



The biotic and abiotic drivers of timing of breeding and the consequences of breeding early in changing world

Sutton, Alex; Freeman, Nikole E

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1 **Review**

2

3 **The biotic and abiotic drivers of timing of breeding and the consequences of breeding early**
4 **in a changing world**

5

6

7 **Abstract**

8 The decision of when to breed is an important determinant of individual fitness. However,
9 despite a multitude of studies investigating the intra-specific relationship between timing of
10 breeding and reproductive performance, less is known about why the strength of this relationship
11 varies between species. Furthermore, environmental change has the potential to alter the
12 relationship between lay date and fitness, but there is still a limited understanding of what
13 mechanisms drive these differential responses to changing environmental conditions. We
14 propose that the potential effects of environmental change on the relationship between timing of
15 breeding and fitness is dependent on two primary factors: 1) the potential constraints imposed by
16 breeding early and 2) the drivers of higher fitness of early breeders. We first summarise multiple
17 hypotheses proposed to explain why breeding early, either based on absolute date or relative to
18 conspecifics, increases fitness. We then summarise the factors that may constrain when
19 individuals initiate breeding, including limits on the ability to advance their lay date or extend
20 the length of their breeding season under favourable conditions. Understanding constraints on the
21 timing of breeding allows for the identification of obligate (single brooded species that do not
22 attempt to breed after a specific date) and facultative (predominantly multi-brooding species that
23 have long breeding seasons) early breeding species that are likely differently affected by climate

24 change. Finally, we propose a simple mathematical formula that incorporates the costs and
25 benefits associated with early breeding to quantify how climate change could influence the
26 benefits of early breeding and either mitigate or exacerbate the costs. Our cost-benefit approach
27 provides a clear framework to predict how species may shift the timing of their breeding to
28 maximise fitness in a changing world.

29

30 *Keywords:* climate change, fitness, lay date, mismatch, ornithology, phenology, phenological
31 change, reproductive success

32

33 **Lay Summary**

- 34 • When individuals breed has important impacts on reproductive performance and
35 individual fitness
- 36 • We synthesise the literature on why breeding early is beneficial and why not all
37 individuals can breed early
- 38 • Environmental change will alter the benefits of breeding early and may impact some
39 species more than others
- 40 • We propose a cost-benefit framework to determine how environmental change influences
41 fitness and to predict future responses to a changing world
- 42 • We also provide guidance on how data could be extracted from existing datasets to apply
43 our cost-benefit framework to bird species in the wild

44 INTRODUCTION

45 When individuals breed is a key determinant of reproductive performance and individual fitness
46 (Winkler et al. 2020). The timing of breeding can have a variety of cascading effects that
47 determine the quality of territories available (Piersma 2013), the amount of resources available
48 throughout the breeding season (Both et al. 2006, 2010; Love et al. 2010), predation risk (Brown
49 and Brown 2000), and even the probability of offspring recruitment (Tomotani et al. 2016, 2018;
50 Zabala et al. 2020). Thus, if individuals breed outside of optimal conditions, they face short- and
51 potentially long-term consequences on reproductive performance and fitness. In the short term,
52 adults breeding in suboptimal conditions typically are unable to invest as much in reproduction.
53 This results in smaller clutches, smaller broods, and nestlings in poorer condition (Rowe et al.
54 1994, Varpe 2017) due to balancing investment in reproduction and their own survival. In the
55 long term, nestlings produced outside of optimal conditions are likely to have lower survival and
56 are less likely to recruit into the population (Zabala et al. 2020). Additionally, there can also be
57 consequences of breeding during suboptimal conditions that carry over to influence the
58 performance and survival of the breeder during subsequent periods of the annual cycle (Harrison
59 et al. 2011, Tomotani et al. 2018).

60 The drivers of optimal breeding conditions can be species specific but may also vary
61 across a species range (Winkler et al. 2002, Burgess et al. 2018, Bailey et al. 2022). Generally,
62 resource availability is thought to be the primary driver of optimal conditions, with individuals
63 aiming to time peak resources needs with peak resource abundance in the environment (Both et
64 al. 2006). Mismatches between peak need and peak abundance have been proposed to be a
65 leading cause of population declines, especially in seasonal environments (Visser et al. 1998,
66 Both et al. 2010, Dunn et al. 2011, Ceballos et al. 2017, Dunn 2019). Despite widespread focus

67 on the availability of resources, several other factors can influence the cost of breeding.
68 Predation, either of eggs, nestlings, fledglings, or adults, can be a major limiting factor
69 influencing the decision of when to breed. The risk of predation is typically not constant
70 throughout a breeding season and individuals may therefore time breeding to limit predation risk
71 during key periods of reproduction (Pienkowski 1984, Götmark 2002, Fontaine and Martin 2006,
72 Lima 2009).

73 Weather conditions can also play a major role in determining optimal breeding
74 conditions. Temperature can limit both the start and end of breeding seasons, with individuals
75 needing to wait for warm weather to initiate breeding and, in some habitats, finish reproducing
76 before temperatures become too hot to successfully raise young or significantly impact
77 reproductive performance (Salaberria et al. 2014, De la Cruz et al. 2022). Similar to temperature,
78 precipitation can also limit the timing of reproduction. Many species, especially at high latitudes
79 and elevations, must wait for snow to melt before they can start to reproduce (Pienkowski 1984,
80 Love et al. 2010, Lameris et al. 2019, Sander et al. 2021, 2023; Meltofte et al. 2021) while some
81 species use rain as a cue to initiate breeding (Dawson 2008, Hidalgo Aranzamendi et al. 2019).
82 Seasonal shifts in precipitation can also alter reproductive performance, and extremes (i.e. severe
83 drought or severe rainfall) may even prevent individuals from continuing to breed (Keast and
84 Marshall 1954, Drake and Martin 2020, Boyle et al. 2020). Collectively, individuals should
85 balance this suite of environmental conditions to determine when to breed in order to maximise
86 their reproductive performance.

87 A large number of studies have investigated the drivers of optimal breeding conditions,
88 but our understanding of these drivers and ecological phenomena more broadly (Pettorelli et al.
89 2021), is largely biased towards temperate ecosystems of Europe and North America. Temperate

90 ecosystems typically follow seasonal rhythms with distinct seasons characterized by concurrent
91 changes in temperature and precipitation (Gilliam 2016), each imposing well characterized
92 challenges for individuals. In contrast, many tropical ecosystems are more stable throughout the
93 year with respect to temperature, or follow different seasonal patterns, such as wet and dry
94 seasons (Murphy and Lugo 1986). This could in turn produce very different patterns of resource
95 availability that deviate away from more well studied patterns in temperate ecosystems. The
96 effects of seasonal shifts in environmental conditions in the global south and tropical ecosystems
97 have not been as widely investigated, meaning we still have an incomplete understanding if
98 avian responses to abiotic conditions and climate change in northern temperate ecosystems are
99 consistent with those in the global south or tropical ecosystems. As a result, it is important to not
100 over-generalize existing results and investigate potential mechanisms in a broad range of habitats
101 to work towards a more complete understanding of how these effects may vary geographically.

102

103 **Why breed early?**

104 Early breeding is widely advantageous regardless of species and geographic location (Sibly and
105 Calow 1986, but see Sander et al. 2021, 2023). Breeding early is associated with direct increases
106 in reproductive performance, resulting in higher clutch and brood sizes (Öberg et al. 2013,
107 Winkler et al. 2014, Meltofte et al. 2021), nest success (Saino et al. 2004, Norris et al. 2004,
108 Rockwell et al. 2012, de Zwaan et al. 2022), number of fledglings (Hochachka 1990,
109 Goodenough et al. 2009, Öberg et al. 2013), and juvenile recruitment (Hochachka 1990,
110 Verboven and Visser 1998, Norris et al. 2004). Additionally, breeding early can increase the
111 probability of success in a given season by providing additional time to reneest should a nest fail
112 (Halupka et al. 2021). Furthermore, for multi-brooded species, it can also allow enough time to

113 raise two or more broods in a given season and has been implicated as an important mechanism
114 to increase lifetime fitness (Saino et al. 2004, Jackson and Cresswell 2017, Zabala et al. 2020). In
115 addition to the positive benefits on reproduction, early breeding has previously been associated
116 with lower mortality of adults, potentially due to differential rates of predation within a season
117 but this relationship can vary between populations (Callery et al. 2022).

