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RESEARCH ARTICLE

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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ABSTRACT

Research from the intensively studied northern temperate and boreal regions dominates avian reproductive phenology studies. However, in most other areas, long-term, high-quality phenological datasets are not available, limiting our ability to predict how reproductive timing may respond to rapid climate change. Here, we provide novel methods for combining conventional and nonconventional observations to understand phenological patterns in birds across a southern continent. Observations from egg collections, bird banding, nest record schemes, and citizen science were combined to determine egg-laying phenology for ~50% of Australia's mainland breeding species. We investigated start, peak, and length of avian egg-laying periods (1) derived from different data sources, (2) across tropical, subtropical, desert, grassland, and temperate biomes, and (3) comparing 2 representative temperate regions of the northern and southern hemispheres. We found that start and peak egg-laying dates calculated from single-visit observations of young or eggs resulted in similar dates as those from more accurate multi-visit nest observations. This demonstration suggests that future studies aimed at assessing changes in the timing of breeding in response to climate change can utilize such observational data. This will significantly increase sample sizes, rather than restricting such analyses to just intensively tracked nests, for which accurate laying dates are available. We found that egg-laying phenology varies between biomes (tropical, subtropical, desert, grassland, temperate), with birds in the desert biome having the earliest peaks of egg-laying. Finally, the length of the egg-laying period differs significantly between hemispheres. The southern temperate zone species have extensive egg-laying periods and many species breed year-round in marked contrast to the highly predictable, springtime breeding in the north. Therefore, avian phenological patterns and documented responses to climate change from the well-sampled, but highly seasonal, northern hemisphere may not be transferrable across the globe.

Keywords: big-data, natural history collections, macroecology, breeding biology, breeding phenology, population monitoring

Caracterización de la cría oportunista a escala continental usando todas las fuentes de datos fenológicos disponibles; una evaluación de 337 especies a través del continente australiano

RESUMEN

Las regiones templadas del norte y las boreales han sido intensamente estudiadas y dominan los estudios de fenología reproductiva de las aves. Sin embargo, en la mayoría de las otras áreas, no están disponibles bases de datos de fenología de largo plazo y de alta calidad, limitando nuestra habilidad para predecir como la cronología reproductiva podría responder al rápido cambio climático. Aquí, brindamos métodos novedosos para combinar observaciones convencionales y no convencionales para entender patrones fenológicos de las aves a través de un continente del sur. Combinamos observaciones de colecciones de hueves, anillado de aves, registros de nidos y ciencia ciudadana para determinar la fenología de la puesta de huevos para ~50% de las especies reproductivas continentales de Australia. Investigamos el inicio, el pico y la duración del período de puesta de huevos de la aves (1) derivado de diferentes fuentes de datos, (2) a través de biomas de tipo tropical, subtropical, desértico, pastizal y templado, y (3) comparamos dos regiones templadas representativas de los hemisferios norte y sur. Encontramos que el inicio y el pico de las fechas de puesta, calculadas a partir de observaciones de una única visita a los polluelos o a los huevos, brindaron fechas similares que las observaciones más precisas generadas a partir de visitas repetidas a los nidos. Este resultado sugiere que futuros estudios dirigidos a evaluar los cambios en la cronología reproductiva en respuesta al cambio climático, pueden utilizar estos datos de tipo observacional. Esto permitirá ampliar significativamente los tamaños de muestra, en lugar de restringir estos análisis únicamente a nidos intensamente monitoreados para los cuales hay disponibles datos precisos de puesta. Encontramos que la fenología de puesta de huevos varía entre los biomas (tropical, subtropical, desértico, pastizal, templado), con los primeros picos en la puesta de huevos para las aves del bioma del

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desierto. Finalmente, la duración del período de puesta de huevos difiere significativamente entre hemisferios. Las especies de la zona templada del sur presentan largos períodos de puesta de huevos y muchas especies crían todo el año, en fuerte contraste con el altamente predecible periodo reproductivo de primavera del norte. Por ende, los patrones fenológicos de las aves y las respuestas documentadas al cambio climático provenientes del hemisferio norte, bien muestreado pero altamente estacional, podrían no ser transferibles a todo el globo terráqueo.

Palabras clave: biología reproductiva, colecciones de historia natural, datos masivos, fenología reproductiva, macroecología, monitoreo poblacional

INTRODUCTION

Phenological shifts in response to changing climate are a widely documented phenomenon across the globe (Crick et al. 1997, Crick and Sparks 1999, Walther et al. 2002, Parmesan and Yohe 2003, Carey 2009, Dunn and Winkler 2010, Chen et al. 2011, Thackeray et al. 2016). For birds, the impact of climate change on the timing of the breeding season has primarily been studied in highly seasonal locations, in particular, regions of the United Kingdom and North America (Crick et al. 1997, Crick and Sparks 1999, Dunn and Winkler 2010). Despite these well-documented phenological shifts in the northern hemisphere temperate region (NHTR), research in other regions of the globe is relatively scarce. The geographic bias toward the NHTR 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).

