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4 **Effects of El Niño Southern Oscillation on avian breeding**
5 **phenology**

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7 Running title:

8 **ENSO AND AVIAN BREEDING PHENOLOGY**

9

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11 Daisy Englert Duursma^{1*}, Rachael V. Gallagher¹, Simon C. Griffith¹

12 1. Department of Biological Sciences, Macquarie University, North Ryde, NSW

13 2109, Australia

14

15 ***CORRESPONDENCE TO BE ADDRESSED TO:**

16 Daisy Englert Duursma

17 Department of Biological Sciences

18 Macquarie University, North Ryde, NSW 2109

19 Australia

20 Ph: +61 02 9850 1302

21 Fax: +61 02 9850 8254

22 Email: daisy.duursma@gmail.com

23 **KEYWORDS:**

24 breeding phenology, climate change, climate oscillations, egg-laying, El Niño

25 Southern Oscillation, ENSO

26 **ABSTRACT**

27 *Aim*

28 Climate oscillations are known to influence the reproductive phenology of birds.
29 Here, we quantify the effects of cyclic climatic variation, specifically El Niño
30 Southern Oscillation (ENSO), on birds that breed opportunistically. We aim to show
31 how inter-decadal climate fluctuations influence opportunistic breeding. This
32 knowledge is essential for tracking the phenological responses of birds to climate
33 change.

34 *Location*

35 Temperate and arid Australia.

36 *Methods*

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

44 *Results*

45 During La Niña phases, which are characterised by mild/wet conditions, most bird
46 species in the temperate and arid regions exhibited longer egg-laying periods relative
47 to Neutral phases. However, there was substantial variation across species. This effect
48 was strongly seasonal; species breeding in spring experienced the greatest increases in
49 egg-laying periods during La Niña. Further, we found only small differences in peak
50 egg-laying dates during Neutral and La Niña in the arid region; suggesting that hot

51 temperatures may constrain breeding regardless of rainfall. The effects of El Niño on
52 breeding phenology were not consistent in the temperate and arid regions and may be
53 confounded by highly mobile species opportunistically moving and breeding with
54 localized rainfall during dry periods.

55

56 ***Main Conclusions***

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

61

62 **INTRODUCTION**

63 Large-scale climate oscillations such as the El Niño Southern Oscillation (ENSO) and
64 the North Atlantic Oscillation influence year to year variation in avian breeding
65 phenology (Forchhammer, Post, & Stenseth, 1998; Gibbs, 2007; Jaksic & Fariña,
66 2010; Wilson & Arcese, 2003), breeding intensity (Gibbs, 2007; Gibbs, Chambers, &
67 Bennett, 2011; Vilina, Cofré, Silva-García, García, & Pérez-Friedenthal, 2002;
68 Wilson & Arcese, 2003) and migration phenology (*reviewed in* Beaumont,
69 Hartenthaler, Keatley & Chambers, 2015; Gordo, 2007). It is well known that long-
70 term climatic cycles influence extinction rates amongst species (i.e. during growth
71 and retreat of glaciers; Wanner et al., 2008), whereas short-term variability in climate
72 affects phenology and population numbers in subsequent years (McCain, Szewczyk,
73 & Bracy Knight, 2016).

74 By contrast, species breeding responses to decadal climatic cycles are
75 relatively poorly studied, particularly for land birds in the Southern Hemisphere.
76 Although there have been several Australian studies of variation in breeding
77 phenology in relation to ENSO (Chambers, Gibbs, Weston, & Ehmke, 2008; Gibbs,
78 2007; Gibbs et al., 2011), they are typically characterised by low sample sizes and
79 focus on just a few species. Low sample sizes are largely due to the lack of long-term
80 time-series data rather than any likely absence of an effect of contemporary climate
81 change on species in the Southern Hemisphere (Hughes, 2003) and is in contrast to a
82 number of long-term datasets that are available in the Northern Hemisphere (Clutton-
83 Brock & Sheldon, 2010).

84 The absence of traditional time series data for terrestrial birds in the Southern
85 Hemisphere is a major obstacle to understanding responses to a changing climate. An
86 objective of this study was to use a combination of conventional and non-

87 conventional sources of avian breeding observations to document variation in avian
88 breeding phenology in relation to the three phases of ENSO.

89 ENSO affects a number of climatic parameters, including ambient
90 temperature, precipitation and wind (Fiedler, 2002; Nemani et al., 2003; Trenberth,
91 1990) and is a global source of decadal climate variation affecting both marine and
92 terrestrial ecosystems. Three distinct phases of ENSO are recognised (El Niño, La
93 Niña, and the Neutral state), and their impacts vary widely across regions. For
94 instance, altered rainfall patterns are common in eastern and northern Australia, India
95 and parts of the Americas during ENSO cycles (Chiew, Piechota, Dracup, &
96 McMahon, 1998; Nicholls, 1991). During El Niño phases sea surface temperatures
97 increase, resulting in heavier than average rainfall in areas of the Americas (Shimizu,
98 Ambrizzi, & Liebmann, 2017), including the Arctic region (Trenberth, 1990) and
99 drier conditions in Australasia. In the central Pacific and East Asia, extreme La Niña
100 phases cause anticyclones with fine, calm weather (Wang, Wu, & Fu, 2000). The
101 Neutral state is when neither El Niño nor La Niña is occurs, and conditions are
102 generally moderate.