118 Given the multitude of positive benefits to breeding early (summarized in Table 1), a
119 large body of literature has proposed a variety of mechanisms to understand what factors
120 facilitate early breeding and why all individuals are not breeding early (Verhulst et al. 1995,
121 Verhulst and Nilsson 2008; Table 2). Two primary hypotheses have been proposed to explain the
122 strong relationship between lay date and reproductive performance; the ‘timing’ hypothesis
123 (Perrins 1970, Verhulst and Nilsson 2008) and the ‘individual quality’ hypothesis (Price et al.
124 1988, Verhulst and Tinbergen 1991, Harriman et al. 2017). The ‘timing’ hypothesis posits that
125 absolute timing of breeding (i.e. ordinal date) is important because of deteriorating
126 environmental conditions as the breeding season progresses (Perrins 1970, Siikamäki 1998,
127 Verboven et al. 2001). In contrast, the ‘individual quality’ hypothesis suggests that individuals of
128 lower quality breed later in the season or are forced to occupy lower quality territories, thus
129 limiting reproductive performance (Harriman et al. 2017, Winkler et al. 2020). These hypotheses
130 are not mutually exclusive and there has been support for each hypothesis separately or acting
131 together to drive seasonal declines in reproductive performance in the same system (Verhulst et
132 al. 1995, Verhulst and Nilsson 2008). However, while the ‘timing’ and ‘individual quality’
133 hypotheses are important generalisations, they often fail to focus on specific mechanisms that are
134 responsible for the observed relationship between lay date and performance.

135 The ‘timing’ hypothesis has been used to describe the general impact of absolute date on
136 reproductive performance and food availability is most often cited as the major driver of seasonal
137 trends (Verboven et al. 2001, Visser et al. 2021). While this can be helpful, it does not account
138 for inter-annual variability in timing of multiple resources or concurrent seasonal changes that
139 may influence optimal timing of breeding. As described above, there are several other
140 environmental variables that can limit reproductive performance and that vary throughout and
141 between breeding seasons. An overview of the possible mechanisms that underlie the ‘timing’
142 hypothesis is provided in Table 1, including reduced parasitism (Oien et al. 1996) and predation
143 (Callery et al. 2022), and increased offspring quality (Hochachka 1990, Verboven and Visser
144 1998) among a variety of others. Taking a more mechanistic approach and understanding the
145 primary drivers responsible for the general pattern of increased fitness of early breeders will be
146 essential to understand how the fitness benefits of early breeding may vary in the face of
147 environmental change.

148 While the ‘timing’ hypothesis focuses generally on the optimal time to breed, the
149 ‘individual quality’ hypothesis largely focuses on endogenous and exogenous conditions that
150 prevent individuals from breeding early or limit reproductive performance (Jacobs and Wingfield
151 2000). It is broadly expected that an individual will breed as early as it can in an effort to
152 maximise its fitness based on current conditions (Winkler et al. 2020, Zabala et al. 2020, Berzins
153 et al. 2020). The mechanisms that limit individual performance and as a result influence timing
154 of breeding are outlined in Table 2, but include individual condition (Rowe et al. 1994, Bêty et
155 al. 2003, Nomi et al. 2018, de Zwaan et al. 2022) and experience (Whelan et al. 2016, Johns et
156 al. 2017, de Villemereuil et al. 2019, Winkler et al. 2020). These mechanisms are largely related
157 to the endogenous sources of energy available to an individual, but also draw on the growing

158 field of ecophysiology to understand how individual responses to external conditions can limit
159 the amount of energy that can be devoted to reproduction. Central to the ‘individual quality’
160 hypothesis is a trade-off between investment in survival and reproduction (Sibly et al. 2012,
161 Callery et al. 2022). Lower quality individuals may have less energy, skewing the investment of
162 limited resources to their own survival rather than reproduction. These lower quality individuals
163 may in turn be forced to breed on lower quality territories (e.g., by late arrival to the breeding
164 grounds for migratory species (Janiszewski et al. 2014) or competition for space (Acker et al.
165 2022)) that further limit their ability to acquire key resources and invest energy in reproduction
166 (Price et al. 1988, Harriman et al. 2017). The ‘individual quality’ hypothesis is particularly useful
167 because it identifies that, despite the benefits of breeding early, individuals are constrained by a
168 suite of factors that may limit their ability to breed early to maximise fitness.

169

170 **Constraints on the timing of breeding**

171 Given the widespread fitness benefits of breeding early (Dunn and Møller 2014), a central
172 question in phenological research should be why not all individuals breed early. The most likely
173 explanation is that endogenous and exogenous factors can constrain initiation of reproduction,
174 preventing individuals from breeding during optimal windows. Endogenous factors have long
175 been a focus of research investigating constraints on early breeding (Jacobs and Wingfield 2000,
176 Williams 2012). One factor that has received particular attention is female condition (Rowe et al.
177 1994, Bêty et al. 2003, Nomi et al. 2018, de Zwaan et al. 2022), with a strong focus on fat stores
178 (Sandberg and Moore 1996, Smith and Moore 2003). The importance of endogenous energy
179 stores on reproduction cannot be understated, but several other factors (e.g., female age and
180 experience or decisions made during other periods of the annual cycle) have also been shown to

181 potentially constrain timing of breeding. Female experience could act as a major constraint, with
182 younger or more inexperienced individuals breeding later (Whelan et al. 2016, Johns et al. 2017,
183 de Villemereuil et al. 2019, Winkler et al. 2020, Burant et al. 2022). Decisions a female makes
184 throughout the annual cycle can also have indirect effects on when they initiate reproduction
185 (Norris et al. 2004, Selonen et al. 2021, de Zwaan et al. 2022). For example, decisions of where
186 to settle during the non-breeding period can directly influence energy supplies (Sandberg and
187 Moore 1996, Norris et al. 2004, Rockwell et al. 2012) and, for migratory species, the timing of
188 migration to the breeding grounds can have a strong influence on reproductive performance
189 (Smith and Moore 2005). Exogenous constraints on timing of breeding have also been proposed
190 but are likely to be more habitat and species-specific than endogenous constraints. Mate and
191 habitat quality can constrain timing of breeding, with lower quality mates and habitat generally
192 being associated with later lay dates (mate quality: Béziers and Roulin 2016, Whelan et al. 2016;
193 habitat quality: Kentie et al. 2018, Sumasgutner et al. 2020, Bailey et al. 2022). The effects of
194 endogenous and exogenous constraints can be further modulated by environmental conditions
195 and resource availability that can either strengthen or alleviate constraints on the timing of
196 individual breeding (Verhulst and Nilsson 2008, Johns et al. 2017, Kentie et al. 2018).

197 Some species are undeniably constrained with respect to breeding early, but there may
198 also be strong selective pressure against reproducing after a certain point in the breeding season.
199 For migratory species, there is a clear end to the breeding season, with individuals needing to
200 finish breeding in time to prepare for migration (Verhulst and Nilsson 2008). This preparation
201 can include moulting (Nilsson and Svensson 1996, Svensson and Nilsen 1997, Tomotani et al.
202 2016, 2018), developing necessary fat stores to fuel migration (Mitchell et al. 2011, Tomotani et
203 al. 2016), and moving from the breeding habitat to a staging ground used in the lead up to

204 migration. Aside from migration to non-breeding grounds, there may be other constraints on
205 timing of breeding that could influence reproductive decisions for both migratory and resident
206 species. One wide-spread phenomenon is single-brooded species not attempting to breed after a
207 given date (Gwinner 1989), suggesting that there may be strong selective pressure against
208 breeding too late in a given season despite seemingly having enough time to successfully rear
209 young with respect to developmental timelines (e.g., time taken from clutch initiation to fledge).
210 For example, Canada jays (*Perisoreus canadensis*) raise a single brood per season, have long
211 developmental periods, and will not attempt to breed after April 10 (Strickland and Ouellet
212 2020). Due to the time required to rear young to independence, many species remain single
213 brooded despite the potential to have a second brood even as breeding seasons are becoming
214 elongated with changing climate (Møller et al. 2010, Hällfors et al. 2020). For these species, in
215 conjunction with the potential benefits of breeding early, there may also be strong selective
216 pressure to breed early because they cannot successfully rear young later in the season.