Although ideal phenological datasets may not always be available, there are numerous types of alternative observations that, when combined, offer powerful substitutes (Sparks 2007, Dickinson et al. 2010). For birds, combining conventional observations on phenology (e.g., nest record schemes) with less orthodox observations on breeding occurrences from museum egg collections, bird-banding records, and citizen science initiatives can provide robust baseline observations. However, care must be taken to account for potential biases, both spatial and temporal, in order for these observations to be useful. In this study, we bring together the datasets mentioned above to answer questions about spatial variation in avian egg-laying phenology using the continental bird fauna of Australia as an example. We focus on the egg-laying phenology of 337 of the most collected species and compare (1) egg-laying phenology calculated from 4 different observation sources, (2) how the start, peak, and length of egg-laying differ among biomes (i.e. 5th, 50th, and number of days between the 5th and 95th percentiles, respectively), and (3) how egg-laying phenology in the Australia Capital Territory (representing a spatially discrete area of the southern hemisphere temperate region (SHTR)) is fundamentally different than in England (a well-sampled region in the NHTR).

Timing reproduction correctly may be important for the long-term fitness of bird populations, particularly under rapid environmental change. Energy expenditure is often greatest during reproduction; for many species the timing of egg hatch and the fledging period is strongly linked to food availability (Both 2010). Most species have discrete breeding periods, and even species that breed opportunistically in unpredictable environments typically exhibit some degree of seasonality (Sharp 1996, Tökölyi et al. 2011). Seasonal breeding is present at all latitudes (Wyndham 1986, Sharp 1996, Stouffer et al. 2013) and birds use climatic or environmental signals to cue and optimize breeding events (Lack 1950, Carey 2009). For instance, in nearly all birds the endocrine pathway, which controls reproduction, responds to the annual cycle of day length, providing an initial reference point by which birds prepare physiologically to breed (Cockrem 1995). Environmental drivers and limitations on breeding may vary markedly with climate, and therefore an assessment of differences in reproductive phenology across biomes and hemispheres is warranted.

Australia includes 5 distinct biomes (tropical, subtropical, desert, grassland, temperate) where strong differences in environmental conditions are likely to influence breeding phenology in birds. For instance, in the Australian tropical biome, high rainfall seasonality has a negative relationship with the spatial abundance of birds and this rainfall pattern may create bottlenecks in food availability limiting both breeding density and success (Williams and Middleton 2008). By contrast, in arid regions (desert and grassland biomes), birds are faced with hot summer temperatures (>33°C average daily maximum temperatures (Bureau of Meteorology 2009)) and low rainfall, which is typically aseasonal and highly unpredictable in both timing and magnitude (Morton et al. 2011). Temperate and subtropical biomes experience seasonal and spatial variations in temperature and precipitation resulting in regions with dry summers or winters or having no dry season at all (Stern et al. 2000). Assuming that it is advantageous to time breeding in response to predictable climatic variation, we expected egg-laying phenology to differ between biomes within Australia and between comparable temperate zones in the northern and southern hemispheres.

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TABLE 1. Types of breeding bird observations for Australia, their sources, mean year of collection and the number of observations. NRS is Birdlife Australia's Nest Record Scheme; ABBBS is the Australian Bird and Bat Banding Scheme.

Observation type	Source	Year of collection (mean ± SD)	Number of observations
Multi-visit	Multiple visit NRS	1980 ± 9	25,810
Egg	Single-visit NRS, museum, eBird	1951 ± 34	63,747
Young	Single-visit NRS, ABBBS, eBird	1982 ± 13	45,332
Undefined	Single-visit Atlas, ABBBS	2004 ± 6	144,078

METHODS

Observations

Occurrence records (latitude and longitude coordinates) for breeding birds were collated from Birdlife Australia's Atlas Survey Records (Barrett et al. 2003) (50%) and Nest Record Scheme (NRS, 27%), historical museum egg collection records (14%), Australian Bird and Bat Banding Scheme (ABBBS, 8%), and eBird (eBird 2015) (1%). Species with <50 breeding observations in at least one biome and those whose breeding habitats were limited to rocky coasts and islets, beaches, and mangroves according to Garnett et al. (2015) were excluded. For Atlas occurrence records that did not include exact observation dates, but instead recorded the start and end dates of the survey, the date of observation was set to the mid-point of the survey and we excluded occurrences where the exact observation date was unknown and the surveys occurred over more than 10 days. This resulted in 278,967 unique observations for 337 bird species. For a complete list of contributing institutes and persons, please see Supplementary Material. Taxonomy follows Clements et al. (2016).

First Egg-Laying Dates

To back-calculate first egg-laying dates (FEDs, days of the year when the first egg in each nest was laid) for the Australian observations, we examined 5 life-history traits: average clutch size, incubation period, fledging age, the rate of lay, and degree of development at hatching. Life-history traits were extracted from the *Handbook of Australian, New Zealand & Antarctic Birds* (Marchant and Higgins 1990, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, 2006; Higgins and Peter 2002), the online *Handbook of Birds of the World* (www.hbw.com, accessed April 2015), and Australian Bird Data Version 1 (Garnett et al. 2015). Average clutch size is the number of eggs typically laid during one breeding event. The incubation period is the number of days eggs are kept at constant temperatures before hatching. Fledging age was defined differently for altricial and precocial species. For altricial species, fledging was estimated as the number of days from the point of hatch until birds leave the nest. For precocial species, fledging corresponds to the point when birds can fly or, for precocial species that do not fly (e.g., Emu [*Dromaius novaehollandiae*]), it is when the juvenile reaches 1/3 adult size. The rate of lay is the average interval, measured in days, between when consecutive eggs in a clutch are laid. The degree of development at hatching is the level of maturity—altricial or precocial.

