1 **Why do earlier-arriving migratory birds have better breeding success?**

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10

11 **Abstract**

12 In migratory birds, early arrival on breeding sites is typically associated with greater breeding

13 success, but the mechanisms driving these benefits are rarely known. One mechanism

14 through which greater breeding success among early arrivers can potentially be achieved is

15 the increased time available for replacement clutches following nest loss. However, the

16 contribution of replacement clutches to breeding success will depend on seasonal variation

17 in nest survival rates, and the consequences for juvenile recruitment of hatching at different

18 times in the season. In particular, lower recruitment rates of late-hatched chicks could offset

19 the benefits to early arrivers of being able to lay replacement clutches, which would reduce

20 the likelihood of replacement clutch opportunities influencing selection on migratory timings.

21 Using a simulation model of time-constrained capacity for replacement clutches,

22 paramaterised with empirically-derived estimates from avian migratory systems, we show

23 that greater reproductive success among early-arriving individuals can arise solely through

24 the greater time capacity for replacement clutches among early-arrivers, even when later re-

25 nesting attempts contribute fewer recruits to the population. However, these relationships

26 vary depending on the seasonal pattern of nest survival. The benefits of early arrival are

27 greatest when nest survival rates are constant or decline seasonally, and early arrival is least

28 beneficial when nest success rates increase over the breeding season, although replacement

29 clutches can mitigate this effect. The time benefits of early arrival facilitating replacement

30 clutches following nest loss may therefore be an important but overlooked source of selection

31 on migratory timings. Empirical measures of seasonal variation in nest survival, re-nesting and

32 juvenile recruitment rates are therefore needed in order to identify the costs and benefits

33   associated with individual migration phenology, the selection pressures influencing migratory

34   timings, and the implications for ongoing shifts in migration and breeding phenology.

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Introduction

For migratory species, the timing of migratory journeys can have important fitness consequences. Declines in breeding success with date of arrival on the breeding grounds have been widely demonstrated in many species (Aebischer *et al.* 1996; Currie, Thompson & Burke 2000; Norris *et al.* 2004; Sergio *et al.* 2007; Saino *et al.* 2004, Rockwell, Bocetti & Marra 2012; McKellar, Marra & Ratcliffe 2013; Velmala *et al.* 2015), and a range of mechanisms have been proposed to explain this association, but empirical evidence of the mechanisms driving arrival date-breeding success links is still scarce. Declines in breeding success with arrival date could arise as a result of variation in individual capacity to both migrate early and breed successfully, irrespective of the conditions encountered during the breeding season. If better quality individuals both arrive first and have greater breeding success (Verhulst & Nilsson 2008), for example because they are older (Daunt et al. 1999), have a greater capacity to attract a mate (Bensch & Hasselquist 1992), lay larger clutches (Bêty, Gauthier & Giroux 2003) and/or provision and protect their offspring, then arrival date may be a correlate, rather than the driver, of breeding success, and selection pressure on arrival timings may be weak. Alternatively, greater breeding success among early-arrivers could result from local environmental variation, with early-arrivers potentially having more opportunities to occupy better quality habitats and territories (Currie *et al.* 2000, Harris *et al.* 2006**, Jonzén *et al.* 2006**) in which, for example, eggs or chicks may be at lower risk of predation or greater resource availability may improve offspring growth and survival (Arnold et al. 2004). However, breeding dispersal events are relatively rare (Paradis *et al.* **1998**), suggesting that any association between arrival timing and site quality must arise in the year of recruitment and persist thereafter. An alternative, and often neglected, driver of associations between migratory timings and breeding success is variability in the time available for replacement clutches following nest loss, or for rearing multiple broods (Saino et al 2004; Hoffmann, Postma & Schaub 2015). If the fitness benefits of early arrival operate primarily through the time available for replacement clutches, then the advances in spring migration that are currently occurring in many species (Rubolini et al. 2007, Knudsen et al. 2011) could have profound implications for both productivity and the phenology of successful nests. Such changes could be contributing to current divergent population trajectories in migratory

70 species with differing rates of advancing spring migration (Møller et al. 2008, Gilroy et al.