217 Constraints on both initiation of breeding and the end of the breeding season likely act
218 synergistically to shape the adaptive benefits of the timing of breeding, in particular the benefits
219 of breeding early (Møller et al. 2010). To date, most research has focused primarily on the
220 constraints limiting the ability of some individuals to breed as early as possible to maximise
221 fitness. However, inter-specific variation in timing of breeding can also be important to consider
222 to better understand the underlying drivers of phenology. We propose that species can be broadly
223 categorised along a continuum into obligate and facultative early breeders based on general
224 patterns of when clutches are initiated (i.e. absolute date), the number of breeding attempts that
225 will be made in a given breeding season, whether multiple broods can be reared in a single
226 breeding season, if there is a date after which reproduction will not be attempted and when this

227 date falls relative to the end of conditions that are seemingly favourable for breeding, and
228 variability in lay date within the population (Figure 1).

229

230 *Obligate early breeders*

231 Obligate early breeders are characterised by several key traits. First, these species will be single
232 brooded because there is not enough time for them to successfully raise multiple broods within a
233 breeding season. Second, these species will have relatively long morphological or cognitive
234 developmental periods (e.g., species of albatross with incubation periods lasting 62 – 75 days
235 (Hasegawa and DeGange 1982, Weimerskirch et al. 1986) and nestling periods lasting an
236 additional 115 – 271 days (Weimerskirch et al. 1986). Slow development can also occur post-
237 fledge with some species having long periods where juveniles are reliant on their parents
238 (Uomini et al. 2020). Young could be reliant on adults after fledging for extended periods of time
239 as they learn specialised foraging behaviours (Uomini et al. 2020), or need to find suitable
240 habitat to begin preparing for subsequent periods of the annual cycle (Strickland 1991, Kokko
241 and Ekman 2002). Together, long incubation, nestling, and post-fledge periods could make it
242 almost impossible to rear multiple broods. Due to prolonged offspring development, obligate
243 early breeders are expected to experience the strongest seasonal declines in reproductive
244 performance (Figure 2a). Any delay in breeding is predicted to have a particularly pronounced
245 impact on juvenile recruitment because young from later in the season will be outcompeted for
246 resources or potentially not have sufficient time to develop. Thus, obligate early breeders may
247 have a hard cut-off point relatively early in the breeding season after which they will not breed,
248 despite conditions seemingly remaining favourable.

249 To facilitate breeding as early as possible, obligate early breeders will likely have
250 physiological or behavioural specialisations that allow them to cope with potentially
251 unfavourable environmental conditions. These could include, but are not limited to, increased
252 cold tolerance, morphological adaptations to environmental conditions such as specialised
253 feathers or feather structures (Lei et al. 2002, Williams et al. 2015), or the use of behavioural
254 strategies like food caching (Vander Wall 1990, Sutton et al. 2016) that allow individuals to
255 initiate breeding out of sync with general resource availability in the environment. Increased
256 tolerance of harsh environmental conditions will reduce variation in lay date because most
257 individuals will be able to breed early, even in unfavourable conditions, as long as they reach
258 breeding condition (Sechley et al. 2014). Inter-annual variation in lay date will still be present as
259 individuals potentially advance breeding to exploit favourable conditions, but initiation of
260 breeding will be relatively synchronous among individuals (Figure 1).

261

262 *Facultative early breeders*

263 In contrast to obligate early breeders, facultative early breeders nest early to maximise their
264 reproductive output, which is achieved by exploiting the benefits of breeding early similar to
265 obligate early breeders or by elongating the breeding season. Facultative early breeders are likely
266 to have the capacity to raise two or more broods within a season (Husby et al. 2009). Thus,
267 breeding early in the season provides more time to have multiple broods and allows subsequent
268 broods to be reared as early as possible. Complimenting their ability to be multi-brooded,
269 facultative early breeders are likely to have short developmental periods that facilitate multiple
270 broods being reared in a single breeding season. These species are also likely to have parental
271 care that allows for the division of labour (Grüebler and Naef-Daenzer 2010) or have non-

272 breeding helpers that allow parents to begin rearing the next brood while helpers care for the
273 fledglings from the first brood (Russell and Rowley 1988). For example, while females are
274 incubating a second clutch, males are caring for fledglings from the first brood (Verhulst and Hut
275 1996).

276 Facultative early breeders are predicted to have higher variation in lay date (Figure 2b),
277 especially when environmental conditions vary between years. Intra-annual variation in lay date
278 will likely be driven by variation in individual condition, while inter-annual variation in lay date
279 will result from natural fluctuations in environmental conditions. Because facultative early
280 breeders are not expected to have adaptations that facilitate early breeding like obligate early
281 breeders, they are predicted to be particularly susceptible to environmental conditions that may
282 delay breeding in some years and advance lay date in others (Figure 1).

283

284 *Inter-population and temporal variation in early breeding strategy*

285 Importantly, many of the characteristics that define obligate and facultative early breeders will
286 vary between species, but some species with large geographic ranges could also display inter-
287 population variation in early breeding strategy, especially at range extremes. For example,
288 European starlings (*Sturnus vulgaris*) are double-brooded across much of their range but will not
289 attempt a second brood above 48° latitude (Cabe 2020). This variation is likely due in large part
290 to environmental conditions truncating the length of the breeding season, preventing additional
291 investment in reproductive attempts. Studying intra-specific and inter-specific variation in early
292 breeding could help to elucidate not only how environmental conditions interact with life history
293 traits to shape patterns of reproductive investment, but also shed light on the benefits of early
294 breeding in the face of environmental change.

295 In changing environmental conditions, it may also be possible to see temporal variation in
296 early breeding strategies, with species shifting from obligate to facultative early breeders as
297 breeding seasons become elongated (Both et al. 2019). If constraints on timing of breeding are
298 generally relaxed, it could be possible for obligate early breeders to successfully raise multiple
299 clutches, depending on factors that set the end date for the breeding season. If this end date is
300 primarily a function of unfavourable environmental conditions, or due to a need to develop
301 sufficiently before the onset of unfavourable conditions (e.g., cold winter conditions), then a shift
302 from obligate to facultative early breeder could be possible in the future. Such a shift would
303 likely be associated with substantial increases in individual fitness (Halupka et al. 2021) but are
304 difficult to predict without understanding the underlying constraints on timing of breeding for a
305 given species.

306

307 *Year-round breeders*

308 Many avian species do not have a single distinct breeding season and instead have the capacity to
309 breed at any point of the year when conditions are favourable. For these species, breeding is
310 often a result of sudden changes in environmental conditions, such as the onset of precipitation
311 events after drought (Hau 2001), or the availability of resources (e.g., food; Benkman 1990, Hau
312 2001). Generally, year-round breeders are understudied and are primarily found in tropical or
313 unpredictable habitats of the global south. Because of the relative lack of study, it is unknown
314 whether similar declines in reproductive performance over the course of a breeding period (e.g.,
315 following the onset of favourable conditions) will manifest in these species. Few detailed studies
316 of these species have investigated the mechanisms driving variation in reproductive performance
317 (but see Benkman 1990, Hau 2001) and therefore more information is needed to quantify

318 patterns of reproductive performance and whether the extensive existing literature investigating
319 seasonal variation in reproductive performance of species with single breeding seasons can be
320 applied to this fascinating group of species.