Occurrence records were divided into 4 types: (1) multi-visit observations where details of 2 or more breeding stages were documented (e.g., nest building activities, presence of eggs, egg hatch, and presence of young), (2) single-visit observations where egg(s) were observed, (3) single-visit observations where young were observed, and (4) undefined breeding observations with no indication as to the breeding stage. Data sources and sample sizes for each of the observation types are summarized in Table 1.

Figure 1 depicts methods, modified from Crick et al. (2003) and Joys and Crick (2004), used to calculate first egg-laying dates (FEDs) for multi-visit observations. Observations where the FED window was >5 days were excluded from analysis.

FEDs from single-visit egg observations were back-calculated by averaging FEDs from the formulas for "first egg" and "last egg." FEDs for single-visit young observations were averages of "young in nest" and "young out of nest." FEDs for single-visit undefined observations were averages of "first egg," "last egg," and "young out of nest" (Figure 1).

We optimize FED back-calculation methods for single-visit observations of young, eggs, and undefined breeding activity to account for varying detectability, for each species, during the nesting cycle. Detectability of a species can vary due to behavior, habitat, flock size, the distance an observer is from a nest or bird, and movement of birds depending on the time of day (Bibby et al. 2000). The first step to optimizing back-calculation methods was to build species-level probability density functions (PDFs) of FEDs for the high-accuracy multi-visit observations. Next, we built PDFs of the FEDs for single-visit observations when we included 0%, 25%, 50%, or 100% of the incubation or fledging period (egg or young and undefined, respectively) to account for species-level variation in detectability. Thus for each single-visit observation type, we had 4 PDFs. However, due to the relatively short length of the incubation period, the majority of these resulted in PDFs that were very similar. Thus we limited PDFs of single-visit

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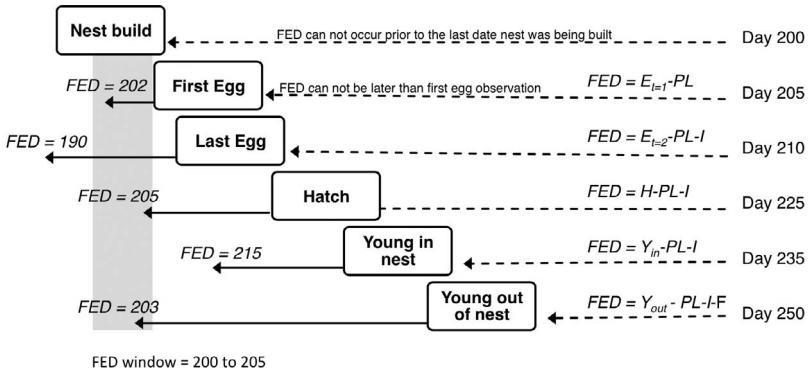


FIGURE 1. A schematic diagram of the first-egg date (FED) back-calculation methods used for multi-visit nest record scheme observations. Observation dates are given as day of the year. The last nest building observation and the first breeding observation is the FED window and limits the dates in which the FED can occur. In this example, the FED window is shown with the gray box and is between nest build on day 200 and first egg observation ($E_{t=1}$) on day 205. Depending on the observation type—$E_{t=1}$, last egg observation ($E_{t=2}$), first observed egg hatching (H), first young in the nest (Y_{in}), and first young out if the nest (Y_{out})—FEDs are back-calculated using the period of lay (PL), incubation (I), and fledging period (F). The final FED is the average of the most similar dates within the FED window. In this example the PL = 3 days, I = 17 days, and F = 26 days and the final FED is rounded up to day 203.

eggs to those including either 25% or 100% of the incubation period. Finally, we calculated the areas under the PDFs for 12 equal-sized bins of 30.5 days and used the chi-square (χ^2) statistic to rank how similar the single-visit PDFs were to the high-accuracy multi-visit observations FEDs. The single-visit FED datasets most similar (in terms of the χ^2 statistic) to the high-accuracy multi-visit observations were kept. If there were not 100 high-accuracy multi-visit observations at the species level, we repeated the above process using observations for the genus, family, order, or the degree of development at hatch, using the lowest taxonomic level or the level of maturity (altricial or precocial), to meet the requirement of 100 high-accuracy multi-visit observations.