71 2016), and altering the benefits of early arrival.

72

73 Among migratory species, having sufficient time to rear multiple broods can be rare but rates

74 of nest loss as a consequence of predation, severe weather or human actions are often high,

75 and replacement clutches are common in migratory bird species (Newton 2008) and occur

76 even at high arctic latitudes (Jamieson 2011; Johnson *et al.* 2011). Most bird species are

77 capable of re-nesting (Martin 1995, Thompson et al. 2001), however, the probability of

78 replacement clutches being laid following nest loss typically declines seasonally (eg Hipfner

79 et al. 1999, Hansson, Bensch & Hasselquist 2000; Brinkhof et al. 2002, Weggler et al. 2006,

80 Jamieson 2011; Pakanen *et al.* 2014), suggesting that opportunities to re-nest will be greater

81 for early-nesting individuals. Given the constraints of post-breeding moult and migration,

82 insufficient time to complete replacement clutches (and thus a lower probability of re-

83 nesting) later in the breeding season is likely to be a feature common to all migratory species.

84 The benefits of laying replacement clutches will be influenced by seasonal variation in both

85 (a) the probability of nest survival and (b) the probability of successful subsequent

86 recruitment of offspring. Seasonal variation in nest success rates can arise through seasonal

87 variation in factors such as local predator abundance and activity (eg Sperry *et al.* 2008;

88 DeGregorio *et al.* 2016), weather conditions (Skagen & Adams 2012) and nest concealment

89 (Borgmann, Conway & Morrison 2013). Seasonal declines in offspring recruitment probability

90 have been reported in many species (Harris *et al.* 1994; Clark *et al.* 2014; Visser *et al.* 2015;

91 Lok *et al.* 2017; Alves *et al.* 2019), potentially reflecting difficulties facing late-hatched young

92 in locating and amassing resources during the post-fledging and winter periods. Lower

93 recruitment of late-hatched young would be likely to reduce the benefits associated with

94 replacement clutches. Consequently, the contribution of replacement clutches to the benefits

95 of early arrival will depend on breeding phenology (including the length of incubation and the

96 time between nest loss and replacement), nest survival rates and offspring recruitment

97 probabilities, and how these rates vary seasonally.

98

99 Here we construct a simulation model to explore the relationships between timing of arrival

100 and breeding success that can arise through variation in the time available to lay replacement

101   clutches. We then explore how these relationships vary with seasonal variation in nest

102   survival and the consequences for offspring recruitment.

103

104

105   **Materials and Methods**

106

107   *Simulation model*

108   We constructed a simulation model in R 3.3.1 (R Core Development Team 2016) of 1000

109   individuals with differing timings of arrival on the breeding grounds. Fifteen simulations were

110   conducted, with each being assigned a maximum number of replacement clutches (either

111   zero, one or three) and one of five different scenarios of seasonality of nest survival rates (see

112   below), and each simulation was run 100 times. In all simulations, each individual could

113   complete a maximum of one successful nesting attempt (i.e. nest successfully hatched) per

114   year, over a 10 year period. To ensure that biologically realistic values were used in the

115   simulations, the modelled distributions and functions (see Figure 1) were constructed using

116   data from published studies of breeding waders in Iceland (Þórisson, 2013; Alves *et al.* 2019),

117   but the key features of the model (individual variation in arrival dates, seasonal variation in

118   nest survival, replacement clutch opportunities and offspring recruitment probabilities) are

119   applicable to all migratory bird systems.

120

121   *Estimating timing of arrival and laying of first clutch*

122   Individuals were assigned an arrival date by randomly sampling from a left-skewed arrival

123   distribution (Figure 1a and SOM 1.1) and the assigned arrival dates for each individual were

124   then fixed for the 10 year period over which simulations were run, as individuals typically

125   show repeatability in their spring arrival dates (Gill *et al.* 2014). For each individual, timing of

126   nesting (lay date) was then calculated as a fixed function of arrival dates (Figure 1b and SOM

127   1.2), with a slightly larger gap **(+29 days)** between arrival and laying at the start of the season,

128   reflecting the greater likelihood of weather constraints on nesting at the start of the season.