103 In Australia, ENSO amplifies inter-annual climate variation and alters
104 vegetation productivity, which underpins the provision of food resources for birds.
105 Birds typically breed when food resources are most abundant (Cockrem, 1995; Dunn
106 & Winkler, 2010) and breeding activity can be driven, maintained or inhibited by
107 food abundance (Both, 2010; Visser, Noordwijk, Tinbergen, & Lessells, 1998; Zann,
108 Morton, Jones, & Burley, 1995). The likelihood of wet/mild climate conditions
109 occurring during the breeding season increases during La Niña phases of ENSO (Fig.
110 1). Conversely, dry/hot conditions are more common during El Niño events (Nicholls,
111 1991; Suppiah & Hennessy, 1998). During El Niño events, a reduction in cloud cover

112 usually results in increased maximum daily temperatures as well as the incidence of
113 frost (i.e. frost is 20% more common in eastern and south-eastern Australia during El
114 Niño) (Alexander & Hayman, 2008; Nicholls, 1991). Variability in temperature and
115 rainfall sometimes results in dramatic year-to-year changes in vegetation, and as a
116 result, some areas of Australia do not have a long-term static vegetation state
117 (Nicholls, 1991).

118 Due to extreme variation in weather patterns caused by ENSO, we expect that
119 some avian breeding responses to climate should be general. For example, mild,
120 warm, wet conditions at the beginning of the breeding season result in earlier
121 breeding (Chambers, Gibbs, et al., 2008; Chambers, Quin, Franklin, & Smales, 2008;
122 Forchhammer et al., 1998; Gibbs, 2007; Vilina et al., 2002; Wilson & Arcese, 2003).
123 Additionally, increases in breeding intensity have been reported under these climatic
124 conditions (i.e. more individuals breeding at a given time or an increased number of
125 fledglings per female), although this may not always lead to population growth
126 (Wilson & Arcese, 2003). Jaksic & Fariña (2010) showed how, during wet phases of
127 ENSO, nesting failure and chick mortality may result from nest flooding, while
128 breeding success was reduced during dry phases as a result of depleted of food
129 resources. In granivorous and insectivorous land birds, increases in primary
130 productivity during the wet phases of ENSO increased abundance, however in some
131 carnivorous species the response is delayed, potentially to coincide with an increase in
132 mammal populations (Jaksic & Fariña, 2010).

133 Here we assess changes in avian breeding phenology, in relation to climate
134 variability associated with ENSO in Australia, over the period 1900 to 2016. We
135 assess 64 species of birds from 11 orders the temperate region, and 15 species in 6
136 orders from the arid region (desert and grassland biomes combined). Species

137 examined include land birds and inland water birds, which meet a minimum
138 requirement of 100 unique observations (date and location), during each of the three
139 phases of ENSO: El Niño, La Niña or Neutral. Using these groups, we evaluate
140 variation in breeding phenology (start, conclusion, and length of breeding period), and
141 we determine the relationships between the timing of egg-laying and decadal climate
142 oscillations. We hypothesise that the intensity and duration of avian breeding will be
143 optimised to occur when food resources are most abundant and physiological stress
144 (due to extremely hot conditions) is low. Thus, there should be significant differences
145 in breeding duration during El Niño and La Niña, relative to the Neutral ENSO phase
146 (a phase which is largely ignored in studies that assess species responses to ENSO
147 phases; Jaksic & Fariña, 2010). Changes in vegetation productivity and associated
148 food resources during La Niña and El Niño phases should influence the start, length,
149 peak and conclusion of breeding (Fig. 1). We predict that relative to Neutral phases:

- 150 (1) the start of the egg-laying period (Fig. 1B) should begin earlier in
151 the year during the La Niña phases (Fig. 1C) and later in the year
152 during the El Niño phases, particularly for desert breeding species
153 which are known to delay, or forego breeding when conditions are
154 not suitable (Morton et al., 2011; Williams & Middleton, 2008);
- 155 (2) the length of the egg-laying period (number of days between start
156 and conclusion of the egg-laying period, Fig. 1B) will be longer
157 during La Niña phases and shorter during El Niño phases (Fig. 1C)
158 with stronger results for species that breed primarily in the spring
159 months;

160 (3) relative to the Neutral phase, the peak and conclusion of the egg-
161 laying period (Fig. 1B) during La Niña phases will be later in the
162 year (Fig. 1C), and earlier in the year during El Niño phase.

163

164 **METHODS**

165

166 *Climate and environmental data*

167 The Australian Government Bureau of Meteorology (<http://www.bom.gov.au/>)
168 defines historical El Niño and La Niña events and records the Southern Oscillation
169 Index (SOI) for Australia. We used these to characterise as many breeding years as
170 possible, since 1900, into one of three phases of ENSO (Fig. 2). A breeding year was
171 defined as the period between July-June (of the following year), rather than a typical
172 calendar year (January-December) because winter months have the lowest breeding
173 incidence in the Australian temperate and arid regions (Englert Duursma, Gallagher,
174 & Griffith, 2017). For this study, a La Niña or El Niño breeding year is defined as
175 those years where these ENSO phases are sustained for at least seven months ($n = 26$
176 La Niña years, and $n = 22$ El Niño years). A Neutral breeding year is defined by the
177 SOI being above -8 and below 8 (Bureau of Meteorology, 2012) and having no La
178 Niña or El Niño events occur for at least ten of the twelve months ($n = 46$ Neutral
179 years). SOI values were downloaded from
180 www.bom.gov.au/climate/enso/soi_monthly.txt (July 25th, 2017). Years that had a
181 high degree of variability and could not be confidently classified as ENSO phases
182 were excluded ($n = 23$ years). See Appendix S1 in Supporting Information for a table
183 of breeding years and the associated ENSO phase.