Egg-Laying Phenology

We assessed differences in egg-laying phenology when calculated from single-visit FEDs of egg, young, or undefined breeding activity with that calculated from the high-accuracy multi-visit observations. This allowed us to assess if the start, peak, or length of egg-laying was skewed by using different types of observations. For all species and each observation type, we calculated the start, peak, and length of the egg-laying period (i.e. 5th, 50th, and number of days between the 5th and 95th percentiles, respectively) within biomes (tropical, subtropical, desert, grasslands, and temperate) using the R (R Core Team 2016) package circular (Agostinelli and Lund 2013). We used circular statistics with a median-unbiased quantile estimator (Hyndman and Fan 1996) to account for species that breed over the turn of a year (i.e. periods encompassing December–January). Analyzed species were limited to those that, within a biome, had >100 FEDs for at least 2 different data types. Biome boundaries were based on a national modified Köppen classification system (Stern et al. 2000, Bureau of Meteorology 2006), and the equatorial biome was combined with the tropical biome in our analyses.

Based on our results from comparing egg-laying phenology from different data types, for each species, we calculated the start, peak, and length of egg-laying at the biome level using multi-visit, young, and egg FEDs. These observation types had a fair to high degree of agreement in our assessment of egg-laying phenology derived from the different observation types. Undefined breeding FEDs were used when there were less than 100 observations from the other categories. Following the constraints imposed by Joys and Crick (2004), we calculated phenology for all species that had 50 or more observations. See Supplemental Material Table S1 for the number of observations for each species and to see if observations of undefined breeding activity were included in phenological measures.

Phenological Comparison between Northern and Southern Hemisphere Temperate Regions

To investigate differences in egg-laying periods between the SHTR and NHTR we used a spatial and temporal subset of Australian egg-laying observations to calculate phenology and compare it with data from the UK reported in Joys and Crick (2004). SHTR observations were spatially restricted to those falling within the Australian Capital Territory (ACT). The ACT is a relatively well-sampled region with mean temperatures in the coldest and warmest quarters similar to those in the NHTR (ACT: 4.5°C and 17.7°C; UK: 3.6°C and 15.3°C, respectively) (Hijmans et al. 2005). Following the temporal constraints presented by Joys and Crick (2004), data was limited to observations after 1990; for species with <100 observations we

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TABLE 2. Mean start, peak, and length of egg-laying periods (ELP) based on 4 types of breeding bird observations. Results are based on liner mixed-effect with biome and observation type as fixed effect and taxonomic order as a random effect. The letters indicate observation types that were significantly different in Tukey's pairwise comparisons ($p < 0.05$).

Observation type	Mean start of ELP (day of year ± SE)	Mean peak of ELP (day of year ± SE)	Mean length of ELP (days ± SE)
Multi-visit	224 ± 7 ^{A}	289 ± 6	134 ± 8 $^{A, B}$
Egg	210 ± 6 ^{B}	282 ± 4 ^{A}	155 ± 6 $^{A, C}$
Young	225 ± 11 ^{B,C}	290 ± 8	140 ± 12 ^{D}
Undefined	202 ± 5 $^{A, C}$	294 ± 4 ^{A}	192 ± 5 $^{B, C, D}$

expanded records to include those between 1966 and 1990. We gave preference to multi-visit, young and egg observations, over the undefined breeding stage observations, following the methods previously outlined. Egg-laying periods across all species ($n = 54$ species) were then calculated as the number of days between the 5th and 95th percentiles for first egg-laying dates (FEDs). Egg-laying periods for the UK were calculated as the number of days between the 5th and 95th percentiles presented in Joys and Crick (2004) ($n = 86$ species). ACT boundaries were from the 2011 edition of the Australian Standard Geographical Classification (http://www.abs.gov.au/AUSSTATS).

Analyses

Three specific statistical analyses were performed to examine (1) similarity in the start, peak, and length of the egg-laying period from different data sources, (2) differences in start, peak, and length of the egg-laying period between biomes, and (3) differences in the length of the egg-laying periods between the NHTR and SHTR. All analyses were carried out in R (R Core Team 2016) and were considered significant at $\alpha = 0.05$.

We assessed the similarity of start, peak, and the lengths of the egg-laying periods back-calculated from multi-visit observations to those calculated from single-visit observations of eggs, young, and undefined breeding using a linear mixed-effects models in the lme4 package (Bates et al. 2015). In our models biome and data type were fixed effects while taxonomic order was a random effect to account for the potential effect of shared ancestry. Differences in phenological measures were tested using Type II Wald F tests using Kenward–Roger approximation for degrees of freedom to test for significant differences between data types, using the car package (Fox and Weisberg 2011) and Tukey's pairwise comparisons using the multcomp package (Hothorn et al. 2008). The coefficient of determination for the linear mixed-effect models were calculated using the MuMIn package (Bartoń 2016).

Differences in the length of the egg-laying period between biomes were assessed using linear mixed-effects models in the lme4 package (Bates et al. 2015). Biome was the fixed effect and taxonomic order was a random effect. Differences among biomes were assessed using Type II Wald F tests using Kenward–Roger approximation for degrees of freedom and Tukey's pairwise comparisons. To assess how the start and peak of the egg-laying period differed between biomes we used the heavy package (Osorio 2016), specifically the function heavyLm to fit least-squares regressions for each taxonomic order with a t-distribution of the residuals to account for heavy-tailed errors. The least-squares regressions were fit for individual orders because using a mixed-effect model with biome as a fixed effect and taxonomic order as a random effect did not explain the variation in start and peak, since the majority of waterbirds in the arid regions respond opportunistically to rainfall verses seasonal variation in temperature, rainfall, and food availability.