129

130   *Predicting nest survival rates*

131   In order to explore how the influence of re-nesting on nesting success might vary with nest

132   survival rates, we first modelled nine different levels of nest survival rate (from 0.1 to 0.9)

which were constant throughout the season. As these models showed that the effects of re-nesting were greatest at intermediate levels of nest survival (see Results), we then explored five realistic scenarios **(see Discussion)** of seasonal variation in nest survival (Figure 1c), all of which had an intermediate mean rate of nest survival (0.5): a) constant nest survival throughout the season, b) sustained seasonal decrease, c) sustained seasonal increase, d) seasonal increase to an asymptote and e) unimodally distributed nest survival, see SOM section 1.3 for details. The success (hatch or fail) of each nesting attempt was determined by a random draw from a binomial distribution, with the probability of success equal to the nest survival rate predicted from the lay date of each nesting attempt in each nest survival scenario.

Modelling replacement clutch occurrence and timing

In simulations in which replacement clutches were possible (up to a maximum of one or three attempts), the lay date of re-nesting attempts was determined by first assigning a nest failure date to each failed attempt, by sampling at random from a distribution of numbers of days between laying and failure of nesting attempts (Figure 1d), and adding a fixed gap between nest failure and re-nesting of four days (re-nesting gap, Þórisson, 2013). This process was continued until either a nesting attempt was successful, the maximum number of re-nesting attempts was reached (one or three) or lay dates exceeded the end of the breeding season on day 181 (last day on which nesting attempts could be initiated, Þórisson, 2013).

Estimating seasonal variation in recruitment probabilities

The probability of offspring recruitment into the breeding population for each successful nesting attempt (one hatched offspring per successful attempt) was estimated as a function of hatch date (Figure 1e, SOM 1.3, **Alves *et al.* 2019).**). Hatch dates were estimated to be 25 days after the laying date of the successful nesting attempt. The outcome of each recruitment event was then determined by a random draw from a binomial distribution with probability of success equal to the recruitment probability. In the cases where a successful nesting attempt did not take place during that breeding season, recruitment probability was set to zero.

164   Each of the 15 simulations was run 100 times, from which the arrival date, mean lay date of

165   successful nests, mean annual number of nesting attempts, mean annual number of

166   successful nesting attempts, mean annual recruitment probability and lifetime number of

167   recruits over the 10 year period was calculated for each individual.

168

169   **Results**

170

171   *Replacement clutch capacity, nest survival rates and breeding success*

172   As nest survival rates increase, the number of successful nesting attempts increases, and the

173   capacity to lay multiple replacement clutches results in a higher number of successful nesting

174   attempts (Figure 2a). The increase in the number of successful nesting attempts is most rapid

175   in populations that have the capacity to lay replacement clutches, however, this increase

176   slows at higher rates of nest survival, as the success of first nests renders replacement

177   clutches increasingly redundant (Figure 2a). Low nest survival rates also result in later average

178   hatch dates of successful nesting attempts when replacement clutches are possible (Figure

179   2b), as a greater proportion of successful attempts are from replacement clutches.

180   Consequently, the correlation between arrival- and lay-dates is **weakened** when replacement

181   clutches are possible (Figure S1). The mean annual number of recruits also increases with nest

182   survival rate and is highest in populations that can lay replacement clutches (Figure 2c), but

183   this benefit diminishes at high nest survival rates, again because of high success of first nests

184   in all populations renders replacement clutches increasingly redundant. These patterns

185   persist when variation in individual arrival dates is introduced (Figure S2)

186

187   *Seasonal variation in nest survival rates*

188   Five scenarios of seasonal variation in nest survival rates were modelled (Figure 3, top row).

189   When nest survival rates are constant throughout the breeding season (Figure 3, first

190   column), the capacity for multiple replacement clutches results in a shift in lay dates of

