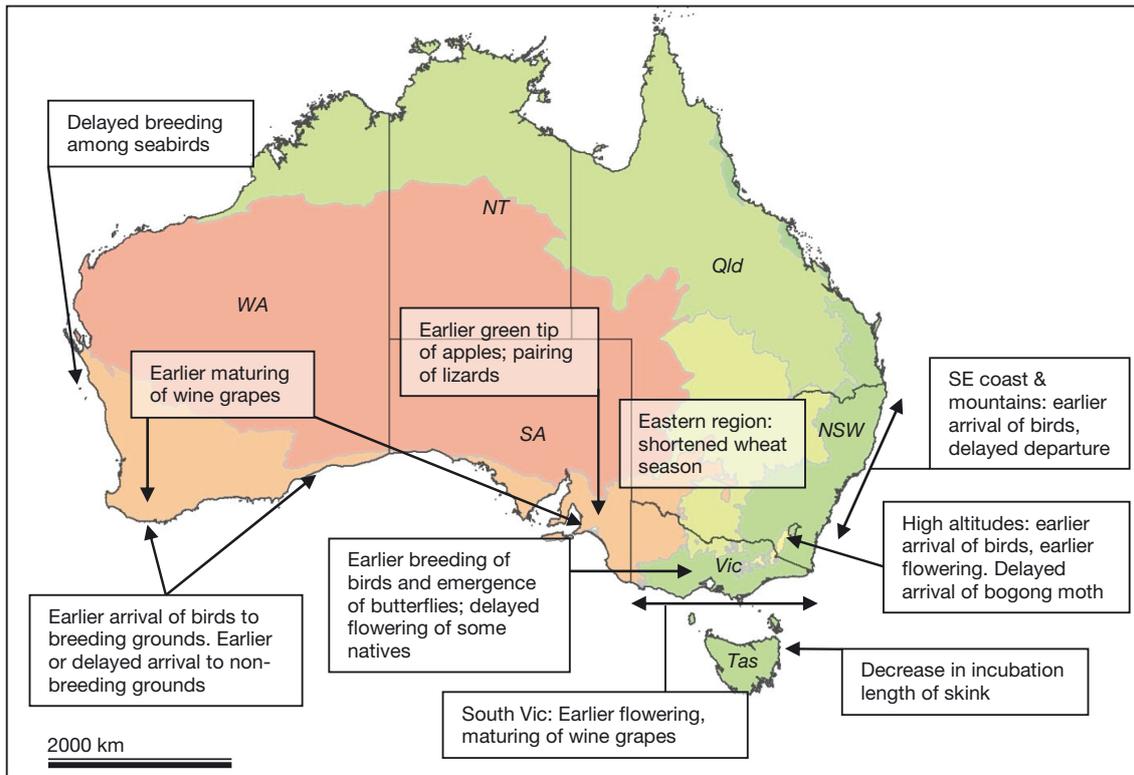


Fig. 1. Examples of recent changes in phenological trends in Australia. Although datasets are variable in length (spanning 9 to 153 years) most assess trends across 2 or more decades from the mid/late 20th century onwards. WA: Western Australia; SA: South Australia; Tas: Tasmania; Vic: Victoria; NSW: New South Wales; Qld: Queensland; NT: Northern Territory. Colours represent boundaries of different biomes. Data sources: WA (Webb et al. 2012, Chambers et al. 2014a, b); SA (Bull & Burzacott 2002, Webb et al. 2012, Darbyshire et al. 2013); Vic (Keatley & Hudson 2007, Webb et al. 2012, Chambers et al. 2014a); Tas (Telemeco et al. 2009); NSW (Beaumont et al. 2006, Sadras & Monzon 2006, Gallagher et al. 2009, Green 2010, Chambers et al. 2014a)

uted to warming, and 1–10 d to a trend in lower soil moisture. They noted, however, that reductions in crop yield, potentially due to management decisions and drought, may have also influenced maturity dates (Webb et al. 2012).