Finally, differences in the length of the egg-laying periods between the NHTR and SHTR were assessed using a linear mixed-effects model with taxonomic order as a random effect. Throughout, summary values are reported as means ± SD.

RESULTS

Comparing Phenology from Different Observation Types

Regression analyses comparing the starts and peaks of egg-laying (ordinal date) when calculated from multi-visit observations and single-visit young and egg observations, respectively, showed high levels of agreement (Figure 2). That is, there was strong correspondence between breeding phenology patterns detected from more reliable, multi-visit observations and single-visit observations of eggs and young, particularly for peak egg-laying (Figure 2A). The length of the egg-laying period when calculated from single-visit egg observations was significantly longer than when calculated using the multi-visit observations (Figure 2B). Additionally, the start of the egg-laying periods when calculated from young observations and egg observations was significantly different (see Table 2 for all pair-wise comparisons).

Phenological Variation across Biomes and within Avian Order

The length of egg-laying period differed between Australian biomes ($F = 12.34$, df = 4 and 719.26, $p < 0.001$; Table

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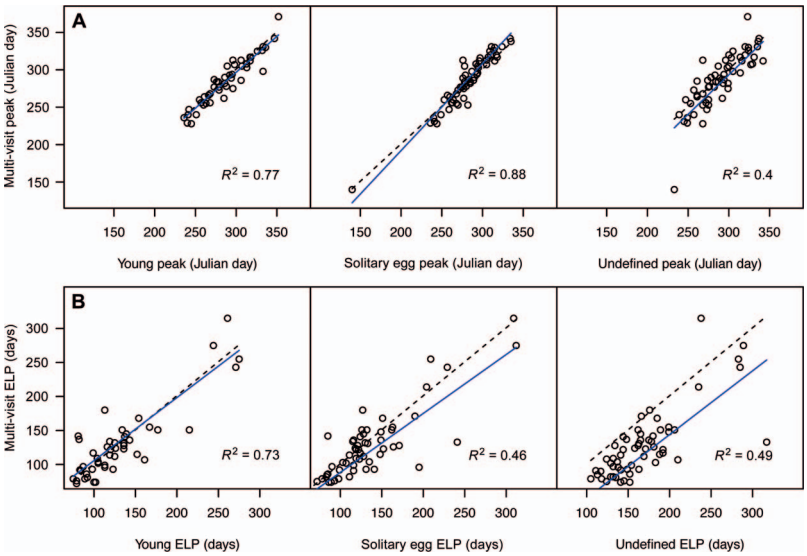


FIGURE 2. Relationships between multi-visit and single-visit observation types (egg, young, undefined) for (**A**) peak breeding (day of the year) and (**B**) length of the egg-laying period (ELP, days). In all graphs, the blue lines depict the line of best fit from the linear mixed-effect model and dashed black lines represent perfect distribution fits (1:1 relationships between *x* and *y* variables). Undefined breeding observations and, to a lesser degree, solitary-egg observations, significantly overestimate the length of the egg-laying period.

3) with egg-laying periods being shortest in the temperate biome and longest in the tropical biome. Data on species-level egg-laying periods and number of observations per species and biome are provided in Supplemental Material Table S1.

The average start and peak of egg-laying periods differed markedly across biomes for the 12 orders of birds that had multiple species breeding in the desert (Tables 4 and 5). Most notable was the trend toward earlier egg-laying phenology in multiple orders found in the desert biome relative to egg-laying phenology in all other biomes: grassland, temperate, subtropical, and tropical (Figure 3). For example, 10 orders had significantly earlier start and 9 had earlier peak of egg-laying in the desert relative to the temperate biome ($p < 0.05$; Tables 4 and 5, respectively). The average start and peak date of the egg-laying (day of the year) in the desert was 145 ± 58 days and 239 ± 40 days compared with the temperate 222 ± 43 days and 292 ± 35 days (see Supplemental Material Table S1 for species-level information). Three of the orders with significantly earlier egg-laying phenology were waterbirds (Anseriformes, Pelecaniformes, Gruiformes). The timing of egg-laying for these waterbird orders coincides with the filling of Kati Thanda-Lake Eyre with summer and autumn rains that flow from regions to the north.

Phenological Variation between Northern and Southern Hemisphere Temperate Regions

When we restricted our observations in the ACT to those after 1990 to match the preferred dates of Joys and Crick (2004), we had 27 species with more than 100 observations. When the date range was expanded back to 1966, as per Joys and Crick (2004), we had an additional 27 species (9 species with >100 observations and 18 species with ≥50 observations) resulting in a total of 54 species in ACT that were used in the assessment of phenological variation between the northern and southern hemispheres.