184 We assessed breeding patterns across two Australian regions: temperate and
185 arid. Region boundaries were based on a national modified Köppen classification
186 system (Bureau of Meteorology, 2006; Stern, de Hoedt, & Ernst, 2000) where the
187 desert and grassland biomes were combined to define the arid region.

188 Elevation and latitude are known to affect the breeding dates of Australian
189 birds (Gibbs et al., 2011) and climate is typically milder in coastal regions (see Fig.
190 1). Gridded data from a digital elevation model of Australia and the distance to a
191 generalized coastline of Australia were obtained from ANUClimate 1.0 (Hutchinson,
192 Stein, & Stein, 2014; Hutchinson & Xu, 2014) via <http://dap.nci.org.au>. The
193 resolution of these data is $0.01^\circ \times 0.01^\circ$.

194

195 *Avian observations*

196 All species used in the analyses met a minimum requirement of having ≥ 100
197 breeding observations during each of the three ENSO phases (i.e. we assessed the
198 same species across all phases). Breeding observations (characterized by their
199 latitude, longitude, and date) were combined from conventional sources of avian
200 breeding (i.e. Birdlife Australia's Atlas (Barrett, Silcocks, Berry, Cunningham, &
201 Poulter, 2003) and the Australian Nest Record Scheme), and non-conventional
202 sources (i.e. historical museum egg collections, Australian Bird and Bat Banding
203 Scheme, and eBird, 2015) following the methods used in Englert Duursma et al.
204 (2017).

205 Breeding observations were limited to those occurring after 1900 to match the
206 temporal range of climate data for characterising El Niño, La Niña, and Neutral years.
207 To prevent potential replication of observations, due to variation in sampling
208 techniques or life history traits (e.g. surveys of species that nest in breeding colonies

209 or intensive mist-netting in one location), observations were limited to one unique
210 observation per location and date for each species. Additionally, for observations
211 from the Nest Record Scheme, where nests are visited more than one time, we
212 calculated a single date when the first egg was laid (following methods used in
213 Englert Duursma et al., 2017).

214 Observations were divided into four types and the date the first egg was laid in
215 each nest (FEDs) was calculated based on the methods and trait data presented in
216 Englert Duursma et al. (2017): *multi-visit* (records where a nest was visited multiple
217 times, and at each visit the breeding stage was recorded; i.e. egg, egg hatch, or
218 young), *egg* (single observation of eggs), *young* (single observation of young), and
219 *undefined* (observation of breeding but no information of breeding stage). Briefly, our
220 approach was to back-calculate the date of each breeding occurrence record to the
221 FEDs by subtracting one or more species-specific life-history periods: the period of
222 lay (number of days taken to lay an average clutch), length of incubation, and
223 fledging period. The exact back-calculation methods differed by the observation type.
224 For example, to find a FED of an *egg*, we assume two possibilities: i) all egg-laying is
225 complete, but incubation has not begun; thus we subtract the period of lay from the
226 observation date. ii) Incubation is complete, but eggs have not hatched. Thus we
227 subtract both the length of incubation and the period of lay. The mid-point of the
228 earliest and latest possible FEDs, is the final FED date.

229 High accuracy observations (*multi-visit*, *young*, and *eggs*) are preferred, and
230 for species that had at least 100 of these observations in each ENSO phase (temperate
231 region, $n = 25$; arid region, $n = 9$), we excluded *undefined* observations because of
232 their lower accuracy in defining breeding stage (Englert Duursma et al., 2017). For
233 species that did not have 100 high accuracy breeding observations, we included

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

240

241 ***Egg-laying phenology***

242 To calculate egg-laying phenology for each species during the three ENSO phases, we
243 used the package *circular* (Agostinelli & Lund, 2017) in R version 3.4.2 (R Core
244 Team, 2017). For each phase and species, we assessed three parameters: start,
245 conclusion and length of the egg-laying period. These parameters correspond with the
246 5th, 95th, and the number of days between the 5th and 95th percentiles, respectively,
247 during El Niño, La Niña and Neutral phases. Circular statistics with a median-
248 unbiased quantile estimator (Hyndman & Fan, 1996) were used to account for
249 breeding over the turn of a year. See Appendix S3 in Supporting Information for the
250 start, conclusion and length of the egg-laying periods for each species in our study.

251

252 ***Statistical analysis***

253 All analyses were carried out in R version 3.4.2 (R Core Team, 2017). In addition to
254 base functions, we used the packages *raster* (Hijmans, 2016), *maptools* (Bivand &
255 Lewin-Koh, 2017) *circular* (Agostinelli & Lund, 2017), *data.table* (Dowle &
256 Srinivasan, 2017), *MuMIn* (Bartoń, 2017) and *visreg* (Breheny & Burchett, 2017) for
257 data extraction, manipulation, and visualisation, and assessment. Statistical tests were
258 considered significant at $p < 0.05$ and results are reported as mean \pm the standard

259 deviation unless otherwise noted. Analyses were performed independently for the
260 temperate and arid regions, and the distinct tests are detailed below.

261 To assess if avian observations were spatially autocorrelated, we fit a linear
262 mixed-effect model and calculated a spatio-temporal sample variogram of the model
263 residuals using the R package *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2017). The
264 linear mixed-effect model was such that we tested if all individual observations of
265 breeding occurrence back-calculated FEDs differed by ENSO phase. Random effects
266 were species nested in taxonomic order, and fixed effects were elevation, distance to
267 coast and latitude of the observation. Elevation and distance to coast were \log_{10}
268 transformed to stabilize variance. The plot of the semi-variance of the model residuals
269 was horizontal indicating little or no evidence of spatial autocorrelation (Zuur, Ieno,
270 Walker, Saveliev, & Smith, 2009).