321

322 **How does lay date change over time?**

323 In ornithology, most studies use lay date to investigate the relationship between timing of
324 breeding and fitness. Lay date is a complex trait and variation in when birds lay is driven by
325 genetic factors (Batt and Prince 1979, Sinervo and Doughty 1996, Van Der Jeugd and McCleery
326 2002, Gienapp et al. 2019), individual condition (Rowe et al. 1994, Bêty et al. 2003, Nomi et al.
327 2018, de Zwaan et al. 2022), species variation (Crick et al. 1997), and environmental drivers
328 (Verhulst and Nilsson 2008, Johns et al. 2017, Kentie et al. 2018). Shifts in lay date have been, at
329 least partially, attributed to a combination of differences in reproductive performance of early
330 breeders compared to late breeders and the heritability of lay date (Winkler et al. 2020).

331 However, a growing number of studies have noted that heritability estimates of lay date across
332 several species are low, but in some populations lay date may still be under selection (Van Der
333 Jeugd and McCleery 2002, Sheldon et al. 2003, de Villemereuil et al. 2019, Evans et al. 2020b,
334 de Villemereuil et al. 2020). Additionally, the influence of heritability on lay date might decrease
335 as individuals age if timing of laying is influenced by experience (Winkler et al. 2020).

336 Lay date may also vary due to intra-individual variation, whereby females adjust lay date
337 to match environmental conditions through plastic responses (Hoover and Schelsky 2020, Burant
338 et al. 2022, Kimmitt et al. 2022). Phenotypic plasticity, when a single genotype can produce
339 multiple phenotypes in response to environmental conditions (Pigliucci 2005), can contribute to
340 variation in lay date between years (Nussey et al. 2005, Brommer et al. 2008). Plasticity in

341 response to a number of environmental conditions has been observed including temperature
342 (Dunn 2004, Barrientos et al. 2009, Watts et al. 2018, McGuire et al. 2020), precipitation (Burant
343 et al. 2022, Mares et al. 2017), and even broad scale climatic oscillations (Wilson et al. 2007).
344 For example, multiple shorebird species began breeding earlier in response to warmer spring
345 conditions (McGuire et al. 2020), while exposure to high amounts of precipitation as nestlings
346 led to female Savannah sparrows (*Passerculus sandwichensis*) advancing their laying date more
347 rapidly than those exposed to lower levels of precipitation (Burant et al. 2022). Phenotypic
348 plasticity is likely the major driver of individual and population variation in lay date between
349 years, but additional biotic factors can determine the extent to which an individual can adjust
350 their lay date to match optimal conditions (Bründl et al. 2020).

351 Not all individuals are equally plastic, resulting in a differential ability to track optimal
352 breeding conditions as they change through time (Nussey et al. 2005, Brommer et al. 2008, de
353 Villemereuil et al. 2020). Certain genotypes are associated with increased plasticity and as
354 environments become increasingly variable, selection may be acting on phenotypic plasticity and
355 increasing the capacity of individuals to adjust their lay dates (Brommer et al. 2008, de
356 Villemereuil et al. 2020). More plastic individuals are expected to be better able to respond to
357 changing environmental cues to better match optimal environmental conditions. Understanding
358 ongoing selection on both timing of breeding and plasticity in lay date is essential to predict
359 future individual and population responses to climate change.

360 Lay date plasticity may also be shaped by extrinsic factors such as mate quality and
361 early-life conditions. Males can contribute to variation in lay date (Whelan et al. 2016, Evans et
362 al. 2020b) and their behaviour (e.g., courtship feeding) or experience can advance lay dates and
363 increase reproductive performance (Brommer et al. 2015, Whelan et al. 2016). Early-life

364 conditions could also play a key role in shaping subsequent female plasticity, with both
365 environmental and social factors acting as important drivers of subsequent plasticity. For
366 example, Savannah Sparrows exposed to higher rainfall as nestlings were able to advance their
367 lay date more strongly throughout their lives than those exposed to less rainfall (Burant et al.
368 2022). Additionally, Canada Jays show differential patterns of senescence associated with
369 initiating reproduction, where individuals who were ejected from their natal territory by their
370 dominant sibling experience greater delays in lay date as they age than the dominant sibling
371 (Sorensen et al. 2022). This work demonstrates that female plasticity is a major driver of
372 variation in lay dates over time, but a combination of genetic and environmental conditions
373 should be considered to understand the scope of individual-level plasticity.

374

375

376 **Understanding the benefits of early breeding**

377 The date when individuals breed both within a year (absolute date) and relative to conspecific
378 and heterospecific competitors (relative date) are important predictors of fitness. The fitness
379 benefit gained from absolute date is expected to be sensitive to both biotic and abiotic
380 environmental conditions. In many systems, both temperature and precipitation regimes become
381 more extreme as the season progresses, which likely explain at least part of seasonal declines in
382 reproductive performance (Salaberria et al. 2014, De la Cruz et al. 2022). Concurrent changes in
383 resource availability, which may also be driven by changing environmental conditions, would
384 also be strongly linked with the relative fitness benefit derived from absolute date. For example,
385 if resources are available for a long period of time and not concentrated in a single peak, there
386 will be less pressure to breed early. In contrast, if resources are generally limited there will be

387 strong selective pressure to match timing of breeding with peaks in resource abundance.
388 Therefore, the shape of the resource peak could drive variation in the benefits of early breeding
389 between habitats or over time (Reneerkens et al. 2016, Bailey et al. 2022).

390 In contrast to fitness associated with absolute date, fitness derived from relative lay date
391 is expected to be largely density-dependent and likely to be driven by habitat availability.
392 Fluctuations in abundance are a common phenomenon in many bird populations (Begon et al.
393 1986) and it is likely that these fluctuations could cause the benefit of breeding early relative to
394 conspecifics to vary between years, especially when resource abundance is fixed. When
395 populations occur near their carrying capacity, it is expected that the benefits of early breeding
396 relative to competitors are most pronounced (Reed et al. 2013). Breeding early relative to
397 competitors is expected to have several primary benefits. If your young are among the earliest to
398 fledge, they may get priority access to resources as they become independent (Freeman et al.
399 2020). They may also gain priority access to territories or be in better condition to compete
400 against juveniles from later-fledging broods (Green and Cockburn 2001, Evans et al. 2020a).

401 There could also be additional benefits from breeding early relative to other species in the
402 broader community if multiple species compete for similar resources. This raises the intriguing
403 possibility that at least a small portion of fitness could be derived from breeding early relative to
404 other species. Already there is documentation that species can differentially respond to changing
405 environmental cues to optimally shift when they breed, and this variation could alter competitive
406 dynamics between species when shared resources are limited. Heterospecific associations could
407 also result in the timing of breeding deviating away from optima. For example, nesting in
408 association with a heterospecific to reduce predation risk can influence when individuals choose
409 to breed and lead to non-optimal timing of breeding. Species may alternatively choose to be

410 asynchronous with heterospecific competitor, for example to reduce inter-specific competition,
411 which could also shift individuals away from breeding at an optimal time (Swift et al. 2018,
412 2020). Therefore, synchronous or asynchronous responses to heterospecific competitors could
413 shape responses to climate change, or future capacities to shift lay date in response to other
414 environmental factors.

415 Based on the importance of both absolute and relative date in determining fitness we
416 propose that the overall fitness benefit of breeding early (ω_{early}) is a function of both absolute
417 ($\omega_{absolute}$) and relative ($\omega_{relative}$) lay date (equation 1):

$$418 \quad (1) \quad \omega_{early} = (\omega_{absolute} + \omega_{relative})$$

419 To better understand how both absolute and relative lay date contribute to the total fitness benefit
420 of early breeding, it is useful to further breakdown the constituent components of fitness (e.g.,
421 fecundity, juvenile survival, and adult survival) because each of these vital rates could be
422 differentially impacted by early breeding. This allows for the mechanisms linking early breeding
423 and each of these components of fitness to be parameterized and to vary independently of one
424 another. This means that specific responses of each component of fitness to early breeding can be
425 quantified and accounted for to estimate a cumulative effect of early breeding on fitness.