As climate change progresses, warmer temperatures are projected to have dual impacts on winegrapes. Firstly, under scenarios for 2030 and 2050, the timing of maturity of Chardonnay and Cabernet Sauvignon across 6 wine-growing regions of Australia is projected to advance, and season length (from budburst to harvest) to decrease (Webb et al. 2007). Secondly, under a mid-range scenario for 2050, harvesting is projected to occur at temperatures 2.2–3.9°C warmer than in 1990, which may alter fruit composition and decrease wine quality (Webb et al. 2007).

Phenological shifts of apple and pear varieties in the Southern Hemisphere (Australia and South Africa) appear to be of smaller magnitude than similar varieties in the Northern Hemisphere, although

comparison of datasets is difficult (Darbyshire et al. 2013). While 6 of 8 datasets of apple and pear varieties from southeast Australia demonstrated advances, this was significant for only one. Green tip (i.e. when green leaf tissue first emerges from the bud tip) in Jonathan apple advanced 2.5 d decade⁻¹ over the period 1963–2009 (Darbyshire et al. 2013).

Agriculture constitutes a significant driver of the Australian economy, with wheat being the single most valuable crop (gross value of \$6.8 billion from 2011 to 2012) (ABS 2013). For the period 1957–2000, phenological models of wheat growth in eastern Australia indicate that for each 1°C increase in temperature the time between sowing and flowering declined 7.5 d, although the decline from sowing to maturing was less at 6.9 d (Sadras & Monzon 2006). This is likely to be because contraction of the pre-flowering phase, a response to a constant increase in temperature, results in post-flowering development taking place during earlier (relatively cooler) conditions, thus leading to an extension of this phase.

2.2. Bird phenology

The timing of key components of avian life-cycles, such as migration, breeding and moult, are generally optimised to coincide with suitable environmental conditions and peak resource availability. In the Northern Hemisphere temperate and high-latitude zones, which currently dominate our understanding of long-term phenological responses of avian species to environmental change, recent temperature increases have been linked to earlier arrivals at breeding grounds and advances in egg laying (e.g. Gordo et al. 2007, Carey 2009).

Although comparatively fewer studies have been conducted in the Southern Hemisphere, phenological research undertaken on Australian birds has also provided evidence that climate change has affected a variety of species (Chambers et al. 2005, 2011; also see Table 1). In particular, warmer temperatures have been linked to earlier spring migration (Beaumont et al. 2006, Chambers et al. 2013, Keatley et al. 2013), particularly in the temperate zone of south-east Australia. For instance, increasing minimum temperatures were associated with earlier arrival of birds by an average of 3.5 d decade⁻¹ since the 1960s, and a delayed departure of approximately 5.1 d decade⁻¹ at numerous locations in south-east Australia (Beaumont et al. 2006). Similarly, shifts in the timing of seasonal arrival and peak abundance of birds in Melbourne were most significantly correlated with minimum temperature (Chambers 2010), while arrival at the Blue Mountains, west of Sydney, has advanced by 4.4 d decade⁻¹, coinciding with increases in temperature along the migration route (Smith & Smith 2012).

The timing of breeding among Australian birds has also been related to temperature, in particular gradients in altitude and latitude, with breeding generally delayed at higher altitudes and further south (Gibbs et al. 2011). No consistent link, however, has been found between the timing of breeding and broad-scale climate indices, such as the Southern Oscillation Index.

Although the results above are consistent with trends found in the Northern Hemisphere, where rising temperatures have led to earlier spring arrival and breeding of birds (Gordo 2007, Carey 2009, Lehikoinen & Sparks 2010), a recent review of Australian bird migration phenology highlights significant species and geographical differences in responses (Chambers et al. 2014a). At least some of this is likely to be driven by species responding to non-temperature-related changes in the climate system. For instance, there is evidence that the interplay of rainfall

with temperature has varied effects on bird phenologies (Chambers 2008, Chambers et al. 2008b, 2013, 2014a, Saunders et al. 2013). For example, a reduction in rainfall and mild warming was linked to earlier breeding, and a possible reduction in the number of eggs laid, by the helmeted honeyeater *Lichenostomus melanops cassidix* in south-eastern Australia (Chambers et al. 2008b). This is significant as the species is critically endangered and if laying continues to advance under a warmer, drier climate, the number of eggs laid in a season may decline and asynchrony with peak food supplies may occur (Chambers et al. 2008b).