271

272 *Peak of breeding*

273 We fit a linear mixed-effect model to determine if all individual observations
274 of breeding occurrence FEDs (i.e. all breeding occurrence records back-calculated to
275 the date that the first egg was laid in a nest) differed significantly across the three
276 phases: El Niño, La Niña or Neutral, using the function *lmer* in the R package *lme4*
277 (Bates, Mächler, Bolker, & Walker, 2015). Species, taxonomic order, year of
278 observation and a binary variable indicating if a species included *undefined* breeding
279 observations were random effects with differing intercepts. We also included a
280 random factor of ENSO phase for each species' FEDs to account for differences in
281 direction and magnitude of breeding within a species between ENSO phases. The
282 binary variable was included to account for potential bias in observational data quality
283 for species that included *undefined* breeding observations. The taxonomic order was

284 included to account for the potential effect of shared ancestry. The model also
285 included elevation, distance to coast and latitude of the observation, as fixed effects.
286 Elevation and distance to coast were \log_{10} transformed to stabilize variance, and we
287 included an interaction between these two variables. ANOVA was calculated using
288 Analysis of Deviance Table (Type II with Satterthwaite approximation for degrees of
289 freedom) using the R package *lmerTest* (Kuznetsova, Brockhoff, & Christensen,
290 2016).

291

292 *Length of breeding*

293 We used linear mixed-effect models to assess the relationships between
294 changes in the length and conclusion of the egg-laying period for each species during
295 the different phases. We used one data-point per species-phase comparison to show
296 the percentage change in the number of days in the breeding period length during a)
297 La Niña and Neutral and b) El Niño and Neutral. Similarly, we used the date of the
298 year that each species concluded breeding during the Neutral phase (e.g. one data-
299 point per species of the date of the 95th percentile of all breeding observations).
300 Comparisons between phases were included as fixed effects in the models with an
301 interaction term with the date of the year. The taxonomic order was included as a
302 random effect with a random slope and intercept for phase comparisons. ANOVA was
303 calculated as described previously.

304

305 *Start and conclusion of breeding*

306 We used linear mixed-effect models to assess if there were significant
307 differences in the start or conclusion of the egg-laying period between a) La Niña and
308 Neutral and b) El Niño and Neutral. As with the length of breeding, for both the start

309 and conclusion of breeding, we used one data-point per species-phase of the date that
310 the species either started egg-laying (e.g. the date of 5th percentile of all breeding
311 observations) or concluded egg-laying (e.g. the date of the 95th percentile of all
312 breeding observations). Comparisons between phases were included as fixed effects
313 in the models, and taxonomic order was included as a random effect with a random
314 slope and intercept for phase comparisons. ANOVA was calculated as described
315 previously.

316

317 **RESULTS**

318 *Start of the egg-laying period*

319 The ENSO phase did not influence the start of the breeding period in a uniform
320 way across all species in the temperate or arid regions ($p = 0.83$ and $p = 0.35$,
321 respectively). In the temperate region, 59% of species had earlier starts to the egg-
322 laying period during La Niña phases when compared to the Neutral phases, and 42%
323 of species had later starts during El Niño compared to the Neutral phases. In the arid
324 region, 87% of species had earlier starts to the egg-laying period during La Niña, and
325 40% started later during El Niño, compared to the Neutral phases (see Table 2 for
326 mean start dates to the egg-laying periods across all species and Appendix S3 for
327 species-level results).

328

329 *Length of the egg-laying period*

330 In the temperate region, La Niña phases affected the length of the egg-laying
331 period particularly for species that concluded egg-laying earlier in the year ($F(1,$
332 $119.2) = 4.97, p < 0.05$; conditional $R^2 = 0.39$; marginal $R^2 = 0.10$). We did not find

333 evidence that species that primarily breed in the spring months were more affected by
334 El Niño (Fig. 3a).

335 In the arid region, both La Niña and El Niño affected the length of the egg-
336 laying period ($F(1, 10.5) = 6.91, p < 0.05$). There was a positive increase in the
337 breeding period length, in both phases, for species that breed early in the year when
338 compared to Neutral phase (Fig. 3b).

339

340 ***Peak and conclusion of the egg-laying period***

341 ENSO influenced the peak of avian egg-laying in Australia's temperate and
342 arid regions. In the temperate region, the average peak dates (linear mixed-effect
343 group means after controlling for covariates) across the 64 species were significantly
344 different depending on ENSO phase ($F(2, 351) = 128.0, p < 0.001$; see Table 1 for
345 model residuals). The peak during Neutral phases, across all species, was on day
346 273.7 ($SE = 5.6$; see Table 2 for peak dates of all regions). Relative to Neutral phases,
347 the peak during the La Niña and El Niño phases were 29.3 days and 15.8 days later,
348 respectively.

349 In the arid region, ENSO phases significantly influenced the peak of avian
350 egg-laying across the 15 species assessed ($F(2, 33.3) = 5.01, p < 0.05$; see Table 1 for
351 model residuals). Based on our linear mixed-effect model, the average peak during El
352 Niño phases (mean FED = 249.7, $SE = 6.5$) was nine days earlier than during the
353 Neutral phases, but there was no significant difference between La Niña and Neutral
354 phases (see Table 2 for all phases' average peak dates).