426 Using the number of recruits produced in a lifetime as a measure of fitness, the increase in total
427 number of recruits produced by early breeders relative to the mean number of recruits produced
428 by the population represents the fitness benefit of breeding early (ω_{early}). ω_{early} can therefore
429 be considered a function of mean fecundity (F), mean juvenile survival (ϕ_j), mean adult survival
430 (ϕ_a), and terms describing how early breeding influences fecundity and survival through both
431 absolute date (a) and relative date (r).

$$432 \quad (2) \quad \omega_{early} = \left((F + a_F + r_F) \times (\phi_j + a_j + r_j) \right) \times$$

433 $(\phi_a + a_a + r_a)$

434 Incorporating both absolute and relative date is important because they can vary independently
435 of each other and could be differentially impacted by abiotic and biotic environmental
436 conditions, influencing survival and fecundity in very different ways. Considering the
437 relationships between lay date and fitness is integral to predicting how individuals and species
438 will persist in a changing world.

439

440 **Breeding in a changing world: how does environmental change influence fitness of early**
441 **breeders?**

442 *Climate change*

443 Climates across the globe have experienced dramatic and long-term shifts in temperature and
444 precipitation (IPCC 2022). In general, temperatures are warming, which has caused winter to
445 become shorter (see Studd et al. 2021, Sutton et al. 2021 for a discussion of multiple definitions
446 of winter and how this relates to changing seasons) and the onset of spring to occur earlier
447 (Møller et al. 2010, Hällfors et al. 2020). Directional shifts in precipitation are more spatially
448 variable, with some regions experiencing drier or even drought-like conditions (Mukherjee et al.
449 2018), while others experience increases in precipitation (Trenberth 2011). Concurrent with
450 these direction changes, temperature and precipitation are becoming increasingly variable,
451 especially at transition points between seasons (IPCC 2022). Variability in temperature can have
452 especially pronounced consequences on wildlife as it can produce unseasonably warm or cold
453 periods relative to long-term directional changes, making directional changes hard to track
454 between years and exposing individuals to severe weather (Shipley et al. 2020). For example,

455 spring may have above average temperatures in one year and cold snaps in the next, which
456 represent very different conditions that an individual must respond to (Moreno et al. 2015).

457 Directional shifts in temperature are likely to increase selective pressure to breed early in
458 species that are temperature limited or use temperature as a cue for reproductive behaviour (de
459 Villemereuil et al. 2020, Visser et al. 2021). Advancing lay date with warming temperatures has
460 been observed in many birds species, with the strength of this relationship varying between
461 species (Møller et al. 2010, Dunn 2019, Hällfors et al. 2020) and even between populations of
462 the same species (Bailey et al. 2022). This pattern has largely been attributed to tracking resource
463 peaks that have also advanced with warming conditions (Visser et al. 1998, Dunn 2019). When
464 populations are unable to track advancing resource peaks reproductive performance declines and
465 population abundance may decline as well (Both et al. 2006, 2010). In addition to changes in the
466 timing of peak resources, warming temperatures could also alleviate some of the costs associated
467 with early breeding. Thermoregulatory costs of incubating eggs and brooding developing
468 nestlings are likely to be highest early in the season, when temperatures typically are coldest
469 (Shipley et al. 2020, Callery et al. 2022). Therefore, warming temperatures could act to decrease
470 costs associated with this key period of the breeding season and facilitate early breeding for more
471 individuals.

472 The consequences of directional shifts in precipitation are more difficult to predict due to
473 potentially contrasting effects on species and the broader ecosystem. Precipitation is likely the
474 primary driver of vegetation growth, especially early in the season (Robinson et al. 2013), and
475 has a variety of cumulative effects on breeding individuals and their food sources (Herrando et
476 al. 2019, Boyle et al. 2020). Vegetation growth is the starting point of trophic cascades that often
477 act through insects to influence when birds breed (Burgess et al. 2018) and any change in

478 precipitation is likely to have dramatic consequences on multiple trophic levels (Thackeray et al.
479 2016). In conjunction with direct effects on prey, precipitation can also influence assessments of
480 habitat quality and subsequent settlement decisions made by an individual (Martin 2001).
481 Vegetation growth leads to differential nest success (Lehman et al. 2008, Conrey et al. 2016,
482 Laidlaw et al. 2020) and female survival throughout the breeding season via effects on nest
483 concealment (Sander et al. 2023). In contrast, growing vegetation can also make some areas
484 undesirable once vegetation has exceeded certain heights (Reintsma et al. 2022). This can result
485 in species avoiding these areas or reducing habitat quality and nesting success.

486 Directional changes in winter precipitation could also have important consequences on
487 timing of breeding, especially at high latitude and elevation (Martin 2001, Sandercock 2003,
488 Sander et al. 2023). For example, snowpack is often a limiting factor that prevents individuals
489 from breeding (Clarke and Johnson 1992, Lameris et al. 2019). Reduced snowfall throughout the
490 winter could allow individuals to breed earlier, or better track advances in spring phenology that
491 are otherwise hard to track due to snow remaining on the ground (Martin and Wiebe 2004), but
492 migrants would still be constrained by the timing of their migration, which could limit their
493 ability to track changes in winter precipitation that would otherwise facilitate earlier breeding.

494 Despite the clear impact of directional shifts in both temperature and precipitation, it is
495 unlikely that these two environmental variables are changing in isolation (Leathers et al. 1991).
496 Instead, concurrent changes in both temperature and precipitation are likely to act in tandem to
497 shape the benefits of early breeding. The extent and direction of correlations between
498 temperature and precipitation can also be important. For example, warm temperatures and
499 increased precipitation could act synergistically to influence arthropod abundance (Halsch et al.
500 2021) resulting in increased resource abundance and potentially higher reproductive performance

501 of breeding birds. However, increased precipitation in cold temperatures could raise
502 thermoregulatory costs (Gardner et al. 2018) and increase the costs of breeding early, thereby
503 reducing performance (Shiple et al. 2020). It is therefore imperative to consider simultaneous
504 changes in both temperature and precipitation to estimate the overall effect of environmental
505 change on reproductive performance and the benefits of breeding early.

506 In addition to directional shifts in mean conditions, climate change is also increasing
507 variability in both temperature and precipitation (IPCC 2022). In order to optimally time
508 breeding, individuals must be able to appropriately respond to environmental cues (Dunn 2019),
509 but increasingly variable conditions make cues difficult to respond to and may impede an
510 individual's ability to adjust the timing of their breeding (Visser et al. 2021). Sudden changes in
511 environmental conditions are likely to increase the likelihood of nests failing or decrease survival
512 (Shiple et al. 2020, Callery et al. 2022). For example, sudden drops in temperature early in the
513 season can be harmful to breeders and developing young (Brown and Brown 1998, 1999; García-
514 Pérez et al. 2014, Clark et al. 2018). Late-spring frosts could decrease adult survival and also
515 lower egg and nestling survival if adults are unable to maintain the temperature of nests above
516 their critical thermal thresholds. These losses could be particularly pronounced for migratory
517 species and other facultative early breeders that likely have lower thermal tolerances than
518 resident species (Shiple et al. 2020). Extreme storms, which are increasing in frequency due to
519 climate change, can also directly influence breeding performance by increasing rates of nest
520 failure (Boersma and Rebstock 2014) and decreasing survival of offspring and adults. Early in
521 the season, snow and ice storms can severely impact breeding individuals (Martin and Wiebe
522 2004), while heavy rainfall or droughts can negatively impact reproductive performance
523 throughout the breeding season (Cimadom et al. 2014).