The egg-laying period was significantly shorter in the NHTR compared to the SHTR ($F = 185.43$, df = 1 and 133.07, $p < 0.001$), with the average egg-laying period significantly shorter in England (61 ± 26 days) than in the ACT (143 ± 42 days). In England, egg-laying periods were narrow: 20 out of 86 species had egg-laying periods of less than 40 days, with only 4 spanning more than 100 days (Figure 4A). By contrast, none of the 54 species assessed in the ACT had egg-laying periods of <40 days, while 48 species had periods of >100 days (Figure 4B).

TABLE 3. Mean length of egg-laying periods (ELP) for bird species occurring in 5 Australian biomes. Biomes with the same letter are not significantly different in Tukey's pairwise comparisons ($p < 0.05$).

Biome	Mean length of ELP (days ± SE)	*n* (species)
Temperate	152 ± 6	257
Grassland	170 ± 4 [A]	183
Desert	177 ± 8 [A]	85
Subtropical	178 ± 7 [A]	158
Tropical	204 ± 9	55

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TABLE 4. Mean start of the egg-laying period for orders of birds occurring in 5 Australian biomes. Species is the number of unique species occurring across all biomes, but not necessarily in all biomes. An asterisk (*) indicates a biome with a start date that is significantly different from the desert ($p < 0.05$). Significance was determined using least-squares regression for each order of birds. Dates are given as day of the year ± SE.

Order	Species	Desert	Grassland	Temperate	Subtropical	Tropical
Passeriformes	185	163 ± 6	209 ± 8*	231 ± 7*	216 ± 8*	236 ± 9*
Accipitriformes	16	148 ± 25	149 ± 30	190 ± 29	136 ± 31	78 ± 35*
Psittaciformes	30	156 ± 17	199 ± 20*	207 ± 19*	180 ± 22	113 ± 44
Anseriformes	17	79 ± 17	158 ± 20*	205 ± 20*	210 ± 20*	355 ± 28*
Pelecaniformes	13	55 ± 27	261 ± 29*	254 ± 29*	258 ± 30*	
Charadriiformes	15	138 ± 19	168 ± 25	227 ± 26*	203 ± 29*	100 ± 35
Cuculiformes	9	111 ± 32	165 ± 40	251 ± 34*	232 ± 34*	271 ± 40*
Coraciiformes	8	214 ± 19	245 ± 21	266 ± 21*	243 ± 21	332 ± 27*
Columbiformes	10	133 ± 19	184 ± 22*	204 ± 22*	185 ± 22*	111 ± 24
Falconiformes	5	189 ± 11	208 ± 15	226 ± 16*	206 ± 25	
Gruiformes	10	82 ± 15	226 ± 18*	245 ± 17*	235 ± 19*	
Suliformes	4	44 ± 51	132 ± 62	158 ± 62	120 ± 65	

DISCUSSION

Using 4 distinctly different types of observations (multi-visit, young, egg, undefined breeding activity) to calculate phenology has allowed us to generalize patterns of phenological variation in the reproductive timing of many species of Australian birds. On average, there is negligible difference in the start and peak of egg-laying periods calculated from multi-visit observations, or single-visit observations of young and eggs. By contrast, undefined breeding observations—where birds are known to be breeding but the stage is not documented—resulted in phenological inferences with higher uncertainty relative to more reliable multi-visit observations, particularly in the length of the egg-laying period (Figure 2B). This discrepancy is likely caused by the lower temporal accuracy of undefined breeding records. However, it is important to highlight that the other observation types may also share a similar temporal bias arising from collectors/observers visiting the field during known or expected times of breeding. This collector behavior may artificially narrow breeding period length and lead to earlier estimates of the start of the breeding season.

Our finding that the starts and peaks of the egg-laying calculated from single-visit egg and young observations were not significantly different from those calculated from the more systematic multi-visit observations has wide-ranging implications for long-term population studies aimed at quantifying phenology. Specifically, it suggests that observation-based research can very efficiently gather data on a larger number of nests rather than a similar effort directed at fewer more intensively tracked nests. For example, if the ultimate goal of researchers is to identify the start or peak in egg-laying then observers should be encouraged to invest the majority of their effort in finding nests and recording if there are eggs, young in nest, or young out of nest rather than intensively tracking nests and visiting them multiple times. To fully assess if the single-visit observation types perform as well as multi-visits, our methods need be tested for highly seasonal

TABLE 5. Mean peak of the egg-laying period for orders of birds occurring in 5 Australian biomes. Species is the number of unique species occurring across all biomes but not necessarily in all biomes. An asterisk (*) indicates that the biome has a peak that is significantly different from the desert ($p < 0.05$). Dates are given as day of the year ± SE.