355 ENSO phase did not influence the conclusion of the egg-laying period in the
356 temperate or arid regions ($p = 0.51$ and $p = 0.98$, respectively).

357

358 **DISCUSSION**

359 We hypothesised that the start of the egg-laying period, for Australian temperate and
360 arid birds, should begin earlier in the year during La Niña phases and later during El
361 Niño phases when compared to Neutral phases. We did not find evidence to support
362 this hypothesis. Instead, it appears that species respond in a variety of ways. For
363 instance, in the temperate region during the La Niña phases, just over half the species
364 (59%) had earlier starts to the egg-laying period (see Appendix S3 for species-level
365 results), while the remaining species had no change, or later starts. In the arid region,
366 87% of species had earlier starts to the egg-laying periods during La Niña but with a
367 large amount of variation across species. On average, egg-laying periods began 19
368 days (\pm 36 days) earlier during La Niña in the arid region (see Table 2 for mean start
369 dates, across all species, to the egg-laying periods). Additionally, during El Niño
370 phases most species did not start breeding later in the year, relative to the Neutral
371 phases, contradicting our initial hypothesis.

372 We found that La Niña events, which are characterised by mild/wet
373 conditions, have a positive impact on avian breeding phenology in the Australian
374 temperate and arid regions, supporting our second hypothesis. Specifically, we found
375 that the length of the egg-laying period is longer during La Niña phases, especially for
376 species that breed in the spring months (Fig. 3). Conversely, we did not find that the
377 length of the egg-laying period was shorter during El Niño phases. For example, 64%
378 of species in the temperate region and 80% of species in the arid region had longer
379 breeding periods during La Niña phases when compared to the Neutral phases, but
380 during El Niño only 44% of species in the temperate region and 40% of species in the
381 arid region had shorter breeding periods when compared to Neutral phases. This
382 pattern suggests that associated increases in vegetation productivity and food

383 resources during the wet/mild conditions of the La Niña phases may play a role in
384 extending breeding seasons in birds, as observed in many studies where breeding
385 begins earlier in the year during the mild and wet phases of climatic oscillations
386 (Chambers, Gibbs, et al., 2008; Chambers, Quin, et al., 2008; Forchhammer et al.,
387 1998; Gibbs, 2007; Vilina et al., 2002; Wilson & Arcese, 2003).

388 In the temperate region, the peak of the egg-laying period was later in the year
389 during La Niña phases, relative to the Neutral phases as hypothesised. In the arid
390 region, there was no difference between the peak during La Niña relative to Neutral
391 phases, but the average peak during El Niño phases was nine days earlier in the year
392 than during Neutral phases (Table 2).

393 The actual effects of climate on breeding phenology in the arid region of
394 Australia may be influenced by the ability of highly mobile species to
395 opportunistically move and breed to exploit localized rainfall in dry periods.
396 Therefore, a species might breed uniformly over a large area during La Niña or
397 Neutral phases and only in a few select locations during El Niño. An assessment of 42
398 species in the arid and semiarid regions of Australia found that species distributions
399 varied considerably over time and key areas of refugia were located in central-north
400 Australia (Runge, Tulloch, Possingham, Tulloch, & Fuller, 2016). If species breed for
401 the same length of time in refugia relative to their wider range, then measures of
402 phenology may not differ despite changes to breeding success and location. This may
403 explain the lack of support we found for our first and third hypothesis and future
404 studies should identify methods to distinguish how differences in breeding patterns
405 may play out across the landscape.

406 Australian birds exhibit a high degree of opportunism and breed in response to
407 localised rainfall patterns (Davies, 1977; Gibbs et al., 2011; Zann et al., 1995),

408 although there is emerging evidence that hot temperatures also constrain breeding
409 times in the desert (Englert Duursma et al., 2017). Birds are typically highly mobile
410 and may seek out more favourable conditions in the landscape, or may forego
411 breeding altogether when conditions are not suitable in a particular year (Morton et
412 al., 2011; Williams & Middleton, 2008). These breeding characteristics may explain
413 some of the similarity of average peak dates during Neutral and La Niña phases in the
414 arid region in this study. Additionally, opportunism likely contributes to the extensive
415 breeding periods we observed for some species (see Appendix S3 for species-level
416 results).

417 While there are numerous studies that have explored breeding responses to El
418 Niño and La Niña phases, fewer studies have tested hypotheses relative to baseline
419 conditions during the Neutral phases (Jaksic & Fariña, 2010). We have demonstrated
420 the importance of including this phase comparison when assessing bird phenology.
421 For instance, if we focus only on La Niña and El Niño years in Australia since 1900,
422 this study would have assessed only 41% of all years of available breeding data. If we
423 further limited our analysis to the strongest events (12 years in La Niña and 12 in El
424 Niño; <http://www.bom.gov.au/>) 79% of years would have been ignored. Further, if we
425 only compared the La Niña and El Niño phases, we would not have identified the
426 seasonal effect of both phases in the arid region (Fig. 3) nor the month later peak
427 during La Niña, relative to the Neutral phase, in the temperate region (Table 2).