524 To understand the effects of climate change on the benefits of early breeding, we can
 525 further refine equation 2 to include terms that describe the costs and benefits associated with
 526 early lay dates. Each absolute and relative lay date term will have an associated cost (c) and
 527 benefit (b) term to allow the impacts of climate change to vary independently (equation 3).

$$528 \quad (3) \quad \omega_{early} = \left((F + a_F(b_F - c_F) + r_F(b_F - c_F)) \times (\phi_j + a_j(b_j - c_j) + r_j(b_j - c_j)) \right) \times$$

$$529 \quad (\phi_a + a_a(b_a - c_a) + r_a(b_a - c_a))$$

530 This approach has several advantages. First, it explicitly incorporates the effects of breeding
 531 early on not only reproductive performance, but also accounts for downstream effects on both
 532 juvenile and adult survival. Second, it also allows climate to independently influence the costs
 533 and benefits of early breeding associated with each of these vital rates allowing climate change
 534 to have different effects on each vital rate. For example, changing environmental conditions
 535 could greatly impact the benefits of early breeding on fecundity, while having a more limited
 536 effect on juvenile survival. In this scenario, we may expect the net effect to be large for fecundity
 537 but remain relatively limited for juvenile survival.

538 Equation 3 also allows for behavioural and physiological processes to be incorporated
 539 into a demographic equation to understand the impact of early breeding on both long- and short-
 540 term processes. Early breeders could augment their overall reproductive performance by
 541 investing in more offspring (increase fecundity, F) or by investing more energy into rearing of
 542 young, which is likely to increase juvenile survival. Russell (2000) hypothesized that species in
 543 tropical habitats could invest more time and energy in post-fledging care, which makes
 544 investment in small clutch sizes more viable to maintain fitness given high predation rates of
 545 nests. Physiological processes, such as senescence, can also account for differences in fitness
 546 over time as a function of conditions when individuals breed or during their early life (Sorensen

547 et al. 2022, Zabala et al. 2022). Patterns of senescence can influence reproductive performance
548 and survival concurrently and if these effects are known, they can be explicitly incorporated into
549 equation 3 to understand the relative impact of both processes on the fitness of an individual.

550 Although it is difficult to parameterize this equation based on current values available in
551 published studies, it should be possible to parameterize this equation using existing long-term
552 data sets. The parameter that is currently less available in the wider literature is an estimate of the
553 effect of breeding early relative to conspecifics. This data is likely available but is usually
554 included in broader analyses aimed at understanding climate as a driver of variation in lay date
555 and thus not explicitly differentiated. Further, effects of relative lay date can be seen largely as
556 density dependent-effects and nest box populations, some of the highest quality long-term
557 studies on birds available, usually publish less frequently on the effect of nest box density than
558 studies which focus on species whose nests are not tied to the location of nest boxes and the
559 effect of nest box density on reproductive performance is equivocal (Male et al. 2006, Serrano-
560 Davies et al. 2017). Despite current gaps in the literature, values for each proposed parameter in
561 equation 3 could likely be estimated from multiple long-term studies, especially blue (*Cyanistes*
562 *caeruleus*) and great tit (*Parus major*) populations in Europe (Culina et al. 2021) and tree
563 swallows (*Tachycineta bicolor*) in North America (Winkler et al. 2020). Additionally, studies
564 using the networks of study populations distributed across broad spatial scales for these species
565 represent an ideal design to quantify how the effect of changing lay date may be differentially
566 influencing individual fitness. Each year data is collected on lay date, and this could be used to
567 quantify both relative and absolute effects given the distribution of lay dates in the population.
568 Intra- and inter-individual effects of lay date on reproductive performance could be used to
569 estimate the benefits and costs of lay date on fecundity (depending on number of individuals

570 monitored and average lifespan). Finally, individual marking and monitoring could be used to
571 estimate the effects of lay date on both juvenile and adult survival. Many long-term studies likely
572 have this data available, but it has not been characterized in this way before, making it difficult at
573 the present time to parameterize equation 3.

574 Despite current limitations in parameterizing equation 3, it is still possible to make
575 predictions about how changes to each parameter would influence the overall fitness benefit of
576 early breeding. At the simplest level, concurrent changes in fecundity and juvenile survival due
577 to early breeding are predicted to be a strong driver of changes in fitness. If these changes
578 increase estimates of both parameters, then fitness of early breeders would increase. In contrast,
579 if estimates of both variables decreased, fitness would be expected to decline sharply. When
580 parameters in equation 3 are not positively correlated (e.g., if early breeding increases the
581 number of young produced, but decreases juvenile or adult survival), it becomes more difficult to
582 predict what the overall impact on individual fitness is and these predictions should be made
583 based on the natural history of the species and with an understanding of the sensitivity of fitness,
584 and by extension population growth (Reed et al. 2013), to each parameter. For example, if
585 fecundity for a species is low (i.e., few young produced every year), a sudden increase in the
586 number of young produced could have an outsized impact on fitness, even if juvenile survival
587 does not change. This relationship between variables is further complicated when we consider
588 the effect of absolute and relative breeding date on individual fitness. If the effect of
589 environmental variables is not consistent across fecundity and survival parameters, it again
590 results in a situation where making general predictions is difficult. For example, Sander et al.
591 (2023) described early breeders as having higher rates of nest failure and young with higher body
592 condition. In this scenario, the overall impact of early breeding on fitness is likely dependent on

593 the relationship between body condition and subsequent recruitment into the population. It is
594 therefore difficult to make general predictions based on this model without considering species-
595 specific attributes and how fecundity, juvenile survival and adult survival are concurrently
596 influenced by early breeding (Reed et al. 2013). Although there may be difficulty in producing
597 broad predictions from equation 3, we believe it represents a novel tool in our potential
598 understanding of how environmental conditions and climate change influence the fitness of
599 individuals as a function of lay date.

600 In our description of equation 3, we have focused primarily on using fecundity to
601 characterize reproductive performance. However, equation 3 could be further modified to
602 include multiple metrics of reproductive performance such as clutch size, brood size, nest
603 survival, and renest probability. Dividing fecundity into its composite parts would allow for
604 relationships between each composite and lay date or environmental conditions to be included in
605 the equation and provide additional information on the drivers of individual fitness. Furthermore,
606 this could help to identify sensitive periods of the breeding season where individuals respond
607 most strongly to biotic or abiotic drivers.

608 In situations where information on one or more demographic parameters are missing it is
609 still possible to use equation 3 to investigate the effects of climate change on the benefit of early
610 breeding. When demographic parameters are missing, it may be best to consider components of
611 fitness separately, rather than in conjunction. For example, if no data on juvenile survival is
612 available, equation 3 could be divided into a fecundity model and an adult survival model, with
613 relative and absolute lay date terms included to understand how these two demographic
614 parameters respond to variation in lay date and climatic conditions. Alternatively, if demographic
615 information exists from another study population or closely related species, this information

616 could be used to parametrize the model and estimate missing parameters. Both these approaches
617 allow the equation to be used to continue to quantify the impact of timing of breeding on fitness
618 but could result in biased estimates. For example, excluding one demographic term means that its
619 potential contribution to variation in fitness is not considered. Despite potential bias, we still
620 believe that using equation 3, even when missing a parameter, could provide considerable insight
621 into the effects of timing of breeding and climate change on the fitness of wildlife while also
622 explicitly considering the mechanisms influencing both the costs and benefits associated with
623 timing of breeding.

624

625 *Applying our model of timing of breeding to year-round breeders*

626 To this point we have framed equation 3 as a valuable tool to estimate the fitness of early
627 breeders in a changing world, but this framework could also be applied to year-round breeders
628 and be used to consider the effect of timing of breeding on fitness. Absolute effects could be
629 used to understand the effect of breeding during different periods of the annual cycle, which
630 likely represent very different challenges to breeding, given that in seasonal environments
631 resources and environmental conditions are highly variable. This means that breeding during a
632 given period of the annual cycle represents a unique challenge and could differentially influence
633 investment in reproduction. The effect of relative lay date could still be used to quantify possible
634 density-dependent effects on reproduction, or important dynamics that result from timing
635 breeding in response to a pulse in resources or a sudden change in environmental conditions. In
636 either of these cases, it would be expected that there would be important effects of how quickly
637 an individual can respond to these events and complete a breeding attempt before conditions
638 become less favourable.