Order	Species	Desert	Grassland	Temperate	Subtropical	Tropical
Passeriformes	185	238 ± 4	268 ± 5*	292 ± 5*	282 ± 6*	311 ± 7*
Accipitriformes	16	242 ± 14	240 ± 18	269 ± 17	242 ± 18	188 ± 20*
Psittaciformes	30	227 ± 8	259 ± 10*	277 ± 9*	260 ± 11*	254 ± 22
Anseriformes	17	196 ± 14	284 ± 17*	280 ± 16*	287 ± 16*	480 ± 22*
Pelecaniformes	13	169 ± 21	329 ± 23*	320 ± 23*	312 ± 24*	
Charadriiformes	15	275 ± 13	277 ± 17	295 ± 18	272 ± 20	169 ± 24*
Cuculiformes	9	230 ± 26	269 ± 32	314 ± 28*	320 ± 28*	372 ± 32*
Coraciiformes	8	280 ± 14	306 ± 16	317 ± 15*	309 ± 15	370 ± 20*
Columbiformes	10	245 ± 9	294 ± 10*	303 ± 10*	291 ± 10*	280 ± 12*
Falconiformes	5	244 ± 5	259 ± 7*	278 ± 7*	260 ± 12	
Gruiformes	10	240 ± 12	287 ± 15*	298 ± 14*	307 ± 16*	
Suliformes	4	165 ± 63	249 ± 78	282 ± 78	263 ± 82	

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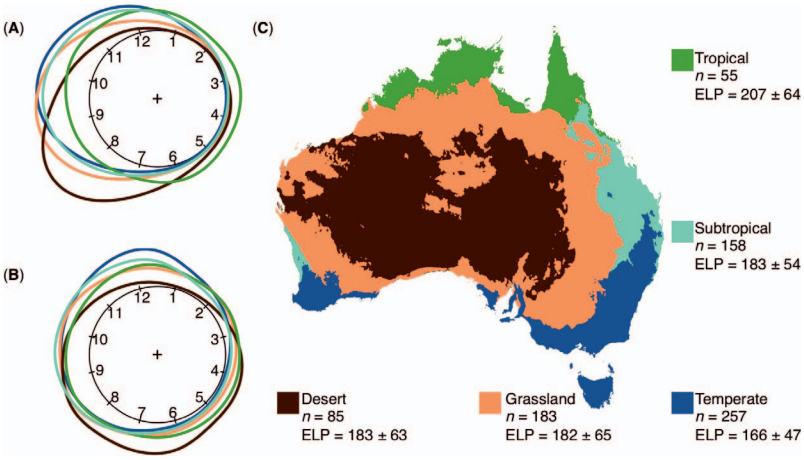


FIGURE 3. Timing of the length of the egg-laying period for 337 bird species within 5 Australian biomes. The egg-laying period is the number of days between the 5th and 95th percentiles of all first-egg dates, and the confidence interval is across species in the biome. (**A**) Colored lines are kernel density estimates of first-egg dates, and the numbers are the months of the year (e.g., January = 1, February = 2, etc.). (**B**) Colored lines are kernel density estimates for the number of species laying eggs in each month within different biomes. (**C**) Map of Australian biomes and the number of species (*n*) and the mean egg-laying period for bird species with more than 50 observations.

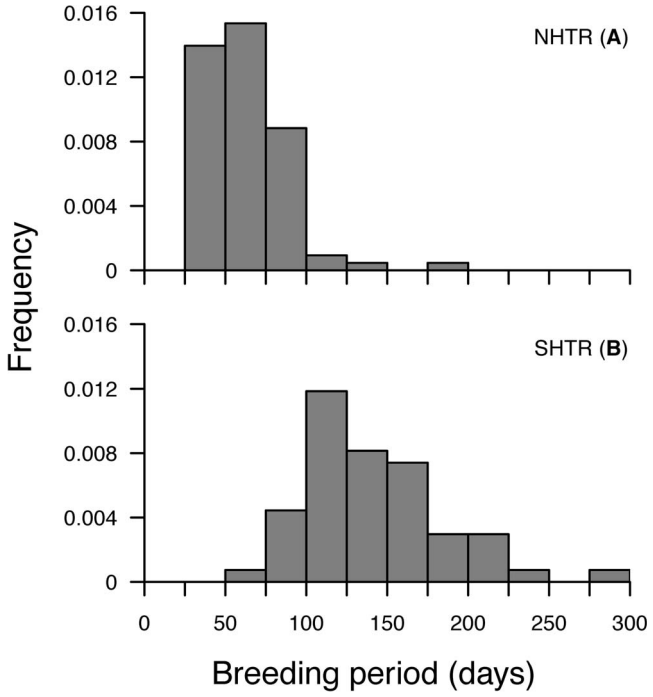


FIGURE 4. Frequency distributions of egg-laying period (number of days between the 5th and 95th percentile of all egg-laying observations) in northern hemisphere (**A**) and southern hemisphere (**B**) temperate regions. Observations in (**A**) are for 86 bird species in England reproduced from Joys and Crick (2004), whereas observations in (**B**) are for 54 bird species from the Australian Capital Territory, Australia. Species include both passerines and nonpasserines, but exclude seabirds.

regions where the total variance is less than in Australia. We have also demonstrated the utility of a variety of datasets such as museum egg collections that could be used to analyze breeding phenology in other regions of the world for which systematically gathered breeding data is not available or is restricted.