428 The differences in breeding responses to decadal climate variation showed in
429 this study support previous findings from both the Southern and Northern
430 Hemispheres. In the Northern Hemisphere, variation in breeding has been noted in
431 response to the North Atlantic Oscillation (Ahola et al., 2004; Sandvik, Coulson, &
432 Sæther, 2008), with a change in the size of the first clutch (Møller, 2002), and

433 fluctuations in the timing and success of breeding (Ahola et al., 2004; Sandvik et al.,
434 2008). In Australia, several studies have shown that breeding intensity increases
435 during the wet, mild years of La Niña but the timing of breeding is not consistently
436 related to the Southern Oscillation Index (Beaumont et al., 2015; Chambers &
437 Keatley, 2010; Gibbs et al., 2011). These studies have been limited to single, or low
438 numbers of, species. Our study is the first to examine patterns across suites of species
439 sharing a biome, offering a novel comparative understanding of birds breeding, and
440 providing more specific conclusions for key regions.

441 It is also worth noting that SOI values – which are routinely used to
442 characterise phases – can be both high and low without La Niña or El Niño events
443 occurring. Therefore, SOI may not be an appropriate metric for many phenological
444 investigations. We found substantial variation in the response across species,
445 indicating general effects of ENSO phases. We also identified a seasonal effect in bird
446 breeding phenology where, on average, species that breed before the turn of the year
447 are affected to a greater degree than those who breed later. This seasonal pattern
448 contributes to differences in breeding times across the 64 temperate species and 15
449 arid species examined.

450 Seasonal trends in breeding were observed in both the temperate and arid
451 regions with spring breeding species having a greater response to ENSO phases. This,
452 in addition to the similarity of the average peak egg-laying dates during Neutral and
453 La Niña phases, supports previous findings that in the desert the timing of breeding
454 may be more constrained by temperature than by rainfall (Englert Duursma,
455 Gallagher, & Griffith, In review; Englert Duursma et al., 2017). During the summer
456 months (Dec – Feb) daily maximum temperatures in the arid region average between
457 33°C and 39°C and can exceed 45°C (Jones, Wang, & Fawcett, 2009). The upper

458 thermal limit of passerine egg temperatures is between 43°C and 44°C, with
459 prolonged exposure to high ambient temperatures being lethal (DuRant, Hopkins,
460 Hepp, & Walters, 2013; Stoleson & Beissinger, 1999; Webb, 1987). Adverse effects
461 on sperm quality have also demonstrated in response to experimental, ecologically
462 relevant heat exposure (Hurley, McDiarmid, Friesen, Griffith, & Rowe, 2018).
463 Therefore, adverse physiological effects on adults and offspring may compromise
464 breeding success during hot summer months.

465

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

467 It is well established that climate influences the demography and recruitment of avian
468 populations (Brawn, Benson, Stager, Sly, & Tarwater, 2017; Crick, 2004; McCauley,
469 Ribic, Pomara, & Zuckerberg, 2017; Sandvik et al., 2008) with several studies finding
470 that this relationship strongest for the first broods of the year (Järvinen, 1996; Møller,
471 2002; Winkel & Hudde, 1997). In Australia, Morton *et al.* (2011) explored the pulse
472 dynamics of the arid zone where heavy periodic rainfall characterises landscapes
473 leading to the episodic growth of perennial plants and flow-on effects to food
474 availability for birds. Australian birds are globally distinct in their levels of
475 opportunism and nomadism, with 30% of Australian desert birds displaying
476 opportunistic breeding, and more than 50 species of waterbirds breeding irregularly in
477 response to periodic flooding (Kingsford, Curtin, & Porter, 1999; Morton et al.,
478 2011). A recent study of opportunistic breeding in over half Australia's terrestrial bird
479 species found that the egg-laying periods in the northern hemisphere temperate region
480 was significantly shorter (61 ± 26 days) than in a climatically comparable region of
481 Australia (143 ± 42 days) (Englert Duursma et al., 2017).

482 Periods of population increase offer crucial opportunities for targeted
483 conservation efforts (Letnic & Dickman, 2010; Marsh & Trenham, 2001; Short,
484 Turner, Majors, & Leone, 1997). Natural increases in population numbers coupled
485 with decreased fire risk and (often) the deliberate reduction of competing or invasive
486 predators can improve species persistence (Garnett et al., 2013). While our study does
487 not explicitly test for changes in species recruitment and abundance during different
488 phases, the average number of observations per breeding year of El Niño and Neutral,
489 were 40% and 36% less than during La Niña years. Given that the data we have used
490 were captured across a range of non-systematic methods, with collection effort
491 presumably random with respect to ENSO phases, we believe that the number of
492 observations collected across the different phases provides some indication of
493 breeding intensity. If this assumption holds true, then birds were breeding at a greater
494 intensity with a higher number of reproductive attempts during the mild/wet La Niña
495 phases. This interpretation is consistent with the findings of Gibbs *et al.* (2011) who
496 reported the intensity of breeding in birds increased during the favourable La Niña
497 phases. This means that the La Niña phases of the ENSO provide an excellent
498 opportunity for conservation efforts for terrestrial species in Australia.

499

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513

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739

740 **DATA ACCESSIBILITY STATEMENT**

741 The data and code used in this study is available upon request.

742

743 **BIOSKETCH**

744 The authors are based at the Department of Biological Sciences, Macquarie

745 University. Their collaboration brings together expertise in spatial ecology and avian

746 biology to explore how climate shape the life history and behaviour of Australia's

747 native bird species. DED, SCG, RVG conceived the ideas; DED collated and vetted

748 data; DED analysed the data; All authors contributed to the writing.

749

750 **TABLES**

751 **Table 1.** Variable importance for explaining the timing of avian egg-laying in the
 752 temperate and arid regions of Australia during the El Niño, La Niña and Neutral
 753 phases of ENSO. Means, standard errors, and the significance are for the regression
 754 coefficients from the linear mixed-effect models for the temperate and arid regions of
 755 Australia.