191   successful nests to later in the season (Figure 3b), more successful nesting attempts overall

192   and a steeper decline in annual number of successful nesting attempts with arrival date

193   (Figure 3c). Thus, with constant nest survival rates, the capacity to lay replacement clutches

194   can generate strong relationships between arrival date and nesting success while, if

195   replacement clutches are not possible, nesting success varies little with arrival date (Figure

196   3c). However, the benefits of replacement clutches can be greatly reduced if the offspring of

197   late nests are less likely to recruit into the adult population. Consequently, seasonal declines

198   in offspring recruitment probabilities reduce the impact of replacement clutches on the

199   lifetime number of recruits, but early arrivers still achieve higher numbers of recruits overall

200   (Figure 3d). Thus, when nest survival rates are constant and replacement clutches are

201   possible, early arrival can facilitate a higher probability of achieving a successful nesting

202   attempt, and these benefits of early arrival can persist even if seasonal declines in recruitment

203   reduce the success of replacement clutches later in the season.

204

205   Seasonal variation in nest survival rates can alter the influence of replacement clutch capacity

206   on breeding phenology and success (Figure 3, e-t). Seasonal declines in nest survival (Figure

207   3e) result in a similar distribution of lay dates of successful nests across all three re-nesting

208   frequencies (Figure 3f), as replacement clutches are only likely to be successful when they

209   occur very early in the season. Consequently, the mean number of successful nesting

210   attempts declines strongly with arrival date, but the capacity to lay replacement clutches only

211   slightly increases the number of successful nesting attempts (Figure 3g) and the lifetime

212   number of recruits achieved (Figure 3h).

213

214   Sustained seasonal increases in nest survival rates (Figure 3i) can introduce costs of arriving

215   early, particularly when replacement clutches do not occur following loss of early nests. In

216   this scenario, the majority of successful replacement clutches occur later in the season (Figure

217   3j), and thus the mean annual number of successful nesting attempts varies little with arrival

218   date when replacement clutches are possible, and increases with arrival date when only single

219   nesting attempts are possible (Figure 3k). However, seasonal declines in recruitment

220   probability can offset benefits of arriving or re-nesting later in the season such that early-

221   arriving re-nesters can achieve more lifetime recruits (Figure 3i).

222

223   When nest survival rates are low at the start of the season and either increase to a plateau

224   (Figure 3m), or decrease after peaking in mid-season (Figure 3q), replacement clutches can

225   again result in more successful nests but with slightly later laying dates (Figure 3n,r).

226   Replacement clutches can mitigate the low nest survival in the early season such that the

227   mean number of successful nesting attempts is lowest for late-arrivers in both scenarios

228   (Figure 3o,s), and seasonal declines in recruitment probability can further enhance the

229   benefits of early arrival and replacement nest capacity for the lifetime number of recruits

230   (Figure 3p,t).

231

232   Thus, replacement clutches can drive benefits of early arrival even when patterns of nest

233   survival vary seasonally, and seasonal declines in recruitment probability can enhance

234   benefits of early arrival and replacement clutches, even when nest survival rates increase

235   through the breeding season.

236

237   **Discussion**

238   Declines in breeding success with date of arrival date on the breeding grounds have been

239   widely reported and a range of potential drivers have been proposed (e.g. Møller 1994; Currie

240   *et al.* 2000, Gunnarsson *et al.* 2006). Our simulation models demonstrate that these patterns

241   can be generated solely by early-arriving individuals having more time to lay replacement

242   clutches, even when recruitment probabilities are lower for later-hatched offspring. Our

243   models also show that replacement clutches are likely to be most beneficial at intermediate

244   nest survival rates (Fig. 2), and that early arrival and the capacity to lay replacement clutches

245   can potentially increase the total number of offspring recruited, even if nest survival rates

246   increase during the breeding season (Fig. 3). Understanding the extent to which the time

247   available for replacement clutches is driving the widely-observed declines in breeding success

248   with spring arrival date of migratory birds will therefore require empirical measures of

249   replacement clutch rates and seasonal variation in nest survival and recruitment rates.