A strong reliance on rainfall as a cue for seasonal movements and breeding was also seen in another endangered species on the opposite side of the continent, Carnaby's cockatoo *Calyptorhynchus latirostris* (Saunders et al. 2013). Furthermore, in the south-west there is a strong correlation between the timing of migration and rainfall, where spring species arrived earlier, while autumn and winter species arrived later (Chambers et al. 2014a). Gibbs et al. (2011) also discovered a significant trend of greater breeding activity with higher rainfall among 16 widespread species. Both Gibbs et al. (2011) and Chambers (2008) found precipitation to have a stronger influence than temperature on species responses.

Regional and between-species differences in responses to changes in local climate variables were also noted by Chambers et al. (2014a). Based on a meta-analysis of 145 datasets for 52 bird species at 10 locations, the authors concluded that climatic conditions during the season of movement were key to determining likely migration timing, and that species with 'strong advances (delays) in phenology are more likely to respond to decreased (increased) rainfall, number of rain days and maximum temperature and increased (decreased) minimum temperature'. This result highlights the difficulties in managing for future changes to Australian (terrestrial and freshwater) bird phenology given current uncertainties in the magnitude and direction of future precipitation patterns over much of Australia (CSIRO BoM 2007, Chambers et al. 2014a).

Global spring and summer phenological responses to climate change among marine species have advanced at the rate of 4.4 ± 1.1 d decade⁻¹, with the response varying by taxonomic and functional groups (Poloczanska et al. 2013). Phenological studies extending into Australia's marine environment are less common than for terrestrial species (Table 1), partially due to the difficulties associated with obtaining data (Chambers et al. 2011, 2013, 2014b, Poloczanska et al. 2013). The general trend for Australian seabirds is

delayed breeding over time (Chambers et al. 2014b). Of 21 datasets covering breeding among 6 species at 8 locations, 10 showed significant delays while only 1 significantly advanced timing of breeding. Most of the species with delayed phenology were Laridae (gulls, noddies, terns) in Western Australia (also see Surman & Nicholson 2009, Dunlop & Surman 2012, Surman et al. 2012). The impact of ENSO on marine resources has been implicated in these delays and an associated reduction in seabird reproductive performance, though other factors may also play a role (Surman & Nicholson 2009, Chambers et al. 2011).

Although there is less evidence of long-term phenological trends in little penguins (*Eudyptula minor*) throughout its distribution (including south-western and south-eastern Australia), the timing of breeding in this species is influenced by variability in oceanographic conditions (Cullen et al. 2009, Cannell et al. 2012, Dann & Chambers 2013). In general, higher ocean temperatures prior to the breeding season lead to earlier laying, resulting in greater breeding productivity, heavier chicks and an increased chance of multiple breeding attempts in a season (Cullen et al. 2009, Cannell et al. 2012). In contrast, some species, such as the wedge-tailed shearwater *Ardenna pacifica*, a long-distance migrant, have highly synchronous breeding and show little inter-annual variation in the timing of breeding (Surman et al. 2012). These species are unlikely to respond to climate-induced changes in marine resources through phenological change. For many seabirds, however, resource availability may influence breeding substantially. For example, if ocean productivity prior to breeding is low, birds may delay their laying date (Cullen et al. 2009, Chambers et al. 2011, Surman et al. 2012). These examples highlight the complexity of anticipating climate-induced phenological shifts, as the interaction between species, such as predator–prey relationships, may influence the magnitude and direction of phenological responses (Chambers et al. 2011).

Among Australian birds, moult phenology in relation to long-term trends and climate influences has been poorly studied. In species such as the little penguin, the moult period is very pronounced and allows for easy observation. As was the case for breeding, moult in this species tended to occur earlier when ocean temperatures prior to this period were higher, possibly indicating more abundant prey resources during the pre-moult fattening period (Chambers et al. 2014b). Moult in this species is more synchronous than breeding, suggesting that environmental constraints may be stronger for moult (Chambers et al. 2014b).