Temperate region		
Fixed effects	Mean (\pm SE)	<i>P</i>
Intercept	238.6 \pm 6.1	
log(Elev)	-1.5 \pm 0.6	<0.05
log(Dist)	-12.4 \pm 0.9	<0.001
Lat	-1.2 \pm 0.1	<0.001
log(Elev) : log(Dist.)	4.9 \pm 0.4	<0.001
Random effects	Variance	
Year	450.4	
Species	825.4	
Order	48.7	
Accuracy	0.0	
<i>Conditional R²</i>	0.55	
<i>Marginal R²</i>	0.06	
Arid region		
Fixed effects	Mean (\pm SE)	<i>P</i>
Intercept	188.8 \pm 7.6	
log(Elev)	-10.7 \pm 2.5	<0.001
log(Dist)	-10.3 \pm 2.0	<0.001
Lat	-2.9 \pm 0.1	<0.001
log(Elev) : log(Dist.)	5.1 \pm 1.2	<0.001
Random effects	Variance	
Year	138.7	
Species	420.9	
Order	0.0	
Accuracy	4.2	
<i>Conditional R²</i>	0.37	
<i>Marginal R²</i>	0.06	

756

757

758 **Table 2.** Average phenology and egg-laying periods for 64 species of birds in the
759 temperate region and 15 species in the arid region of Australia. The start and
760 conclusion of the egg-laying period (i.e. 5th, 95th percentiles of all breeding
761 observations back calculated to the date that the first egg in each nest was laid,
762 respectively), and peak of the egg-laying period are given as the day of the year. The
763 egg-laying period is the number of days between the 5th and 95th percentiles. Values
764 are given as the mean across all the species in a region \pm the standard deviation in
765 days, unless otherwise noted.

	Start	Conclusion	Egg-laying period	Peak (\pm SE)
Temperate				
La Niña	218 \pm 42	10 \pm 42	156 \pm 43	303.1 \pm 5.9
El Niño	222 \pm 39	3 \pm 41	146 \pm 47	289.5 \pm 5.8
Neutral	222 \pm 39	4 \pm 39	147 \pm 46	273.7 \pm 5.6
Arid				
La Niña	163 \pm 49	342 \pm 51	179 \pm 63	260.7 \pm 7.4
El Niño	175 \pm 51	344 \pm 51	170 \pm 68	249.7 \pm 6.5
Neutral	182 \pm 40	345 \pm 50	163 \pm 68	258.9 \pm 5.8

766

767 **FIGURES**

768 **Figure 1.** Variation in rainfall during the three phases of ENSO and the hypothesised
769 effect of variation in climate on avian breeding phenology during El Niño, La Niña,
770 and Neutral phases. (a) Rainfall deciles showing a ranking based on the amount of
771 rainfall during the winter and spring months within each 50km x 50km grid-cell
772 compared to the average for the period 1900 – 2016. A mean rainfall decile of range
773 10 indicates that the grid cell has average rainfall values higher than 90% of other
774 observations. Conversely, a decile value of 1 indicates the grid cell falls in the bottom
775 10% of observations. Rainfall data comes from the Australian Water Availability
776 Project (Jones et al., 2009) via <http://www.bom.gov.au/jsp/awap/>. (b) Histogram
777 depicting an example of a species start and conclusion to the egg-laying period (i.e.
778 the 5th and 95th percentiles of egg-laying dates. Length of the egg-laying period is the
779 number of days between the 5th and 95th percentiles. (c) Hypothesised relationship of
780 egg-laying to ENSO phases. We predict that, on average, egg-laying will last longer,
781 begin earlier, and peak and conclude later in La Niña events relative to the Neutral
782 events as shown.

783

784 **Figure 2.** The density of breeding observations during La Niña, El Niño and Neutral
785 breeding years from 1900 to 2016. The short vertical lines show years defined as La
786 Niña, El Niño and Neutral breeding years. A breeding year is 12 months and extends
787 from July through to June. For more information see Appendix S1.

788

789 **Figure 3.** The relationship between the percentage change in the egg-laying periods
790 (ELP) during the El Niño and La Niña phases when compared to the Neutral phases

791 and the time of the year that egg-laying concludes during the Neutral phases in the (a)
792 Temperate and (b) arid regions of Australia.