639

640 *Differential effects of climate change on obligate and facultative early breeders*

641 Species-specific responses to climate change have been widely documented (Møller et al. 2010,
642 Hällfors et al. 2020), but mechanisms underlying these variable responses remain poorly
643 understood. Inter-specific comparisons have revealed that the breeding season of multi-brooded
644 species has increased in length but decreased for single-brooded (Møller et al. 2010), resident,
645 and short-distance migrant species (Hällfors et al. 2020). Additionally, initiation of breeding is
646 becoming more synchronised between species, with more broods co-occurring during the early
647 breeding season (Hällfors et al. 2020). Collectively, this could indicate that facultative early
648 breeders are exploiting favourable conditions to match the early breeding of obligate species
649 (Figure 2).

650 It is also important to consider how climate change could modulate the overall benefit of
651 strategies used to advance timing of breeding in obligate early breeders. For example, food
652 caching is a widespread behavioural strategy used to cope with low food availability (Vander
653 Wall 1990). However, once food is stored, it will begin to degrade until it is retrieved (Sutton et
654 al. 2016). Climate change is likely to increase rates of cached food degradation, which will
655 reduce the amount of energy available to individuals during periods of resource scarcity (Sutton
656 et al. 2016). Already the effect of this decline in cached food quality has been shown to influence
657 reproductive performance (Sutton et al. 2019), survival (Masoero et al. 2020), and population
658 dynamics (Sutton et al. 2021) of food caching species. This means that strategies used to
659 facilitate early breeding could be negatively impacted by climate change and force obligate early
660 breeders to delay breeding until conditions are more favourable or reduce investment in
661 reproductive performance to maintain survival, resulting in fewer young being produced. If

662 breeding is delayed, it could exacerbate timing constraints and further limit the reproductive
663 performance of late-breeding individuals.

664 If obligate and facultative early breeders compete for similar resources, rapid
665 advancements of facultative lay dates could alter competitive dynamics of bird communities. The
666 resulting increase in competition could then limit the reproductive performance of obligate early
667 breeders. Additionally, if this general advance of mean community lay date causes an associated
668 shift in predator abundance and phenology, benefits of early breeding due to decreased predation
669 risk would be greatly reduced. Increased competition could also translate to reduced juvenile
670 performance and reduced survival during the post-fledging period, when survival is already low.
671 Taken together, it is likely that the traits underlying early breeding will modulate the effects of
672 changing environmental conditions and potentially shape the long-term effects of climate change
673 on populations and the broader avian community.

674

675

676 **Conclusion**

677 Climate change is already directly impacting species and the traits that influence individual
678 fitness such as lay date. It is often difficult to predict individual performance in response to
679 changing environmental conditions, but here we provide an empirical framework to understand
680 the direct effects of environmental change on fitness, acting through both survival and
681 reproductive performance. This empirical framework is also founded on the underlying
682 mechanisms driving seasonal declines in reproductive performance that have been widely
683 documented in a variety of bird species across a diverse range of habitats. We hope that by
684 explicitly incorporating both the benefits and costs of early breeding in a simple mathematical

685 equation, future research will consider how climate change influences both the costs and benefits
686 of breeding in a changing world. This approach would complement demographic modelling to
687 understand how individual level effects of climate change, especially those influencing fitness,
688 and in turn scale up to influence population dynamics and persistence. Additionally, considering
689 characteristics of species and constraints imposed on breeding individuals by environmental
690 conditions can provide insight into how individuals allocate resources to reproduction and
691 survival and how these decisions interact with environmental conditions to shape population
692 dynamics and fitness in a wide range of habitats.

693 Investigations of why breeding early increases individual performance are vital to
694 predicting future responses to environmental change. Correlations between lay date and
695 reproductive performance have been documented for a wide range of species, but it is important
696 to move past correlations and delve into the mechanisms driving this relationship. Here, we have
697 highlighted a range of mechanisms that have been explored in a number of systems and
698 encourage researchers to continue to consider these and additional drivers of the benefits of early
699 breeding in a changing world.

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- 1174

1175 **Tables**1176 **Table 1.** Proposed mechanisms underlying variation in timing of breeding and predicted advantages to breeding early.

Hypothesis	Mechanism	Prediction	Source
Resource matching	Early breeding allows for matching of peak needs with resource abundance peak	Individuals advance lay date with advancing phenology of resources	(Verboven et al. 2001, Visser et al. 2021)
Seasonal declines in environmental quality	Environmental conditions that are optimal for breeding decline over a breeding season	Early breeding individuals have increased reproductive performance	(Perrins 1970, Winkler et al. 2014, Meltofte et al. 2021)
Reduced predation	Early breeders are exposed to fewer predators	Individuals breed prior to peak predator abundance	(Callery et al. 2022)
Reduced parasitism and brood parasitism	Early breeders are exposed to fewer parasites (brood or otherwise)	Early breeding individuals have lower rates of parasitism and brood parasitism	(Oien et al. 1996)
Increased offspring quality	Offspring from early nests are of higher quality	Nestlings of higher quality will be in better body condition. Post-fledging survival and offspring recruitment will be higher for individuals from early nests	(Hochachka 1990, Verboven and Visser 1998)

Time for offspring development	Breeding early provides enough time for offspring to develop morphologically, behaviourally and cognitively	Offspring born too late in the season will not have sufficient time to develop and have lower survival	(Uomini et al. 2020)
Offspring access to resources	Offspring that fledge from early nests have priority access to resources	Offspring from early nests will have preferential access to high quality resources after reaching independence	(Green and Cockburn 2001)
Insurance against failure	Early breeders have more time to attempt renests after nests fail	Early breeders are more likely to attempt to renest if their nest fails	(Becker and Zhang 2011)
Longer breeding season	Multi-brooded species have more time to attempt second or additional nests	Early breeders are more likely to attempt to rear multiple clutches in a given year	(Saino et al. 2004, Jackson and Cresswell 2017, Zabala et al. 2020)
Female choosiness	Early females have longer to assess potential mates and more males are available to be selected early in the season	Females initiating breeding later will have access to fewer potential mates	(Palokangas et al. 1992, Kokko et al. 2006)
Access to higher quality mates	Individuals starting to breed earlier have access to higher quality males	Mate quality will be higher for individuals breeding earlier in the season	(Møller 1994)

Reduced inter-specific competition

Early breeding relative to other species reduces competition for resources

Early breeding species will have reduced competition for resources

(Gustafsson 1987)

Reduced intra-specific competition

Early breeding relative to conspecifics reduces competition for resources

Early breeders will have reduced competition for resources

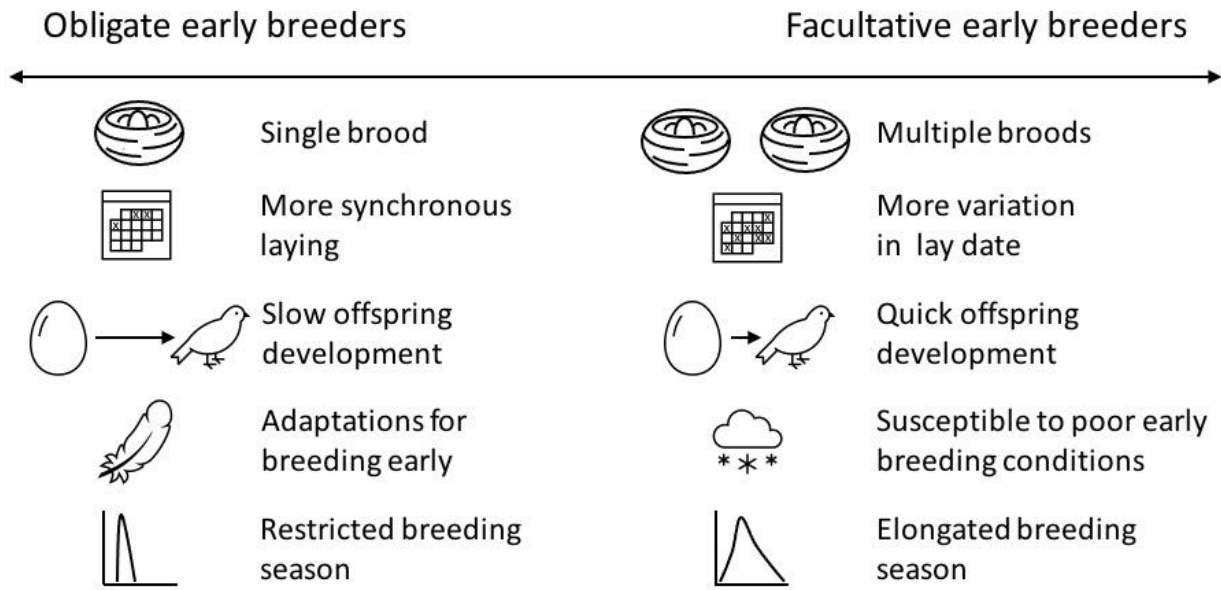
(Alatalo and Lundberg 1984)