250

251   The benefits of replacement clutches for enhancing the probability of achieving a successful

252   nesting attempt are most apparent when nest survival rates are at intermediate levels, as

253   very high nest survival rates inevitably lead to the majority of first broods being successful

254   (and thus limited benefits of re-nesting), while very low nest survival rates lead to the majority

255   of first nests and replacement clutches failing (again limiting the benefit of re-nesting). Our

256   models did not include opportunities to achieve more than one successful nesting attempt

257   within a season but producing multiple broods would be likely to produce similar benefits to

258   early arrival as laying replacement clutches. The probability of laying replacement clutches is

259   also likely to be influenced by length of the breeding season and consequently to vary with

9

260 latitude. However, replacement clutches can occur even at high arctic latitudes (Jamieson

261 2011; Johnson *et al.* 2011), and thus the benefits of early arrival may be particularly strong at

262 higher latitudes, where breeding seasons are very short. Finally, replacement clutches could

263 also incur costs for parents (eg Wendeln et al. 2000), which may influence the frequency with

264 which replacement clutches are laid even if sufficient time is available.

265

266 Nest survival rates in wild bird populations can show seasonal declines (eg Sandercock 1998;

267 Grant *et al.* 2005, Weiser *et al.* 2018), increases (eg Wilson, Martin & Hannon 2007;

268 Reneerkens *et al.* 2016), mid-season peaks (eg Sperry *et al.* 2008) or little seasonal variation

269 in survival (eg Sandercock 1998; Laidlaw *et al.* 2015, Weiser *et al.* 2018), and these patterns

270 may vary spatially and between years as a result of differences in weather conditions,

271 predator abundance and breeding phenology, availability of alternative prey for predators,

272 etc. However, declines in the number of successful nesting attempts with individual arrival

273 date were apparent in all of the seasonal nest survival scenarios modelled here, except for

274 sustained seasonal increases in nest survival (Fig. 3k). In addition, the apparent benefits of

275 late arrival in systems with sustained seasonal increases in nest survival were reduced by re-

276 nesting capacity (Fig. 3k), and reversed by additional seasonal declines in subsequent life time

277 number of recruits (Fig. 3l). Thus, benefits of early arrival are likely to be apparent in most

278 scenarios of seasonal variation in nest survival rates, and having the time to lay replacement

279 clutches can be a major driver of these benefits.

280

281 Seasonal declines in recruitment probability can substantially increase the benefits associated

282 with early arrival and nesting in migrants, even when (later) replacement clutches delay

283 offspring fledging (Fig. 3). Quantifying the recruitment probabilities of individuals that hatch

284 and fledge at different points in the season requires long-term tracking of individuals from

285 the first year of life. Developments in tracking technologies have facilitated an increase in the

286 number of studies capable of generating such data, and seasonal declines in recruitment

287 probabilities are commonly reported in these studies (Clark *et al.* 2014; Visser *et al.* 2015; Lok

288 *et al.* 2017; Alves *et al.* 2019). The mechanisms underpinning the costs of late fledging are

289 likely to include the having less time available to locate resources and suitable wintering

290 locations and, potentially, having fewer opportunities to gain social information from adults

291 which may have already departed for winter sites (Gunnarsson 2005)**, and density-**

dependent costs associated with fledging into local populations comprising large numbers of fledglings from earlier nests (Verhulst 1992). More studies of seasonal variation in individual recruitment rates in migratory species will help to identify the magnitude of these effects and their drivers.