793

794 **SUPPORTING INFORMATION**

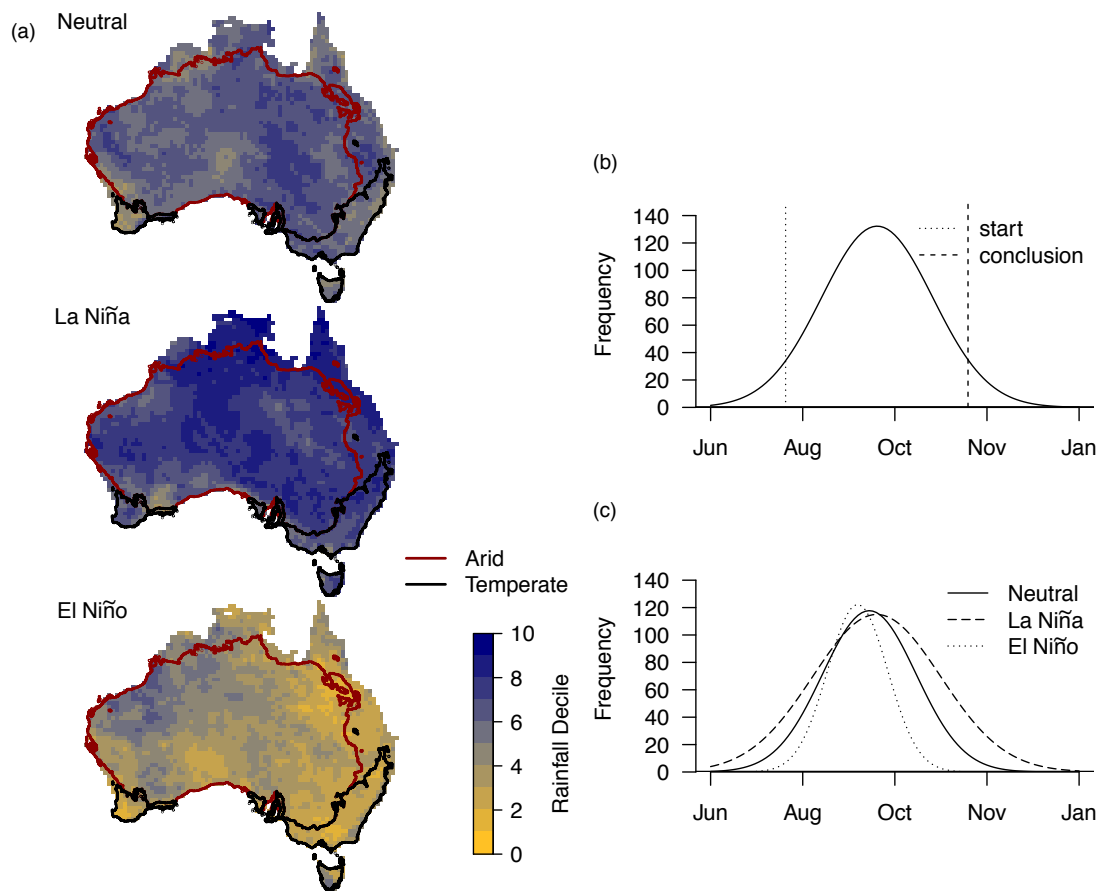
795 **Appendix S1** - La Niña, El Niño and Neutral breeding years from 1900 to 2016.

796 **Appendix S2** - Institutes and persons who either collected data or are custodians of
797 the observations used in this study.

798 **Appendix S3** – Starts, conclusions and length of the egg-laying periods for 64 species
799 of birds in the temperate region and 15 species in the arid region of Australia.

800

801 **Fig 1**



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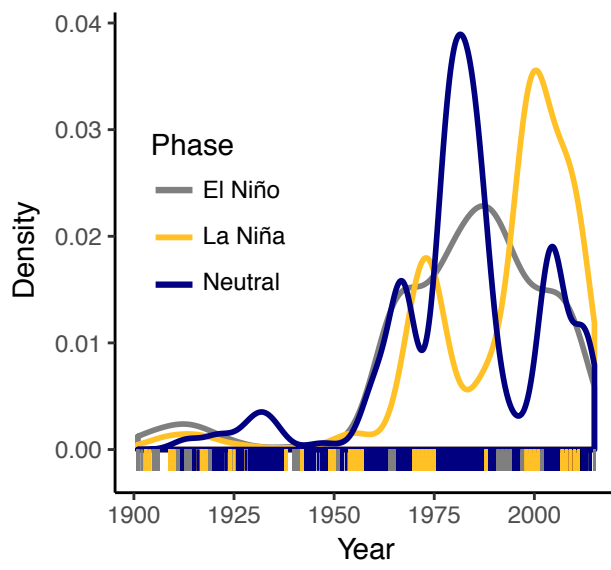
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809 **Fig 2**

810

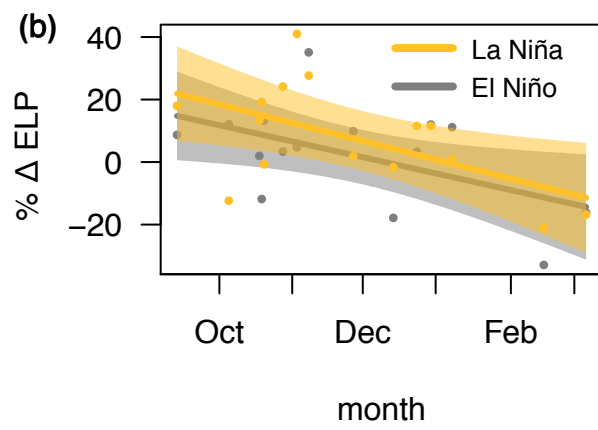
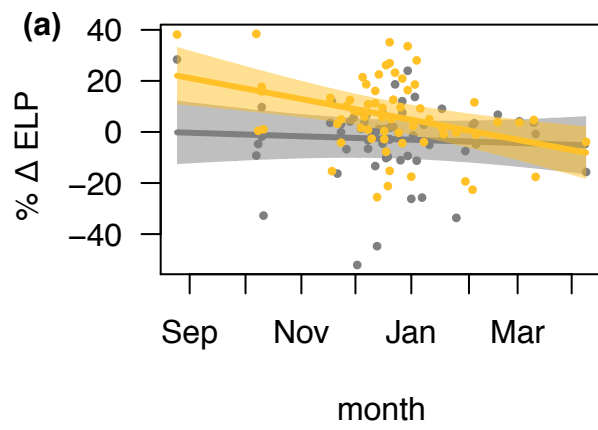


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814 **Fig 3**



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