2.3. Mammal phenology

Despite Australia's many unique mammal species, including a high proportion of marsupials, and being a hot spot for marine mammals, few studies have specifically assessed phenological trends among this group. One notable exception is for the Pinnipedia (marine mammals). Environmental variability affects the timing, duration and success of breeding in Australian sea lions (*Neophoca cinerea*) and Australian fur seals (*Arctocephalus pusillus doriferus*) in south-eastern Australia (Gibbens & Arnould 2009, Goldsworthy et al. 2009), with earlier birthing dates corresponding to a greater number of pups being born.

In contrast to the Pinnipedia, the breeding season for the terrestrial marsupial genus *Antechinus* is controlled by photoperiod, with species having only 1 very brief (1–2 wk) breeding season each year (Naylor et al. 2008). Breeding is highly synchronised within populations and between cohorts, and is suggested to be timed to coincide lactation and weaning with insect abundance (Naylor et al. 2008). As with the wedge-tailed shearwater, as climate change progresses, lack of flexibility in the timing of breeding may lead to an uncoupling of *Antechinus* breeding with the abundance of insect food.

Similar mismatches between predators and their prey may also occur in Australia's alpine zone (Table 1). Here, the arrival of the altitudinal migrant, Richard's pipit (*Anthus novaeseelandiae*), the end of hibernation of the critically endangered mountain pygmy possum (*Burramys parvus*), and the timing of the dusky antechinus' (*Antechinus swainsonii*) single, short breeding season all require a readily available food source: the migratory Bogong moth (*Agrotis infusa*) (Green 2010). However, over recent decades arrival of the moth has been delayed, while the timing of snow melt across the Snowy Mountains has advanced, and it is expected that the mismatch will have a negative impact on these insectivorous vertebrates (Green 2010).

2.4. Reptile and amphibian phenology

As ectotherms, reptiles and amphibians are dependent on environmental heat sources to regulate their body temperature, with environmental temperature affecting activity patterns, fecundity and survival rates (Adolph & Porter 1993). Globally, climate-related shifts in species range margins and local extinctions have been reported for lizards (Sinervo et al. 2010) and amphibians (Blaustein et al. 2010), with am-

phibians also demonstrating the greatest rate of phenological change reported to date (Parmesan 2007).

In Australia, lizards have altered their reproductive behaviour and nesting phenology in response to climate variation and change (Table 1). Monogamous pairing of sleepy lizards (*Tiliqua rugosa*) generally occurs 8 wk prior to mating, and observations over the period 1983–1997 found that pair forming occurred earlier and lasted longer during later years (Bull & Burzacott 2002). Higher local temperatures have also advanced the date of birth among the viviparous lizard *Niveoscincus ocellatus* in Tasmania (Cadby et al. 2010) and ovipositioning of the 3-lined skink *Bassiana duperreyi* in alpine sites on the mainland (Telemeco et al. 2009).

Whilst shifting the timing of breeding activities may enable individuals to cope with climate change, an alternative compensation mechanism is to alter the characteristics of nest sites, such as openness, aspect, or depth (Doody 2009). However, for *B. duperreyi*, neither earlier ovipositioning nor adjustments to nest depth have been sufficient to compensate fully for climate change. As a consequence, incubation length has decreased and hatchlings are emerging earlier and are smaller (Telemeco et al. 2009). There has also been a shift in the mode of sex determination: the threshold below which offspring sex is determined by thermal clues has been reached, resulting in sex determination by genotype and, therefore, a shift away from male-biased to a nearly 50:50 sex ratio among hatchlings (Telemeco et al. 2009).

2.5. Insect phenology

Temperature is the primary environmental factor influencing the development of insects (Drake 1994). As with reptiles and amphibians, ambient temperature has direct consequences on the rate of development, abundance, survival and distribution of insects (Bale et al. 2002). In high-latitude regions, the primary response of insects to warmer winters is likely to be greater survival, while warmer springs and summers will lead to more rapid and earlier development and, in the case of multi-voltine species, may allow additional generations each year (Bale et al. 2002).