Egg-Laying Phenology Differs between Northern and Southern Hemisphere Temperate Regions

Importantly, we show that the length of the egg-laying period in a sample of NHTR species (England) is considerably shorter than that of a comparable sample of SHTR species (ACT). The difference in egg-laying phenology between birds of the northern and southern hemispheres is not so surprising, and widely acknowledged, but to our knowledge has not previously been quantified. This finding demonstrates how egg-laying phenology across a wide suite of birds measured at the same spatial and temporal scales is fundamentally different between the SHTR and the NHTR. This finding has implications for using phenological patterns in the NHTR to infer avian species responses to anthropogenic climate change in other regions of the world. Changes in the timing of breeding in response to climate change which have been documented in NHTR (e.g., Crick et al. 1997, Crick and Sparks 1999, Dunn and Winkler 2010), where most birds breed just once a year and most variation is related to the onset of breeding, may not reflect responses in other areas of the world where breeding seasonality differs.

Well-studied, narrow breeding periods of birds in NHTR are unlikely to provide a useful proxy for bird

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responses to climate change in less seasonal regions globally. Longer duration of egg-laying period in the ACT, and in the biomes of Australia more generally, may be indicative of high levels of flexibility and opportunistic behavior in response to intra-annual climate fluctuation and food resources (Wyndham 1986, Tökölyi et al. 2011). For instance, individuals of some species can likely breed throughout the entire egg-laying period, in other species individuals with different genotypes are breeding at different times with a high degree of inter-annual variation (Chambers and Keatley 2010). More research is needed to further explore how inter-annual variation in climate influences breeding intensity and the spatial distribution of breeding in areas with extensive breeding seasons. Further, the typical practice of looking for changes in the start and conclusion of breeding in response to climate change may not be appropriate in areas with extensive breeding periods. Assessments of species responses to climate change need to include measures of population variation (McCain et al. 2016); this is especially important for areas of the world that experience a high level of inter-annual climatic variation.

Egg-Laying Phenology Varies with Biome

In Australia, there were clear differences in the timing and length of egg-laying periods between biomes and the orders of birds found within them. A likely driver is the distinctive difference in climatic conditions in each biome and their effects on bird reproduction. Although we did not formally test the role of climate in shaping egg-laying phenology, some basic inferences can be made. For example, after excluding waterbirds, the peak period for egg-laying in the desert typically occurs before the highest temperatures in summer, while peak egg-laying in the temperate biome occurs after the coldest temperatures of winter.

Climatic conditions can constrain breeding directly by making the nesting environment uninhabitable (e.g., water-saturated nests in the tropics) and indirectly by changing resource availability (e.g., limited food resources). It has previously been suggested that birds in Australia's arid regions breed opportunistically throughout the year, and often in response to rainfall, which results in high food availability (Zann et al. 1995, Perfito et al. 2007, Robin et al. 2009, Morton et al. 2011). This is analogous to the established paradigm from temperate regions that bird reproductive phenology is primarily determined by peak food availability (Lack 1950, Visser et al. 2005). Rainfall in the arid regions is typically aseasonal and unpredictable (Morton et al. 2011), and while rainfall is no doubt an important trigger for primary productivity in the desert (Lieth and Whittaker 2012), we hypothesize that significantly earlier start and peak in the desert biome (Figure 3, Supplemental Material Table S2) may have evolved to decrease exposure to summer maximum temperatures. More research looking at temperature and precipitation constraints on breeding is needed to understand the climatic mechanisms that cue and limit breeding, particularly in hot arid biomes.

Previous studies examining variation in the length of breeding periods with latitude have largely attributed differences to increases in temperature and day length (Wyndham 1986, Griebeler et al. 2010). Our analysis focuses on a continent with 5 distinct biomes and shows significant variation in the timing and length of breeding periods among them (Figure 3). We report similar patterns as previously reported for latitudinal studies when comparing breeding periods between biomes. That is, the northern tropical biome had longer egg-laying periods than did the more southern temperate biome. Similarly, the hot arid biomes in the center of the continent (i.e. desert, grassland) have significantly longer egg-laying periods than the temperate region. However, the early average start and peak of the egg-laying periods in the desert biome suggest that in the hot arid biomes there are constraints on breeding that have not been previously noted or explored.

Caveats for the Use of Unconventional Data in Phenological Research

There are a wealth of different potential sources of information on organism phenology that are largely untapped (Sparks 2007, Møller and Fiedler 2010). Although these vary in quality, our study demonstrates how they can be combined and analyzed to reveal aspects of basic ecology for many species over wide spatial distributions. The observations used in this study come from a range of digitized resources, including natural history museum egg collections, which contain collection dates, and citizen science databases such as eBird (http://ebird.org), which can include information on life history events. Each resource has its own spatial and temporal biases including well-documented phenomena such as observer error, differences in the quality of data, and variation in sampling effort across space and time (Parmesan 2007, Dickinson et al. 2010, Møller and Fiedler 2010). We recognize that the geographic and temporal distribution of data may influence the egg-laying periods such that they represent the areas with greatest sampling density (Dickinson et al. 2010). The methods demonstrated here might be useful in other regions of the world where phenological events have not previously been defined at a broad scale across lots of species.

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Author contributions: DED, RVG, and SCG conceived and designed the study. DED collated and vetted the observation data. DED and SG collated the trait data. DED performed the analysis. All authors contributed to the writing of the manuscript.

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