1178 **Table 2.** Hypothesized constraints on early breeding and their underlying mechanisms promoting variation in the timing of breeding.

Hypothesis	Mechanism	Prediction	Source
Individual condition	Endogenous energy stores are used to support breeding	Only individuals in good condition with ample energy stores breed early	(Rowe et al. 1994, Bêty et al. 2003, Nomi et al. 2018, de Zwaan et al. 2022)
Individual experience	Experience accumulated by an individual allows them to appropriately respond to environmental cues	Young, inexperienced individuals breed later	(Whelan et al. 2016, Johns et al. 2017, de Villemerueil et al. 2019, Winkler et al. 2020, Burant et al. 2022)
Environmental drivers	Poor weather creates unfavourable breeding conditions	Individuals will not breed in poor weather	(Verhulst and Nilsson 2008, Johns et al. 2017, Kentie et al. 2018)
Tolerance to environmental conditions	Tolerance of and adaptations to harsh environmental conditions enable breeding during poor conditions	Individuals will not breed during conditions they are not adapted to	(Vander Wall 1990, Lei et al. 2002, Williams et al. 2015)
Migratory distance	Individuals that travel farther will be less able to advance lay date	Longer-distance migrants breed later than shorter-distance migrants	(Smith and Moore 2005, Hällfors et al. 2020)
Arrival on breeding territory	Early arrival on breeding territories provides earlier access to resources needed for breeding	Individuals arriving late will always breed late	(Smith and Moore 2005)

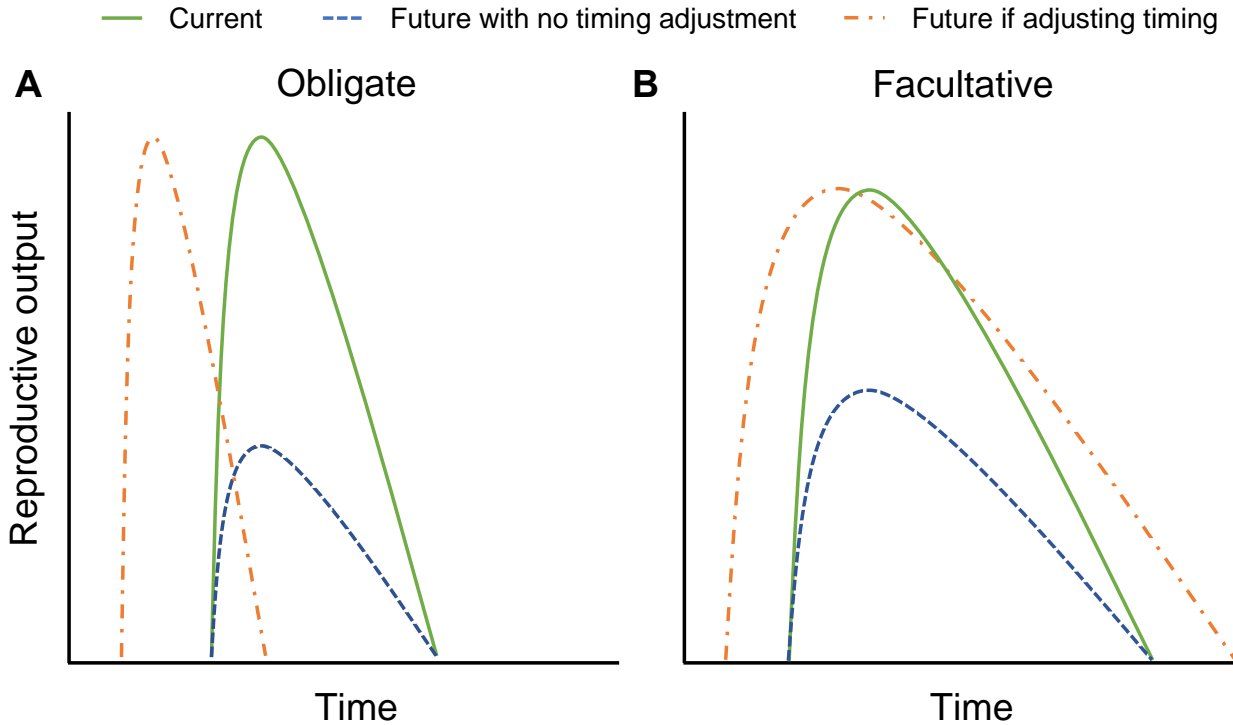
Development time	Length of time required to rear young sets a limit on length of breeding season	Individuals will not breed if there is not enough time to raise young	(Gwinner 1989, Strickland and Ouellet 2020, Uomini et al. 2020)
Resource abundance	Resource abundance during the breeding season determines amount of energy that can be invested in reproduction	Individuals will not breed when resources are low	(Dunn 2019)
Heritable lay date	Timing of breeding is heritable	Offspring of late breeders will be late breeders	(Sheldon et al. 2003, Evans et al. 2020b, Winkler et al. 2020)
Mate quality	Mate experience and condition influences female lay date decisions	Low quality, young, and/or inexperienced males will breed later	(Béziers and Roulin 2016, Whelan et al. 2016)
Lay date plasticity	Individuals may adjust lay date to match environmental conditions	Less plastic individuals will be less able to track changing environmental conditions	(Nussey et al. 2005, Brommer et al. 2008)
Territory quality	Territory quality determines the quality and/or quantity of resources available	Individuals on low quality territories breed later	(Kentie et al. 2018, Sumasgutner et al. 2020, Bailey et al. 2022)

1180 **Figures**



1181

1182 **Figure 1:** Variation in traits for obligate and facultative early breeders. Both species and
1183 populations can be placed along the continuum because intra-specific variation is expected in
1184 species that inhabit broad geographical ranges and/or habitat types.



1185

1186 **Figure 2:** Reproductive output of obligate (A) and facultative (B) early breeders over a breeding
 1187 season and how their reproductive output may change if they shift their timing based on changes
 1188 in environmental conditions (e.g., warming temperatures, earlier green up, and resource peaks).

1189 The two distributions (obligate vs. facultative) differ in two primary ways: the width of the
 1190 distributions and the decline in reproductive output on the right tail of the distribution. The width
 1191 of the distribution is narrower for obligate early breeders (panel A) because the range of possible
 1192 lay dates is constrained, and facultative early breeders can have a longer breeding season
 1193 depending on environmental conditions. The decline in reproductive output for the right tail of
 1194 the distribution is shallower for facultative early breeders (panel B) because reproductive output
 1195 will decline more slowly throughout the breeding season and this decline could be buffered by
 1196 variation in individual quality, especially when high quality individuals are attempting additional
 1197 clutches after successfully rearing their first. In future climates, the width of the distribution is

1198 predicted change more dramatically as the length of the breeding season extends with earlier
1199 onset of favourable conditions.