A striking feature of migratory populations is that, despite the apparent benefits of early arrival on the breeding grounds, the timing of spring migration within populations is typically characterised by high levels of between-individual variation (e.g. arrival may span several weeks) but very low levels of within-individual variation (individuals are typically highly repeatable in their timing of migratory journeys) (Phillips *et al.* 2005; Alerstam, Hake & Kjellén *et al.* 2006; Brodersen *et al.* 2012; Conklin, Battley & Potter 2013; Gill *et al.* 2014; Tibblin *et al.* 2016). This suggests that the benefits of individual consistency in timing may be greater than the benefits of early arrival *per se*, and/or that the benefits of early arrival may be offset by costs that are not distributed equally among individuals. Previous models of migratory timings have assumed the latter, by incorporating variation in individual quality that directly influences timing of arrival (e.g. Kokko 1999, Kokko *et al.* 2006). However, between-individual variation in arrival dates could also arise through factors such as conditions in the year of recruitment (eg weather or individual condition) influencing individual timings, and benefits of consistency in individual timings could subsequently maintain this variation independent of any consistent variation in individual quality. A recent study demonstrated that population-level shifts in spring arrival dates were driven by increases in the frequency of early-arriving recruits in the population, and not by individuals altering arrival dates (Gill *et al.* 2014), suggesting that factors operating prior to recruitment influence individual arrival dates, which are then repeated in subsequent years. Migratory birds are often highly mate-faithful between years and studies have shown high levels of synchrony in arrival of mates (Gunnarsson *et al.* 2004; Phillips *et al.* 2005; Fayet *et al.* 2017). Costs of later arrival may therefore be reduced by synchronous arrival of mates facilitating breeding soon after arrival, and the importance of synchronous arrival may underpin the benefits of consistent individual arrival timings.

Summary

In summary, early arrival of migratory birds on breeding grounds can potentially lead to higher reproductive success solely as a result of the greater time available for laying replacement clutches, should early nesting attempts fail. These patterns persist across a range of seasonal patterns in nest survival rates and even when later nesting attempts are less likely to produce successful recruits. These benefits of replacement clutches are most apparent at intermediate nest survival rates, as very high or very low rates of nest loss will render replacement clutches unsuccessful or unnecessary, respectively. Advances in the timing of spring migration are occurring in many species at present, and there is evidence for population declines being associated with a lack of these shifts in timing (Møller et al. 2008, Gilroy et al. 2016). Our findings highlight the potential role of replacement nests as a driver of these divergent population trends; advances in spring migration could result in increased time available for replacement nests following nest loss, but the benefits of these replacement nests (and thus their potential contribution to population growth) will depend on the seasonal variation in nest survival and offspring recruitment. Empirical studies of the frequency and seasonality of replacement clutches are therefore urgently needed in order to identify the conditions in which they occur and their role as a driver of both the benefits of early arrival and the population-scale consequences of shifts in migration timing.

Author contributions

All authors conceived the ideas and designed the methodology. CAM performed the simulation modelling and JAG and CAM led the writing of the manuscript. All authors contributed to the writing of the manuscript and gave final approval for publication.

Data accessibility

No original data are presented in this manuscript.

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584 **Figure legends**
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587 **Figure 1**: Model structure and the distributions and functions used in the simulations: (a)

588 distribution of individual arrival dates, (b) the relationship between individual arrival date and

589 lay date (solid line; see Equation S1) and the gap between individual arrival and laying (vertical

590 distance between the line of unity (dashed line) and the solid line), (c) the five scenarios of

591 seasonal variation in nest survival rates (details in text), (d) the distribution of days between

592 lay date and nest failure and (e) the relationship between hatch date and the probability of

593 offspring subsequently recruiting into the breeding population (see Equation S2).

594

595 **Figure 2:** Simulated effects of differing nest survival rates on the (a) number of successful

596 nesting attempts, (b) hatching date of successful nesting attempts and (c) annual number of

597 recruits for differing maximum numbers of possible replacement clutches following nest loss

598 (red = zero, blue = one, green = three).

599
600 **Figure 3**: Variation in the consequences of individual spring arrival dates for the probability of

601 successful nesting and offspring recruitment, in simulation models with differing seasonal

602 patterns of nest survival (top row) and maximum number of possible replacement clutches

603 (red = zero, blue = one, green = three). For each seasonal nest survival scenario, the

604 distribution of lay dates of successful nesting attempts (second row), relationships between

605 mean annual arrival date and both number of successful nesting attempts (third row) and

606 **lifetime number of recruits** (fourth row) are shown (see Figure 1 and SOM for model details).