Warming has already had impacts on the seasonality of insects, although studies are mostly restricted to Lepidoptera and Odonata in Northern Hemisphere temperate regions for which advances have been reported for flight dates (Dingemanse & Kalkman 2008,

Altermatt 2010, Diamond et al. 2011, Karlsson 2014). While spring events typically show the strongest advancement, late-season species often demonstrate either no advancement or have delayed flight dates (e.g. see Altermatt 2010, Karlsson 2014).

In Australia, museum and private collection records indicate that, over a 65 yr period, a south-eastern population of the common brown butterfly *Heteronympha merope* advanced its mean emergence date by 1.5 d decade⁻¹. Using physiological models, Kearney et al. (2010) attributed this advance to the concurrent increase in air temperature of ~0.16°C decade⁻¹. Similar collection records were used to explore shifts in the emergence date of 16 butterfly species across various locations in south-east Australia, since the 1950s (McClellan 2011). Of these, 6 species had demonstrated a significant advance in emergence in at least 1 location, with 6 other species demonstrating a significant delay (McClellan 2011).

Currently, long-term assessments of phenological trends among Australian insects have been restricted to Lepidoptera (Table 1). However, other potential indicator species have been identified. Based on 18 mo of continuous sampling of insects at an arid zone site in Australia, Palmer (2010) identified correlations between climate variables and the presence/abundance of several termite, wasp and butterfly species, and suggested phenological monitoring of these species as indicators of climate change. For instance, temperature strongly controlled colony founding among the termite genus *Amitermes*, for which abundance peaked in December and January, while the *Rhopalum* wasp species were restricted to cooler months. Palmer hypothesised that increasing temperatures may result in the earlier appearance of termites and a decline in season length for *Rhopalum*. In contrast, precipitation appeared to be a stronger driver for the development of adult wasps (*Bembecinus* species) and abundance of the butterfly *Nacaduba biocellata*.

As the century progresses, climate change may precipitate a range of other responses among species. In the tropics and subtropics, insect development is often limited by high temperature and moisture stress, and development can be arrested during the dry season (Drake 1994). Such arrests usually occur at a particular developmental stage, e.g. diapausing eggs, with the first rains of the wet season triggering the breaking of diapause and leading to synchronisation of generations (Drake 1994). Hence, trends in the timing of diapause initiation will likely shift as climate changes, and the frequency with which facultative species undergo diapause may alter.

3. LOOKING AHEAD

While there is a considerable body of data documenting phenological shifts in response to climate change, a number of areas remain poorly understood. These include:

- To what extent does species richness stabilise asymmetry in the phenological trends of interacting species (such as plant–pollinator systems) (e.g. Bartomeus et al. 2013)?
- How does thermal sensitivity vary across life-cycle stages, and how will species responses be influenced by constraints and tradeoffs between these stages (Briscoe et al. 2012)?
- What role do non-climatic factors play in driving phenological trends (e.g. impact of altered management practices on the timing of wine-grape ripening Webb et al. 2012)?
- Do populations contain sufficient adaptive genetic diversity to evolve and keep pace with a rapidly changing climate?
- What adaptation options are available to natural resource managers to influence rates of phenological change and to manage for potential phenological mismatches in dependent species?

Variability in precipitation across large parts of the Australian continent has a significant impact on the distribution and abundance of resources. As such, precipitation can play a key role in the timing and direction of phenological shifts (e.g. Chambers et al. 2013). This highlights the importance of assessing climate drivers beyond those that are temperature related. However, uncertainties in projections of the direction of future precipitation regimes make it difficult to predict species responses *a priori*.

Carefully designed studies, including experimental studies of CO₂ enhancement and temperature on plant phenology, can address some of the above knowledge gaps. Similarly, renewed interest in citizen science programs, such as ClimateWatch (www.climatewatch.org.au), and the development of online recording tools (Dickinson et al. 2012) and mobile apps should facilitate the capture of much needed scientific information over coming years. Observation networks within smaller geographic areas may be beneficial, enabling observations of multiple species within a location to be recorded simultaneously (Chambers & Keatley 2010). Standardised data collection and on-going development of statistical techniques to account for/remove biases in data collections (Gonsamo & D'Odorico 2014) will be key in elucidating patterns from citizen science collections.

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