607 Colour intensity (rows 3 and 4) represents the average annual number of nesting attempts

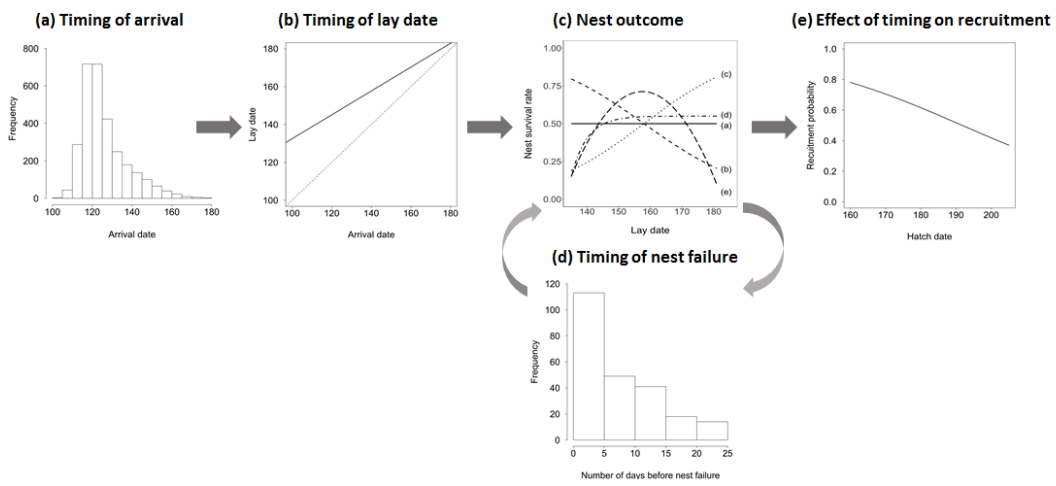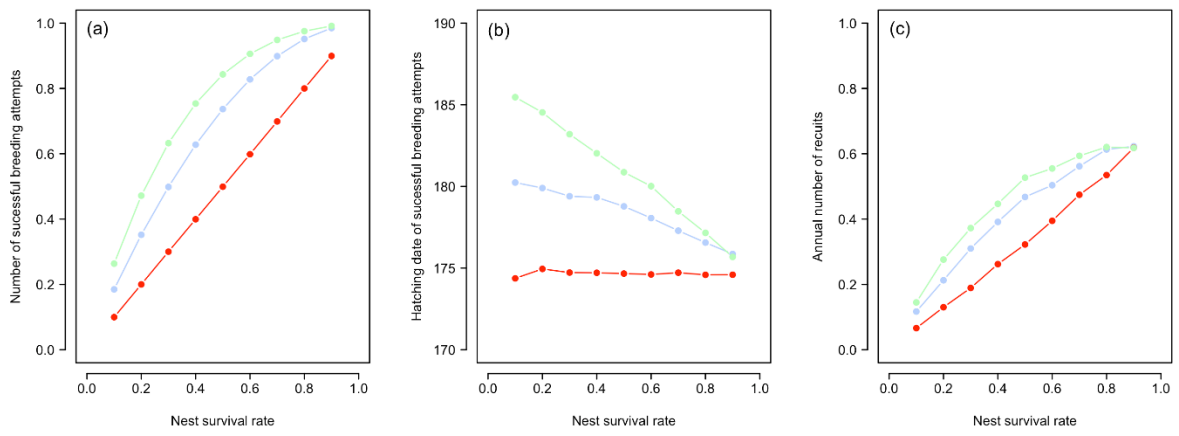608 (darker = more nesting attempts (range: 0.5-2.5)).

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615   **Figure 1:**

(a) Timing of arrival
(b) Timing of lay date
(c) Nest outcome
(e) Effect of timing on recruitment
(d) Timing of nest failure

616
617

618   **Figure 2:**

619

Figure 3: