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Lifespan and reproductive cost explain interspecific variation in the optimal onset of reproduction

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1 **Full title**

2 **Lifespan and reproductive cost explain interspecific variation in the optimal onset of**

3 **reproduction**

4 **Running title**

5 Evolution of delayed onset of reproduction

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110   Fitness can be profoundly influenced by the age at first reproduction (AFR), but to date the

111   AFR-fitness relationship only has been investigated intraspecifically. Here we investigated

112   the relationship between AFR and average lifetime reproductive success (LRS) across 34 bird

113   species. We assessed differences in the deviation of the Optimal AFR (i.e., the species-

114   specific AFR associated with the highest LRS) from the age at sexual maturity, considering

115   potential effects of life-history as well as social and ecological factors. Most individuals

116   adopted the species-specific Optimal AFR and both the mean and Optimal AFR of species

117   correlated positively with lifespan. Interspecific deviations of the Optimal AFR were

118   associated with indices reflecting a change in LRS or survival as a function of AFR: a delayed

119   AFR was beneficial in species where early AFR was associated with a decrease in subsequent

120   survival or reproductive output. Overall, our results suggest that a delayed onset of

121   reproduction beyond maturity is an optimal strategy explained by a long lifespan and costs

122   of early reproduction. By providing the first empirical confirmations of key predictions of

123   life-history theory across species, this study contributes to a better understanding of life-

124   history evolution.

125

126   **KEY WORDS: Age at first reproduction, comparative method, cost of reproduction, family**

127   **formation theory, life-history theory.**

128   **DATA ARCHIVING:**

129   Data are provided in the appendix.

130   **ABBREVIATIONS**: AFR, age at first reproduction; LRS, lifetime reproductive success; LRT,

131   likelihood ratio test

132   Life-history theory predicts that the timing of reproductive events during an individual's life

133   affects its fitness (Cole 1954; Caswell 1982). An early age at first reproduction (hereafter

134   AFR) can increase the number of lifetime reproductive events and shorten generation time,

135   which, in a stable or growing population, should be favored by natural selection (Cole 1954;

136   Bell 1980; Roff 1992; Charlesworth 1994). However, an early AFR may also be costly and

137   reduce future survival or reproductive investment (Lack 1968; Roff 1992; Stearns 1992).

138   Additionally, individuals could benefit from deferring breeding beyond sexual maturity if this

139   enhances parenting skills ('constraint hypothesis': Curio 1983), secures access to higher

140   quality territories or mates ('queuing hypothesis': Zack and Stutchbury 1992; van de Pol et

141   al. 2007), increases reproductive output with age ('restraint hypothesis': Williams 1966;

142   Forslund and Pärt 1995) or decreases reproductive senescence ('senescence hypothesis':

143   Charmantier et al. 2006). If AFR is shaped by natural selection, then individuals should adopt

144   the AFR that is associated with the highest fitness return, which may depend on individual

145   quality and annual variation in environmental conditions.

146   Individuals of some species express no variation in AFR, while there is a large range

147   in AFR in other species. In the latter case, only certain AFRs are associated with a high

148   lifetime reproductive success (hereafter LRS), but the exact association appears to vary

149   among species (Clutton-Brock 1988; Newton 1989; Oli et al. 2002; Krüger 2005; Charmantier

150   et al. 2006; Millon et al. 2010; Kim et al. 2011; Tettamanti et al. 2012; Zhang et al. 2015).

151   Moreover, the relationship between the species-specific AFR that is associated with the

152   highest LRS (hereafter termed Optimal AFR) and age of sexual maturity can vary across

153   species (Komdeur 1996; Pyle et al. 1997; Oli et al. 2002; Krüger 2005). Yet, the reasons

154   underlying this among-species variation remain unclear as we currently lack comparative

155   studies that investigate the evolution of AFR and deviation in the timing of Optimal AFR

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156   during reproductive lifespan across species. Such a study could contribute to our

157   understanding of the general patterns of variation in this crucial life history trait.

158   Whether species-specific Optimal AFR either approximates or is shifted beyond the

159   age of sexual maturity of the species may depend on interspecific variation in life-history or

160   ecological factors. Across species, the pace of life (i.e. slow or fast life history) is likely to be

161   a major factor influencing variation in AFR and timing of the species-specific Optimal AFR

162   relative to the age of sexual maturity (Roff 1992; Stearns 1992; Charlesworth 1994). A short

163   lifespan should be associated with little or no variation in AFR, and with an Optimal AFR that

164   is close to the species' age of maturity, as any postponement would increase the risk of

165   death before reproduction. In contrast, a long lifespan allows for a larger range in AFR and

166   increases the likelihood of a delayed Optimal AFR, an outcome that is supported by field

167   studies (Pyle et al. 1997; Tettamanti et al. 2012). In addition to lifespan, other life-history,

168   ecological or social traits may influence the deviation from the age of sexual maturity in the

169   species-specific Optimal AFR. Species could benefit from delayed AFR when there is a high

170   level of parental care (e.g. altricial species), or when requiring time to learn specialized skills

171   to survive or reproduce successfully. Conversely, a prolonged association of juveniles with

172   their parents (i.e. family-living; Drobniak et al. 2015) may facilitate skill learning and lead to

173   an earlier species-specific Optimal AFR ('skill hypothesis': Skutch 1961; Langen 1996). An

174   earlier Optimal AFR may also be found in cooperatively-breeding species, since helpers may

175   buffer the reproductive costs of early AFR ('load-lightening hypothesis': Khan and Walters

176   2002; Santos and Macedo 2011).

177   Here, we use data from 34 bird species to investigate the extent of variation in

178   reproductive strategies and to assess the potential benefits some species may gain from

179   delaying AFR beyond sexual maturity. We examine interspecific variation in the fitness

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180 consequences of AFR using within-species relationships between AFR and a fitness proxy

181 averaged over all individuals within a specific AFR-class. For each of the 34 species, we

182 identified the species- and sex-specific Optimal AFR and several derived metrics,

183 summarized in Table 1, to assess changes in LRS or survival as a function of AFR. Information

184 on species-specific Optimal AFR was previously unavailable for typical meta-analysis

185 approaches due to the substantial challenge of obtaining fitness estimates of populations

186 from several species. Its investigation allows us to make inferences about the selection

187 pressures on AFR that could not be achieved via a simple analysis of interspecific variation in

188 AFR. As a fitness proxy, we used the most commonly provided measure of an individual's

189 productivity, the lifetime number of fledglings or recruits produced (LRS) (Clutton-Brock

190 1988; Newton 1989 and other references in Table S1). Although it depends on population

191 dynamics, while rate-sensitive fitness estimates (e.g. lambda λ_{ind}) theoretically are more

192 accurate proxies than LRS (Cole 1954; Lewontin 1965; Caswell and Hastings 1980), a number

193 of studies have shown that LRS is a reliable estimate of fitness (Brommer et al. 2002; Link et

194 al. 2002; Dugdale et al. 2010).

195   Specifically, we addressed the following three questions: (i) How does AFR vary

196 within and among species? (ii) Is variation in AFR associated with differences in LRS, and is

197 the typical AFR of a species the one associated with the highest LRS? (iii) Which life-history

198 (chick developmental mode, LRS and survival change with AFR, lifespan), social (family-

199 living, helper presence) and ecological (latitude, nest predation) factors are associated with

200 among-species variation in deviation of the Optimal AFR from age at maturity? We used a

201 generalized linear mixed model approach in a model selection framework for the analyses,

202 with further control for similarity in phenotype among taxa due to a shared phylogenetic

203 history.

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204

Materials and Methods

206 **DATA COLLECTION**

207 We used data from published (N = 15) and unpublished (N = 21) studies on the age at first

208 reproduction (AFR) and lifetime reproductive success (LRS) for 34 avian species (Table S1).

209 To find published data, we searched online databases (ISI Web of Science, Scopus) using the

210 terms "age at first reproduction", "age at first breeding", or "age at maturity" in

211 combination with "lifetime reproductive success", "lifetime reproductive output", or

212 "fitness" and "avian" or "bird". We included data from long-term studies (years of

213 monitoring exceeding the mean lifespan) in which individuals were followed for a sufficient

214 period to accurately measure LRS (mean duration of study: 20.75 years; range: 8 to 48

215 years) and where LRS (including its mean, standard deviation and sample size) was reported

216 separately for each category of AFR. We used GetData Graph Digitizer 2.25

217 (http://www.getdata-graph-digitizer.com/) to extract values from published data that were

218 only presented in figures. Unpublished data were requested from researchers who

219 coordinated long-term monitoring studies.

220 We collected species-specific data on key life-history, ecological and social lifestyle

221 factors that might influence the effect of AFR on LRS (italicized words represents variable

222 names used in the models), including *chick development mode* (altricial or precocial), *mean*

223 *lifespan*, *mean body mass*, *latitude*, *nest predation risk*, *family-living* and *helper presence*.

224 We also collected data on the age of maturity for the estimation of an index used as

225 variables in the model (see INDICES AND ESTIMATES). Age of maturity corresponded to the

226 age at which an individual is physiologically able to reproduce, or the minimum age

227 recorded for breeders. Among ecological factors that can contribute to nest predation risk,

228 nest location is well known and important (Martin and Li 1992; Martin 1993). Based on this

229 information, we ordinally ranked the nest predation risk as high risk – ground nesters,

230 medium risk – nests in shrubs, low risk – nests in trees, or very low risk – cavity breeders or

231 species that build their nest floating on water and thus difficult for nest predators to access.

232 We considered species to be family-living when offspring remain with the parents beyond

233 independence and non-family living when juveniles disperse soon after becoming

234 independent (Drobniak et al. 2015). Species were categorized with helper when offspring

235 regularly engage in cooperative breeding and without helper when offspring do not engage

236 in cooperative breeding. Variables not provided for the populations studied were obtained

237 from the Animal Ageing and Longevity database (http://genomics.senescence.info/species/)

238 or the Handbooks of the Birds of the World (del Hoyo et al. 1992-2006).

239

240 **DATA COMPOSITION**

241 The 34 species included in our study (Figure S1) comprise 10 taxonomic orders and 22

242 families, with mean lifespan ranging from 1.4 to 18.5 years and mean LRS ranging from 0.67

243 to 21.16 fledglings produced over the lifetime, or from 0.54 to 2.53 recruits. For blue tits

244 (*Cyanistes caeruleus*) and western gulls (*Larus occidentalis*), we included data from two

245 different populations that were analyzed separately. While age at first reproduction might

246 be influenced by individual quality (Forslund and Pärt 1995; Kim et al. 2011), only few

247 studies provide such information, limiting our ability to include this factor in our analyses.

248 Data collected consisted of average values per species (i.e. body mass) or per AFR age-class

249 category combining data from all cohorts and years. Therefore, annual or cohort variation

250 could not be addressed here but we hope to do so in future work. Note that not controlling

251 for intraspecific individual quality and combining data across cohorts and years is

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252   conservative as it reduces the chance of observing biological patterns. Values of mean LRS

253   (N = 34 species) and lifespan (N = 21 species), as well as their standard deviation and sample

254   size (number of individuals), were determined for each AFR age-class category (e.g. from all

255   individuals starting to reproduce at AFR = 1-year old, at AFR = 2, at AFR = 3, and so on), and

256   for each sex if possible. While it would have been more appropriate to use the geometric

257   rather than the arithmetic mean, as it takes into account variability in fitness (see Liou et al.

258   1993), such data were unavailable. Age at first reproduction was defined as the age at which

259   an individual first reproduced during its life. In most species, this value corresponds to the

260   age when a female laid at least one egg, although in some species the value reflects when a

261   female laid a full clutch. For males, AFR corresponds to the age where its mate laid eggs,

262   and, accordingly, reproductively competent males that failed to acquire a mate were not

263   considered as reproductive at that time. The LRS data were based on the number of

264   fledglings or recruits produced over the lifetime of an individual (Table S1). All LRS values

265   were centered and scaled within species and sexes to convert the original units to those of

266   standard deviations and make them comparable (Schielzeth 2010). For species with only

267   one AFR age-class category, only a single data point was available. Thus we could not

268   estimate the standard deviation necessary for scaling. Instead, we used the standard

269   deviation of the same sex of a species with a similar value of unscaled LRS to calculate the

270   scaled LRS. Accurate estimation of AFR and fitness proxies is challenging as it requires

271   known-aged individuals and intensive individual-based monitoring of reproductive output

272   throughout the lifespan of a representative sample of individuals, as well as data on the

273   survival and reproduction of descendants. Age at first reproduction and fitness proxies may

274   be biased due to extra-pair paternity, or because not all reproductive events of individuals

275   are   followed   due   to   emigration   from   or   immigration   into   the   study   population.

276   Consequently, AFR might be overestimated and LRS underestimated for males and

277   overestimated for females. Such biases affect the interpretation of the relationship between

278   AFR and fitness components, and add noise to the data. However, because a relation

279   between AFR and extra-pair paternity and or migration has never been documented, we do

280   not know how and to what extent such a bias would affect our interpretation.

281

282   **INDICES AND ESTIMATES**

283   Interspecific variation in deviations of the Optimal AFR from the age at sexual maturity

284   might be explained by the association of an early or a late AFR with an increase or a

285   decrease in subsequent survival or reproductive output. However, given the heterogeneity

286   of the data distribution between species and sexes, conventional methods are unable to

287   estimate changes in reproductive output or survival with a changing AFR. Thus, we

288   calculated five derived metrics from the raw data per AFR age-class category to investigate

289   this hypothesis (i.e. average values over all individuals from a specific AFR age-class,

290   combining cohorts and years, for each species and where possible split by sex). These

291   included the Delay Index, which assessed the deviations of the Optimal AFR from the age at

292   sexual maturity, and four indices which assess the relationship between AFR and LRS or

293   survival: the Before Variation Index and the After Variation Index, the Choice Index, and the

294   Lifespan Effect Index (see Table 1).

295   We visually determined the species-specific AFR that maximized LRS ("Optimal AFR"-

296   Table 1). The use of a single statistical optimization method was not feasible due to the large

297   diversity of patterns in the relationship between AFR and LRS.

298   Based on the Optimal AFR, the age at sexual maturity and the latest AFR observed

299   within focal species and sex, we assessed the "Delay Index" representing the timing of the

300   Optimal AFR in relation to the reproductive lifespan (illustrated in Table 1):

$$\text{Delay Index} \; = \; \frac{\text{Optimal AFR} - \text{maturity age}}{\text{latest AFR} - \text{maturity age}}$$

301   A Delay Index equal to zero always resulted from the Optimal AFR being the age of maturity.

302   For 35 out of 62 cases several AFR categories had mean LRS values near that of the

303   Optimal AFR. Hence, we determined the range of the species-specific optimum ages for the

304   onset of reproduction, referred as the "Optimal AFR Range". The Optimal AFR Range

305   included the AFR categories adjacent to the Optimal AFR, with mean LRS values included in

306   the calculation of the standard error bar for the mean LRS of the Optimal AFR (Table 1). The

307   AFR categories forming the Optimal AFR Range are therefore assumed to be similarly

308   beneficial in terms of LRS than the Optimal AFR.

309   Based on the Optimal AFR Range, we estimated the Before Variation Index and the

310   After Variation Index. These indices correspond to the slope of the relationship between LRS

311   and AFR from the earliest and the latest AFR to the center of the Optimal AFR Range. The

312   slopes were estimated in the whole data set with all AFR age-class categories, and in a data

313   set only including categories with more than 5% or 10% of the individuals (Table 1). Before

314   and After Variation Indices represent the average of the three estimated slopes. We

315   assumed that a delayed AFR should be favored if an early AFR is associated with a lower LRS,

316   while an earlier AFR should be favored if a late AFR is associated with a lower LRS.

317   Therefore, we expected the Delay Index to be positively correlated with the Before Variation

318   Index but negatively with the After Variation Index.

319   Based on the Optimal AFR Range and the actual value observed for the AFR, we

320   calculated the Choice Index (Table 1), which represented the probability that individuals

321   adopt AFR(s) with highest fitness return:

$$\text{Choice Index} = \frac{\text{Optimal AFR Range}}{\text{number of AFR categories}}$$

322   In cases with only one AFR category (N = 6 out of 62 cases), the Choice Index was assigned a

323   zero, as in such cases there is no variation in AFR. We assumed that species with a large

324   Optimal AFR Range relative to the number of AFR categories (i.e. with a large Choice Index)

325   would have a lower probability of suffering a LRS cost when initiating reproduction earlier or

326   later than the Optimal AFR. Consequently, such species may have a higher likelihood of

327   benefiting from delayed reproduction than species with only a low number of beneficial

328   AFR. Therefore, we expected the Delay Index to be positively correlated with the Choice

329   Index.

330   The association between AFR and subsequent survival was calculated via the

331   Lifespan Effect Index, i.e. the correlation coefficient of the reproductive lifespan plotted

332   against AFR per age-class category. We were able to estimate the Lifespan Effect Index for

333   21 out of 34 species only, due to missing data for mean lifespan for the different AFR age-

334   class categories for 13 species. As causes and consequences cannot be disentangled from a

335   correlation, negative values could indicate a reproductive cost in terms of survival for

336   individuals with a late AFR or an early AFR favored by high intrinsic mortality. By contrast,

337   positive values could indicate a survival cost of early AFR or a late AFR favored by low

338   intrinsic mortality (Table 1, Figure S2). We assumed a survival cost of early AFR to be

339   associated with a late Optimal AFR. Therefore, we expected the Delay Index to be positively

340   correlated with the Lifespan Effect Index.

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341   We verified the robustness of our results based on the indices involving the Optimal

342   AFR Range by considering a second method to estimate it. In this second method, the

343   Optimal AFR Range included AFR(s) adjacent to the Optimal AFR with their 90% CIs

344   overlapping those of the Optimal AFR. The first method (method used in the manuscript

345   abovementioned) represents the logic of a null-hypothesis-like test, which assumes an error

346   distribution around the hypothesis (the Optimal AFR's LRS mean), and if our statistics (the

347   other AFRs' LRS mean) do or do not fall within this range. We also considered this first

348   method to be more straightforward while the use of the second method is more

349   conservative. This is because the use of 90% CI indicates that the LRS population's mean of

350   the focal AFR will fail in 90% of the time, while for the use of the standard error it would do

351   so in around 68% of the time. However, we preferred to present the results from the first

352   method in the manuscript for two reasons. First, most of our data comes from studies with

353   intensive monitoring of a population (Table 1, some of which pretty much sample all

354   individuals in the population) and thus, the LRS means approach the population mean with

355   little error. Second, for some AFRs the LRS estimates were based on a single individual (thus

356   without CI). Note that one could prefer to consider one or the other method depending on

357   their data characteristics and questions.

358

359   **STATISTICAL ANALYSIS**

360   **General procedure**

361   All statistical analyses were carried out in R version 3.0.2 ((R Core Team 2013),

362   http://www.R-project.org/) using linear mixed-effects models (lmer function, lme4 package:

363   Bates et al. 2014) that allow for the non-independence of data from a single species by

364   including species as a random factor in the model. To account for differences in sample size

365   (N, Table S1) and decrease noise by giving greater emphasis to the more reliable species-

366   specific estimates, all models were weighted (Garamszegi and Møller 2011) by incorporating

367   N-1 in the "weights" argument of the lmer function (Hansen and Bartoszek 2012). Note that

368   removing the weighting did not change the results (Table S2 to S7). To compare coefficients,

369   all continuous predictors were centered (around the mean) and scaled (by the standard

370   deviation) before incorporation in the models (Schielzeth 2010), but we present raw data in

371   the figures. Model assumptions of normality and homogeneity of residuals were checked by

372   visually inspecting histograms and qq-plots of the residuals as well as by plotting residuals

373   against fitted values. For each analysis, we used a model selection process to identify the

374   predictors that best explained variation in the response variable. Model selection was based

375   on minimization of the corrected Akaike's information criterion (AICc) (Burnham and

376   Anderson 2011). Support for an effect of an explanatory variable on the response variable

377   was based on comparison of AICc values between the full model with the effect of interest

378   included vs. excluded, and when ΔAICc ($AICc_{included} - AICc_{excluded}$) was less than or equal to

379   minus five (Burnham and Anderson 2011). The 95% confidence interval (CI) of the predictor

380   estimates was obtained using the confint function (stats package: R Core Team 2013).

381   The influence of phylogenetic similarity among species was tested in the "best

382   model" obtained during the lmer model selection process (model including only explanatory

383   variables with ΔAICc $\leq$ -5). This was done by running a phylogenetically controlled mixed-

384   effects model in ASReml-R (VSN International, Hempstead, U.K.; www.vsn-intl.com) with the

385   same set of predictors as the lmer "best model" for each analysis. The phylogeny was

386   included as a random effect in the form of a correlation matrix of distances from the root of

387   the tree to the most recent common ancestor between two species. The phylogenetic effect

388   was tested by performing a REML likelihood ratio test (comparing the REML likelihood of the

389   same ASReml model with and without phylogeny; the log-likelihood ratio test statistic was

390   assessed against a χ^2 distribution with one degree of freedom). The phylogenetic tree used

391   in this comparative study was adapted from a recent species-level molecular phylogenetic

392   assessment (Jetz et al. 2012; Ericson backbone phylogeny) (Figure S1).

393

394   **Variation in age at first reproduction**

395   To determine how AFR varied within and among species, we noted how often an AFR was

396   the most frequently observed AFR within a species (mode) (Figure S3A) and considered the

397   frequency of a specific AFR age-class across all species (Figure S3B). Then, mean AFR and its

398   standard deviation were calculated for each of the 34 species. We tested the influence of

399   sex, mean lifespan and social lifestyle (family-living and presence of helpers) on variation in

400   mean AFR across the 24 species for which we had data for both sexes (Table S1). We used a

401   weighted linear mixed-effect model with population mean AFR as the unit of analysis, and

402   included species as a random effect. Since AFR cannot exceed the mean lifespan, AFR and

403   mean lifespan should be correlated positively. Therefore, we tested whether the estimated

404   correlation between AFR and mean lifespan differed significantly from the null expectation.

405   To do so, we performed a conservative permutation analysis (following Charmantier et al.

406   2006; Lane et al. 2011). For each mean lifespan, a mean AFR value was randomly selected

407   with replacement from our dataset. During re-sampling we fixed the rule that AFR was

408   smaller than mean lifespan. Data were re-sampled 500 times and analyzed using the same

409   weighted linear mixed-effect model as described above. We estimated the average

410   estimates and 95% CIs over the 500 model outputs and compared them to those observed.

411

412   **Fitness consequences of age at first reproduction**

18

413   To determine whether variation in AFR has consequences for LRS, the correlation between

414   AFR and LRS (within-species) as well as its average influence (among-species effect) was

415   investigated using within-subject centering (van de Pol and Wright 2009). The within-species

416   effect was calculated for each sex and species by subtracting the species- and sex-specific

417   mean AFR from each AFR age-class category observed within sex and species (within-species

418   AFR effect; van de Pol and Wright 2009). The among-species effect was determined as the

419   mean AFR within sex and species (between-species AFR effect; van de Pol and Wright 2009).

420   To test for non-linear effects of AFR on LRS within species, a quadratic term of the within-

421   species AFR effect was included in the model. The AFR values were centered to reduce

422   collinearity between the within-species AFR effect and the within-species AFR^2 effect.

423   Centering enabled independent interpretation of the linear and the curvature effect

424   (Schielzeth 2010). Due to apparent interspecific variation in the relationship between AFR

425   and LRS, the ideal analytical framework would have been a random intercept and slope

426   model that estimated separate intercepts and slopes for each species. However, our sample

427   size did not provide sufficient power to support such a model (Martin et al. 2011; van de Pol

428   2012). Therefore, we ran a standard weighted linear mixed-effect model using the average

429   LRS within AFR age-class categories, with sex and population as units of analysis. Species

430   was included as a random effect in this analysis, along with the natural log of mean body

431   mass as a covariate. We included lifespan in this model as a covariate, since reproductive

432   performance corrected for survival estimates approximates real fitness better (Roff 1992).

433   While the output of the analysis with and without lifespan were similar, lifespan is strongly

434   correlated with the between-species AFR effect. Therefore, we present the analysis without

435   lifespan to avoid issues caused by collinearity (Dormann et al. 2013).

19

436   To assess whether the most frequently observed AFR within each species was an

437 optimal strategy, the AFR mode within each species was correlated with the AFR that

438 maximized LRS (i.e., Optimal AFR, Table 1). Then, the species-specific Optimal AFR was

439 compared to the age at sexual maturity to identify species with optimal delayed

440 reproduction (i.e., species with Optimal AFR > Age at maturity). Finally, the Optimal AFR was

441 correlated with lifespan to identify if a benefit from delaying the onset of reproduction

442 beyond sexual maturity coincided with long lifespan.

443

444 **Among-species variation in the relative timing of optimal age at first reproduction**

445 We used a model selection and model averaging approach (Grueber et al. 2011) to

446 determine the factors that explain interspecific variation in deviations of the Optimal AFR

447 from the age of sexual maturity (i.e., Delay Index, Table 1). All life-history, social and

448 ecological factors listed above were included (see DATA COLLECTION), as well as indices

449 reflecting the relationship between LRS and AFR: the Choice Index, and the Before and After

450 Variation Indices (see above, Table 1). In a second analysis, the Lifespan Effect Index was

451 included for the 21 species for which we had detailed data on lifespan mean for each AFR

452 age-class category (Table 1, Figure S2). Due to reduced statistical power of the latter (as on

453 restricted dataset, see above), in the results section we present only the estimates and 95%

454 CI of the analysis excluding the Lifespan Effect Index. Each of the before mentioned

455 variables, and the biologically relevant interactions (Before Variation Index x After Variation

456 Index, Choice Index x Before Variation Index, Choice Index x After Variation Index, Choice

457 Index x Family-living, Choice Index x Helper presence, Mean lifespan x Family-living, Mean

458 lifespan x Helper presence, Nest predation risk x Family-living, Nest predation risk x Helper

459 presence; Table S8 lists predictions associated with these interactions) were tested against

460   the Delay Index in a weighted linear mixed-effect models with Delay Index for each sex and

461   population as a unit of analysis. Species was added as a random effect. Sex and the natural

462   logarithm of body mass were included as default fixed-effects variables to control for

463   allometry and any differences between sexes. Due to a large number of possible

464   combinations between all predictors, we used the R package MuMIn (Barton 2013) to

465   perform model selection. The candidate model set included models with Δ AICc $\leq$ 5, Δ AICc

466   being the AICc of the focal model minus the AICc of the best model (see Table S9 for analysis

467   excluding Lifespan Effect Index and Table S10 for analysis including Lifespan Effect Index). To

468   estimate the relative importance of a factor, we summed the Akaike's weights of the models

469   in the set of best models including the focal factor, following the method described by

470   Symonds and Moussalli (2011).

471

Results

473   **VARIATION IN AGE AT FIRST REPRODUCTION**

474   Across species (N = 34), age at first reproduction (AFR) ranged from one to 20 years. In 11

475   species, the modal AFR was one year (Figure S3A). In 70% of species, AFR was age 3 or less

476   and only 20% of species had an AFR that was greater than 6 years of age (Figure S3B).

477   Within species, the number of AFR categories ranged from one to 15 (average = 4.8 years;

478   SD = 3.1; N = 34) and the mean AFR and its standard deviation varied among species (Figure

479   1). Removing sex or social variables (i.e. family-living, helper presence) from the model did

480   not influence mean AFR (Table 2). However, mean AFR correlated positively with mean

481   lifespan (parameter estimate for mean lifespan = 0.87, 95% CI (hereafter given in brackets

482   after all estimates): 0.72 to 1.02, Table 2), and this correlation exceeded that expected from

483   the mathematical interdependence of AFR and mean lifespan (estimated by the

484   permutation test: mean of 500 simulations: 0.63 (0.87 to 0.79), Δ AICc = -22.24). A positive

485   relationship between AFR and mean lifespan was also apparent when comparing the AFR

486   age-class categories within each species (Figure 2). The phylogenetic effect on mean AFR

487   was significant (likelihood ratio test: LRT = 6.99, df = 1, p < 0.01).

488

489   **FITNESS CONSEQUENCES OF AGE AT FIRST REPRODUCTION**

490   Our within-subject centering approach revealed no among-species effect of AFR on LRS, but

491   a within-species effect of both AFR and AFR^2 (Figure 3). Within species, there was strong

492   directional selection for an early AFR (within-species AFR effect estimate = -0.54 (-0.70 to -

493   0.39), Table S11), as well as stabilizing selection (within-species AFR^2 effect estimate = -0.26

494   (-0.43 to -0.10), Table S11) (Figure 3). The phylogenetic effect on mean LRS for the

495   corresponding AFR was not significant (likelihood ratio test: p = 1). Twenty-six out of 34

496   species (76%) had an Optimal AFR delayed beyond the age at maturity, and this delay

497   correlated positively with a longer mean lifespan (slope = 0.28, $r_{Spearman}$ = 0.61, p < 0.005;

498   Figure 4). Both the most-observed AFR and mean AFR correlated with the AFR with the

499   highest LRS (Optimal AFR vs. modal AFR: slope = 0.98, $r_{Spearman}$ = 0.80, p < 0.0001; Optimal

500   AFR vs. mean AFR: slope = 0.95, $r_{Spearman}$ = 0.84, p < 0.0001). The latter was true even when

501   only looking at species with a large number of observed AFR age-class categories (Table

502   S12).

503

504   **AMONG-SPECIES VARIATION IN THE RELATIVE TIMING OF OPTIMAL AGE AT FIRST**

505   **REPRODUCTION**

506   While the Delay Index was associated with indices that reflect a change in LRS and survival

507   as a function of AFR (i.e. Choice, Before Variation and Lifespan Effect Indices; Table 1, all

22

508   predictor weights ≥ 0.45), it was only marginally related to social (predictor weights < 0.45)

509   or ecological factors (predictor weights ≤ 0.30; Tables 3 and 4). A delayed optimal onset of

510   reproduction (i.e. large Delay Index) was found in species with a large range of optimal AFR

511   relative to reproductive lifespan (Choice Index: estimate = 0.44 (0.15 to 0.72), Table 3).

512   Moreover, a large Delay Index was found in species in which early AFR was associated with a

513   decreased LRS (Before Variation Index estimate = 0.30 (0.07 to 0.54), Table 3 and Figure 3)

514   and a reduced reproductive lifespan (Lifespan Effect Index estimate = 0.54 (0.37 to 0.72),

515   Table 4). Finally, larger species showed later optimal onset of reproduction than smaller

516   species (ln (body mass) estimate: 0.35 (0.01 to 0.69), Table 3). These results remained

517   quantitatively similar when using indices estimated with the Optimal AFR Range determined

518   under the criterion where AFR categories included in the Optimal AFR Range were AFR(s)

519   adjacent to the Optimal AFR with their 90% CIs overlapping those of the Optimal AFR

520   (Tables S13 to S16).

521

Discussion

523   Age at first reproduction (AFR) is a key life-history parameter with consequences for

524   individual reproductive output, and hence its effect on fitness has been studied in a number

525   of intraspecific studies (see references in Table S1). Here we provide a first comparative

526   analysis using a representative amount of averaged within-species information to examine

527   interspecific variation in the relationship between AFR and lifetime reproductive success

528   (LRS). Identifying the species-specific AFR that results in the highest LRS (i.e. Optimal AFR)

529   allowed us to investigate not only within- and among-species variation in the relationship

530   between AFR and LRS, but also differences in the benefits and costs associated with variable

531   timing in the onset of reproduction among species. Our results demonstrated that the most

23

532   commonly observed AFR within a species corresponds to the species-specific Optimal AFR.

533   Among species, Optimal AFR varied considerably. This study showed that lifespan was a

534   major predictor of the relative timing of the Optimal AFR within the reproductive lifespan

535   and that they correlated positively. Additionally, our analyses revealed that Optimal AFR

536   beyond the age of maturity was associated with a decrease in fitness and survival that arose

537   from starting to reproduce at earlier ages than the Optimal AFR.

538   Age at first reproduction varied considerably both within and among species (Figure

539   1). Some species displayed no variation in AFR (e.g. long-tailed tit *Aegithalos caudatus*,

540   indigo bunting *Passerina cyanea*, common buzzard *Buteo buteo*), while others exhibited

541   large variation (e.g. mute swan *Cygnus olor*, wandering albatross *Diomedea exulans*,

542   eurasian oystercatcher *Haematopus ostralegus*). Most species that expressed variation in

543   AFR experienced negative consequences for LRS from initiating reproduction either too

544   early or too late in life (e.g. the Optimal AFR was at an intermediate point in the

545   reproductive lifespan: between the age of sexual maturity and the oldest AFR observed

546   within a population), while for others the earliest or latest observed AFR resulted in the

547   highest LRS (Figure 3). This suggests simultaneous directional and stabilizing selection. If the

548   pattern observed is a footprint of selection acting at the individual level, this should lead to

549   a decrease in average AFR and a reduction in its evolvability. However, a comparative study

550   directly investigating individual variance would be needed to assess this hipothesis.

551   While there was no overall interspecific relationship between AFR and LRS, a within-

552   species relationship between AFR and LRS (Table S11) indicates that evolutionary processes

553   operate at different scales. On the one hand, large-scale evolution acts on all individuals

554   within a population, which might confound the detection of a relationship between AFR and

555   LRS. On the other hand, local-scale evolution acts on individuals, such as on variation in

556 individual quality (Van Noordwijk and De Jong 1986; Kim et al. 2011), food availability

557 (Brommer et al. 1998), territory quality (Krüger 2005), population density (Krüger 2005) or

558 climatic conditions (Gibbs and Grant 1987; Kim et al. 2011), which also might drive the

559 relationship between AFR and LRS. Differences among cohorts in the relationship between

560 AFR and LRS (Brommer et al. 1998; Kim et al. 2011) might additionally explain the absence

561 of a between-species effect of AFR on LRS, but our data did not allow us to take potential

562 differences in individual or cohort quality into account.

563   Among-species variation in mean AFR correlated positively with lifespan (Table 2),

564 supporting the life-history paradigm that the pace of life fundamentally affects reproductive

565 timing (Roff 1992; Stearns 1992; Charlesworth 1994). Furthermore, the species-specific

566 optimal reproductive strategy varied among species, where species with a mean lifespan of

567 up to six years (median mean lifespan: 1.9 years) had an Optimal AFR of one year, providing

568 a quantitative benchmark to differentiate between short- and long-lived bird species. At the

569 other extreme, species with a longer lifespan had a later mean AFR (Table 2) and a later

570 Optimal AFR (Figure 4).

571   When relating the position of the Optimal AFR to the age of sexual maturity of a

572 species, our results revealed that the Optimal AFR was beyond the age of maturity in 26 of

573 34 species. Thus, individuals in these species appear to benefit from delaying their onset of

574 reproduction (e.g. female tawny owl *Strix aluco* (Millon et al. 2010); female goshawk

575 *Accipiter gentilis* (Krüger 2005); sexes combined short-tailed shearwater *Puffinus tenuirostris*

576 (Wooller et al. 1989)). The association of an Optimal AFR beyond the age of sexual maturity

577 with a long mean lifespan suggests that the positive effect of lifespan on mean AFR is not

578 caused by physiological constraints associated with maturity. Indeed, longer-lived species

579 mature later and still adopt an AFR past their age of maturity, and they experienced a larger

25

580   LRS as a consequence (Figure 4). Such a benefit from delayed AFR until after the age of

581   sexual maturity was found not only in long-lived species, but also in six out of 11 short-lived

582   species with a mean lifespan of less than three years (Figure 4).

583   When controlling for reproductive lifespan, we found that interspecific variation in

584   deviation of the Optimal AFR from the age at maturity was primarily associated with a

585   change in survival and fitness with AFR (Tables 3 and 4). Moreover, our results confirmed

586   that an early AFR might be favored by a short reproductive lifespan and vice versa (Roff

587   1992; Stearns 1992; Charlesworth 1994) (Table 4 and Figure 2). Species in which an early

588   onset of reproduction was associated with a reduced reproductive lifespan benefited from

589   delaying AFR (Table 4 and Figure S2), which supports the restraint hypothesis (Williams

590   1966; Forslund and Pärt 1995). Moreover, the cost of early reproduction, measured as a

591   decrease in LRS relative to the optimum, correlated positively with the optimal delayed

592   reproductive onset (Table 3). An early reproductive onset might be costly because of

593   differences in individual competitive ability, if this early onset leads to unequal probabilities

594   of acquiring a high-quality territory (Ens et al. 1995; Ekman et al. 2001; Prevot-Julliard et al.

595   2001; Cooper et al. 2009) or to high physiological costs (Hawn et al. 2007). This pattern

596   suggests that different factors affect the evolution of sexual maturity and the onset of

597   reproduction. Interestingly, in species where there was limited change in LRS relative to

598   AFR, postponing the onset of reproduction beyond sexual maturity was chosen over other

599   earlier AFR leading to similar fitness. Therefore, not reproducing as soon as physiologically

600   capable might provide further benefits. Our results provide empirical support for the

601   hypothesis that costs of reproduction shape the onset of reproduction (Lack 1968; Roff

602   1992; Stearns 1992).

603   It has been argued that variation in AFR might be sub-optimal, reflecting constraints

604   on early breeding, such as limited access to high-quality mates or to high-quality breeding

605   sites (Lack 1968; Emlen 1982; Stearns 1989; Koenig et al. 1992). However, our results

606   suggest that the onset of reproduction most likely is an optimal strategy, since the most

607   commonly observed AFR coincides with the Optimal AFR. A number of theories developed

608   to explain the evolution of cooperative breeding depicts the decision of offspring to remain

609   with their parents beyond sexual maturity as a "best of a bad job" strategy that reflects

610   dispersal constraints (Emlen 1982; Koenig et al. 1992; Arnold and Owens 1998; Hatchwell

611   and Komdeur 2000). The lack of a strong correlation between the Delay Index and the

612   different social lifestyles suggests that delayed onset of reproduction might not have

613   evolved due to constraints (Ekman et al. 2004; Ekman 2007), but instead constitutes a

614   beneficial life-history decision, which correlates positively with lifespan (Covas and Griesser

615   2007). Still, the lack of a correlation between social factors and variation in the optimal

616   timing of reproduction could reflect the fact that our data is skewed towards pair-breeding,

617   northern hemisphere species. Including more tropical and southern hemisphere species

618   might alter our results and magnify the role of social factors in our analyses, as the latter

619   two groups are often long-lived (Valcu et al. 2014), stay longer with their parents (Russell

620   2000) and are more likely to breed cooperatively (Jetz and Rubenstein 2011). The current

621   paucity of long-term studies in these regions potentially biases our view of life-history

622   evolution (Martin 2004).

623   Although we found no significant effect of sex in our study, the relationship between

624   AFR and LRS, and the optimal timing of reproduction, sometimes differed between sexes

625   (Figures 3 and S4). Twelve out of 24 species showed sex-specific differences in the Delay

626   Index; females benefited more from earlier onset than males in seven species, whereas the

27

627 opposite was true in five species (Figure S4). Intraspecific studies have demonstrated sex

628 differences in the relationship between LRS and AFR (e.g. western gull *Larus occidentalis*

629 (Pyle et al. 1997); green woodhoopoe *Phoeniculus purpureus* (Hawn et al. 2007); blue-

630 footed booby *Sula nebouxii* (Kim et al. 2011)), highlighting the need to consider sex-specific

631 variation in life-history traits (McDonald 1993; Santos and Nakagawa 2012). The positive

632 correlation between the relative timing of Optimal AFR and body mass concurs with findings

633 in mammals where AFR is correlated strongly with body mass (larger mammals having later

634 AFR; Estern 1979; Wootton 1987). Nevertheless, we additionally demonstrated that, in

635 birds, larger species benefited more from delaying the onset of reproduction beyond sexual

636 maturity than smaller species. Therefore, body mass seems to be an important factor

637 associated with variation in reproductive strategy. Animals with a large body size invest

638 substantial amounts of resources into growth. Although, in birds, growth after sexual

639 maturity is negligible (Ricklefs 1983), postponing the onset of reproduction might

640 counterbalance the cost endured during the development phase and increase the

641 probability of a high lifetime reproductive output.

642   In conclusion, AFR varies both within and among species, and this variation is

643 reflected in LRS. The most frequently observed AFR within a species results in the highest

644 LRS. Where an AFR delayed beyond physiological maturity co-occurred with the highest LRS,

645 this delay was mainly associated with a long lifespan and a decrease in LRS and future

646 survival linked to early reproduction. Our study is the first to provide empirical confirmation

647 of several key predictions of life-history theory across species that lifespan and costs of

648 reproduction shape reproductive timing (Lack 1968; Roff 1992; Stearns 1992; Charlesworth

649 1994). Moreover, the finding that, in long-lived species, postponing the onset of

650 independent reproduction is an optimal strategy has important implications for long-held

651   perspectives on the evolution of sociality. Hitherto, the decision of young birds to remain

652   with their parents and become helpers has been viewed as a sub-optimal response to the

653   lack of breeding opportunities (Emlen 1982; Koenig et al. 1992; Arnold and Owens 1998).

654   Our results clearly indicate that this decision can be a strategy to mitigate the costs of early

655   reproduction. Overall, our results are consistent with life-history theory and challenge

656   current theories on the evolution of family formation and cooperative breeding.

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667

668   **LITERATURE CITED**

669   Arnold, K. E. and I. P. F. Owens. 1998. Cooperative breeding in birds: a comparative test of

670   the life history hypothesis. Proc. R. Soc. B 265:739-745.

671   Barton, K. 2013. MuMIn: Multi-model inference. R package version 2.0.0. http://R-Forge.R-

672   project.org/projects/mumin/.

673   Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models

674   using Eigen and S4. R package version 1.1-7, http://CRAN.R-project.org/package=lme4.

675   Bell, G. 1980. The costs of reproduction and their consequences. Am. Nat. 116:45-76.

676   Brommer, J. E., J. Merilä, and H. Kokko. 2002. Reproductive timing and individual fitness.

677   Ecol. Lett. 5:802-810.

678   Brommer, J. E., H. Pietiainen, and H. Kolunen. 1998. The effect of age at first breeding on

679   Ural owl lifetime reproductive success and fitness under cyclic food conditions. J. Anim.

680   Ecol. 67:359-369.

681   Burnham, K. P. and D. R. Anderson. 2011. AIC model selection and multimodel inference in

682   behavioral ecology: some background, observations, and comparisons. Behav. Ecol.

683   Sociobiol. 65:23-35.

684   Caswell, H. 1982. Life history strategies. Pp. 285-305 *in* J. M. Cherrett, ed. Ecological

685   Concepts. Blackwell Scientific Publications, Oxford.

686   Caswell, H. and A. Hastings. 1980. Fecundity, developmental time, and population-growth

687   rate - An analytical solution. Theor. Popul. Biol. 17:71-79.

688   Charlesworth, B. 1994. Evolution in Age Structured Populations. Cambridge University Press,

689   Cambridge.

690   Charmantier, A., C. Perrins, R. H. McCleery, and B. C. Sheldon. 2006. Quantitative genetics of

691   age at reproduction in wild swans: Support for antagonistic pleiotropy models of

692   senescence. Proc. Natl. Acad. Sci. U.S.A 103:6587-6592.

693   Clutton-Brock, T. H. 1988. Reproductive Success. University of Chicago Press, Chicago.

694   Cole, L. C. 1954. The population consequences of life history phenomena. Q. Rev. Biol.

695   29:103-137.

696   Cooper, N. W., M. T. Murphy, L. J. Redmond, and A. C. Dolan. 2009. Density-dependent age

697   at first reproduction in the eastern kingbird. Oikos 118:413-419.

698   Covas, R. and M. Griesser. 2007. Life history and the evolution of family living in birds. Proc.

699   R. Soc. B 274:1349-1357.

700   Curio, E. 1983. Why do young birds reproduce less well? Ibis 125:400-404.

701   del Hoyo, J., A. Elliott, J. Sargatal, and D. A. Christie. 1992-2006. Handbook of the Birds of

702   the World. Lynx Edicions, Barcelona.

703   Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B.

704   Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B.

705   Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a

706   review of methods to deal with it and a simulation study evaluating their performance.

707   Ecography 36:27-46.

708   Drobniak, M. S., G. Wagner, E. Mourocq, and M. Griesser. 2015. Family living: an overlooked

709   but pivotal social system to understand the evolution of cooperative breeding. Behav.

710   Ecol. 26:805-811.

711   Dugdale, H. L., P. Nouvellet, L. C. Pope, T. Burke, and D. W. MacDonald. 2010. Fitness

712   measures in selection analyses: sensitivity to the overall number of offspring produced in

713   a lifetime. J. Evol. Biol. 23:282-292.

714   Ekman, J. 2007. Delayed dispersal: youth costs carry lifetime gains. Curr. Biol. 17:R417-R418.

715   Ekman, J., J. L. Dickinson, B. J. Hatchwell, and M. Griesser. 2004. Delayed dispersal *in* W. D.

716   Koenig, and J. L. Dickinson, eds. Ecology and Evolution of Cooperative Breeding in Birds.

717   Cambridge University Press, Cambridge.

718   Ekman, J., S. Eggers, M. Griesser, and H. Tegelström. 2001. Queuing for preferred territories:

719   delayed dispersal of Siberian jays. J. Anim. Ecol. 70:317-324.

720   Emlen, S. T. 1982. The evolution of helping. 1. An ecological constraints model. Am. Nat.

721   119:29-39.

722   Ens, B. J., F. J. Weissing, and R. H. Drent. 1995. The despotic distribution and deferred

723   maturity - two sides of the same coin. Am. Nat. 146:625-650.

724   Estern, D. 1979. Size, life history and ecology in mammals. Afr. J. Ecol. 17:185-204.

725   Forslund, P. and T. Pärt. 1995. Age and reproduction in birds: hypothesis and tests. Trends

726   Ecol. Evol. 10:374-378.

727   Garamszegi, L. Z. and A. P. Møller. 2011. Nonrandom variation in within-species sample size

728   and missing data in phylogenetic comparative studies. Syst. Biol. 60:876-880.

729   Gibbs, H. L. and P. R. Grant. 1987. Ecological consequences of an exceptionally strong El-

730   Niño event on Darwin Finches. Ecology 68:1735-1746.

731   Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in

732   ecology and evolution: challenges and solutions. J. Evol. Biol. 24:699-711.

733   Hansen, T. F. and K. Bartoszek. 2012. Interpreting the evolutionary regression: the interplay

734   between observational and biological errors in phylogenetic comparative studies. Syst.

735   Biol. 61:413-425.

736   Hatchwell, B. J. and J. Komdeur. 2000. Ecological constraints, life history traits and the

737   evolution of cooperative breeding. Anim. Behav. 59:1079-1086.

738   Hawn, A. T., A. N. Radford, and M. A. du Plessis. 2007. Delayed breeding affects lifetime

739   reproductive success differently in male and female green woodhoopoes. Curr. Biol.

740   17:844-849.

741   Jetz, W. and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography

742   of cooperative breeding in birds. Curr. Biol. 21:72-78.

743   Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity

744   of birds in space and time. Nature 491:444-448.

745 Khan, M. Z. and J. R. Walters. 2002. Effects of helpers on breeder survival in the red-

746   cockaded woodpecker (*Picoides borealis*). Behav. Ecol. Sociobiol. 51:336-344.

747 Kim, S. Y., A. Velando, R. Torres, and H. Drummond. 2011. Effects of recruiting age on

748   senescence, lifespan and lifetime reproductive success in a long-lived seabird. Oecologia

749   166:615-626.

750 Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The

751   evolution of delayed dispersal in cooperative breeders. Q. Rev. Biol. 67:111-150.

752 Komdeur, J. 1996. Influence of age on reproductive performance in the Seychelles warbler.

753   Behav. Ecol. 7:417-425.

754 Koricheva, J., J. Gurevitch, and K. Mengersen. 2013. Handbook of Meta-analysis in Ecology

755   and Evolution. Princeton University Press, Princeton.

756 Krüger, O. 2005. Age at first breeding and fitness in goshawk *Accipiter gentilis*. J. Anim. Ecol.

757   74:266-273.

758 Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

759 Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, D. W. Coltman, M. Buoro, S. Raveh,

760   and F. S. Dobson. 2011. A quantitative genetic analysis of hibernation emergence date in

761   a wild population of Columbian ground squirrels. J. Evol. Biol. 24:1949-1959.

762 Langen, T. A. 1996. Skill acquisition and the timing of natal dispersal in the white-throated

763   magpie-jay, *Calocitta formosa*. Anim. Behav. 51:575-588.

764 Lewontin, R. C. 1965. Selection for colonizing ability. Pp. 77-91 *in* H. G. Baker, and G. L.

765   Stebbins, eds. The Genetics of Colonizing Species. Academic Press, New York.

766 Link, W. A., E. G. Cooch, and E. Cam. 2002. Model-based estimation of individual fitness. J.

767   Appl. Statist. 29:207-224.

768   Liou, L. W., T. Price, M. S. Boyce, and C. M. Perrins. 1993. Fluctuating environments and

769   clutch size evolution in Great Tits. Am. Nat. 141:507-516.

770   Martin, J. G. A., D. H. Nussey, A. J. Wilson, and D. Réale. 2011. Measuring individual

771   differences in reaction norms in field and experimental studies: a power analysis of

772   random regression models. Methods Ecol. Evol. 2:362-374.

773   Martin, T. E. 1993. Nest predation and nest sites - New perspectives on old patterns.

774   Bioscience 43:523-532.

775   Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright

776   future? Auk 121:289-301.

777   Martin, T. E. and P. J. Li. 1992. Life-history traits of open-nesting vs cavity-nesting birds.

778   Ecology 73:579-592.

779   McDonald, D. B. 1993. Demographic consequences of sexual selection in the Long-tailed

780   Manakin. Behav. Ecol. 4:297-309.

781   Millon, A., S. J. Petty, and X. Lambin. 2010. Pulsed resources affect the timing of first

782   breeding and lifetime reproductive success of tawny owls. J. Anim. Ecol. 79:426-435.

783   Newton, I. 1989. Lifetime Reproductive Success. Academic Press, London.

784   Oli, M. K., G. R. Hepp, and R. A. Kennamer. 2002. Fitness consequences of delayed maturity

785   in female wood ducks. Evol. Ecol. Res. 4:563-576.

786   Prevot-Julliard, A. C., R. Pradel, R. Julliard, V. Grosbois, and J. D. Lebreton. 2001. Hatching

787   date influences age at first reproduction in the black-headed gull. Oecologia 127:62-68.

788   Pyle, P., N. Nur, W. J. Sydeman, and S. D. Emslie. 1997. Cost of reproduction and the

789   evolution of deferred breeding in the western gull. Behav. Ecol. 8:140-147.

790   R Core Team. 2013. R: A language and environment for statistical computing. R Foundation

791   for Statistical Computing, Vienna, Austria.

792   Ricklefs, R. E. 1983. Comparative avian demography *in* R. F. Johnston, ed. Curr Ornithol.

793   Plenum Press, New York.

794   Roff, D. A. 1992. The Evolution of Life Histories. Chapman and Hall, New York.

795   Russell, E. M. 2000. Avian life histories: Is extended parental care the southern secret? Emu

796   100:377-399.

797   Santos, E. S. A. and R. H. Macedo. 2011. Load lightening in southern lapwings: group-living

798   mothers lay smaller eggs than pair-living mothers. Ethology 117:547-555.

799   Santos, E. S. A. and S. Nakagawa. 2012. The costs of parental care: a meta-analysis of the

800   trade-off between parental effort and survival in birds. J. Evol. Biol. 25:1911-1917.

801   Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients.

802   Methods Ecol. Evol. 1:103-113.

803   Skutch, A. F. 1961. Helpers among birds. Condor 63:198-226.

804   Stearns, S. 1992. The Evolution of Life Histories. Oxford University Press, Oxford

805   Stearns, S. C. 1989. Trade-offs in life-history evolution. Funct. Ecol. 3:259-268.

806   Symonds, M. R. E. and A. Moussalli. 2011. A brief guide to model selection, multimodel

807   inference and model averaging in behavioural ecology using Akaike's information

808   criterion. Behav. Ecol. Sociobiol. 65:13-21.

809   Tettamanti, F., W. Witvliet, and P. Bize. 2012. Selection on age at first and at last

810   reproduction in the long-lived Alpine Swift *Apus melba*. Ibis 154:338-344.

811   Valcu, M., J. Dale, M. Griesser, S. Nakagawa, and B. Kempenaers. 2014. Global gradients of

812   avian longevity support the classic evolutionary theory of ageing. Ecography 37:930-938.

813   van de Pol, M. 2012. Quantifying individual variation in reaction norms: how study design

814   affects the accuracy, precision and power of random regression models. Methods Ecol.

815   Evol. 3:268-280.

816   van de Pol, M., I. Pen, D. Heg, and F. J. Weissing. 2007. Variation in habitat choice and

817   delayed reproduction: Adaptive queuing strategies or individual quality differences? Am.

818   Nat. 170:530-541.

819   van de Pol, M. and J. Wright. 2009. A simple method for distinguishing within- versus

820   between-subject effects using mixed models. Anim. Behav. 77:753-758.

821   Van Noordwijk, A. J. and G. De Jong. 1986. Acquisition and allocation of resources: their

822   influence on variation in life history tactics. Am. Nat. 128:137-142.

823   Williams, G. C. 1966. Natural selection, costs of reproduction, and a refinement of Lack's

824   principle. Am. Nat. 100:687.

825   Wooller, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1989. Short-tailed Shearwater. Pp.

826   405-417 *in* I. Newton, ed. Lifetime Reproductive Success. Academic Press, London.

827   Wootton, J. T. 1987. The effects of body-mass, phylogeny, habitat, and trophic level on

828   mammalian age at 1st reproduction. Evolution 41:732-749.

829   Zack, S. and B. J. Stutchbury. 1992. Delayed breeding in avian social-systems - The role of

830   territory quality and floater tactics. Behaviour 123:194-219.

831   Zhang, H., M. Rebke, P. H. Becker, and S. Bouwhuis. 2015. Fitness prospects: effects of age,

832   sex and recruitment age on reproductive value in a long-lived seabird. J. Anim. Ecol.

833   84:199-207.

834   **Conflict of Interest**

835   We have no conflict of interest.

836   **Author contributions**

837   P.B., S.B., R.B., A.C., C.C., R.E., M.H., H.H., O.K., J.M., A.M., S.N., R.P., A.N.R., A.R., J.T., J.V.,

838   M.V.P., I.G.W., I.S.W., A.W. provided unpublished data on lifetime reproductive success.

839   E.M. compiled the data, performed the statistical analysis and wrote the first draft of the

840   manuscript. All authors contributed to revisions (especially M.G.) and gave final approval for

841   publication. M.G. helped with data compilation and reflection on the manuscript. S.M.D.,

842   S.N. and M.G. helped with the statistical methods and estimation of the indices. S.M.D.

843   wrote the R script to automate the estimation of two indices.

844   **Data accessibility**

845   The datasets supporting this article have been uploaded as part of the Supporting

846   Information.

847 **Table 1.** Definitions and descriptions of the parameters and indices estimated for each sex (when

848 possible) and each species followed by a graph illustrating the description based on the case of the

849 Eurasian sparrowhawk (*Accipiter nisus*). See also *Indices and estimates* section in *Materials and*

850 *Methods*.

Species parameter	Definition	Biological description	Technical description
Optimal AFR	AFR that results in the highest LRS	Reflects the species-average optimum strategy of onset of reproduction	AFR that maximizes mean LRS excluding AFR categories with <10% individuals. Extracted visually
Optimal AFR Range	Range of optimal AFR(s)	Reflects the range of the species-average optimum strategy of onset of reproduction	Number of AFR(s) adjacent to the Optimal AFR with mean LRS values overlapped by the standard error bars of the Optimal AFR. Extracted visually. Range from 1 to 15
Before Variation Index	LRS cost of initiating reproduction before the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy which is earlier than the range of species-average optimum strategy of onset of reproduction	Slope before the Optimal AFR Range (center of the range) between mean LRS and AFR; Average of slopes obtained when all individuals were included, when excluding AFR categories with <5% and <10 % individuals (mean standard error slope = 0.21). A large positive value indicates a strong negative fitness impact of reproducing before the Optimal AFR Range
After Variation Index	LRS cost of initiating reproduction after the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy which is later than the range of species-average optimum strategy of onset of reproduction	Slope after the Optimal AFR Range (center of the range) between mean LRS and AFR; Average of slopes obtained when all individuals were included, when excluding AFR categories with <5% and <10 % individuals (mean standard error slope = 0.18). A large negative value indicates a strong negative fitness impact of reproducing after the Optimal AFR Range
Delay Index	Relative position of the Optimal AFR during the reproductive lifespan	Reflects when – during the average-reproductive lifespan of a species – individuals from a species benefit the most from initiating their reproduction	Varies between 0 and 1. Delay Index 0: the optimal strategy is to start reproduction at physiological maturity; Delay Index 1: the optimal strategy is to delay the onset of reproduction to maximum AFR
Choice Index	Range of optimal AFR(s) relative to the number of AFR observed	Reflects the species-average span of "beneficial choice" in AFR, (i.e. AFRs leading to higher LRS)	Varies between 0 and 1. Choice Index of 0: species has only one optimal AFR; Choice Index of 1: all AFR are optimal
Lifespan Effect Index	Effect of AFR on the mean reproductive lifespan (for each AFR category: see Figure S2)	Reflects the species-specific average effect of the onset of reproduction on survival	Correlation coefficient between mean reproductive lifespan and AFR (Fisher's z transformed) (Koricheva et al. 2013). Positive values suggest a cost of early onset of reproduction, while negative values suggest a cost of late onset

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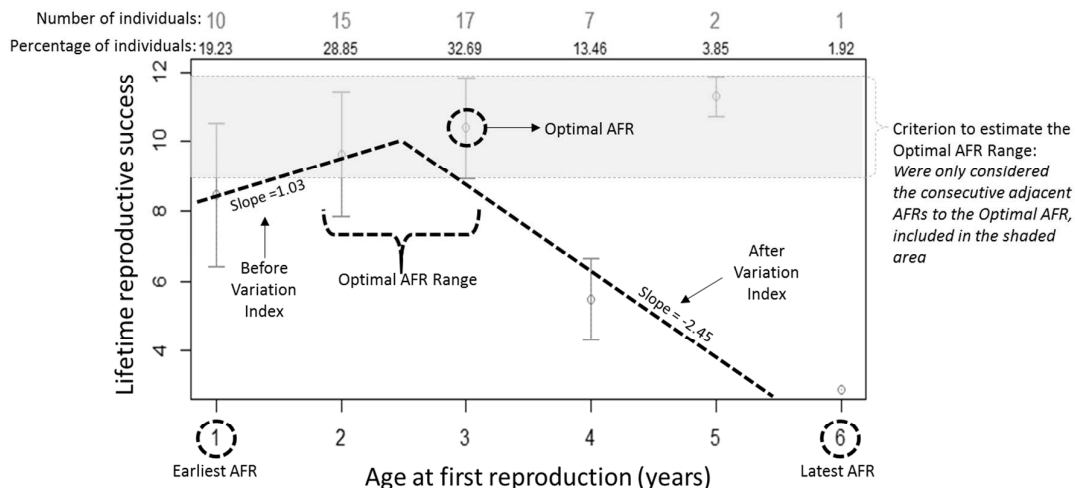
852   **Table 2.** Effect of sex, mean lifespan of species, family-living and presence of helpers on mean AFR

853   within a species (N = 26 populations, 24 species for which data were available for both sexes).

854   Estimates and 95% confidence intervals (CI) are presented. Δ AIC$_c$ corresponds to the change in AIC$_c$

855   when the specific parameter was included vs. excluded from the full model.

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	Standard deviation	Estimate	95% CI	Δ AIC$_c$
Fixed effects:				
intercept		0.10	(-0.14, 0.34)	-
sex: Female		0.00	na	-2.51
sex: Male		0.03	(0.01, 0.05)	
mean lifespan $_{species}$*		0.87	(0.72, 1.02)	-61.65†
family-living: NO		0.00	na	2.58
family-living: YES		-0.12	(-0.89, 0.64)	
helper presence: NO		0.00	na	2.08
helper presence: YES		-0.33	(-1.16, 0.50)	
Random effects:				
species	0.52		(0.40, 0.70)	
residuals	0.93		(0.72, 1.26)	

869   * factor centered and scaled; na – not applicable; † support for inclusion of the factor
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871   **Table 3.** Relative importance of predictors included in the full model for the analysis of Delay Index

872   variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging

873   estimates (based on 53 models with Δ AICc (AICc $_{focal\ model}$ – AICc $_{best\ model}$) ≤ 5, see Table S9).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.14	(-0.71, 1.00)
ln(body mass)	0.49	1.00	0.35	(0.01, 0.69)
sex	0.49	1.00	Both: 0.00 Female: -0.06 Male: -0.24	na (-0.94, 0.82) (-1.12, 0.65)
Choice Index ¶	0.49	1.00	0.44	(0.15, 0.72)
Before Variation Index ¶	0.48	0.98	0.30	(0.07, 0.54)
family-living	0.40	0.82	NO: 0.00 YES: 0.01	na (-1.45, 1.48)
helper presence	0.40	0.82	NO: 0.00 YES: 0.49	na (-2.12, 3.31)
nest predation risk	0.28	0.56	0.03	(-0.34, 0.43)
Choice Index: helper presence	0.25	0.51	NO: 0.00 YES: -0.67	na (-2.45, -0.18)
mean lifespan	0.25	0.50	0.09	(-0.26, 0.60)
Choice Index: family-living	0.23	0.46	NO: 0.00 YES: 0.57	na (-0.50, 3.00)
mean lifespan: helper presence	0.22	0.44	NO: 0.00 YES: 2.48	na (2.66, 8.49)
mean lifespan: family-living	0.21	0.43	NO: 0.00 YES: -1.91	na (-6.12, -2.72)
nest predation risk: family-living	0.21	0.43	NO: 0.00 YES: 0.91	na (1.23, 2.97)
Before Variation Index: Choice Index	0.17	0.35	0.13	(-0.08, 0.82)
After Variation Index ¶	0.14	0.28	-0.04	(-0.37, 0.05)
nest predation risk: helper presence	0.10	0.21	NO: 0.00 YES: -0.41	na (-3.82, -0.13)
chick development mode	0.05	0.11	Altricial: 0.00 Precocial: -0.02	na (-1.20, 0.74)
latitude	0.03	0.07	-0.01	(-0.41, 0.23)
Before Variation Index: After Variation Index	0.00	0.01	0.00	(-0.08, 0.19)

874   *: sum of model weights from Table S9 including the focal predictor. na – not applicable;

875   †: predictor weight relative to the highest weighted predictor.

876   ‡: model averaging estimates according to full model averaging approach since the best AIC$_c$ model

877   is not strongly weighted (weight = 0.05) (Symonds and Moussalli 2011).

878   §: reference levels of categorical variables have an estimate of 0; estimates reflect difference in

879   slope between the reference level and focal level.

880   <u>Note:</u> The relative importance of body mass and sex is due to their inclusion by default in each

881   model to control for allometry and sex differences. All continuous variables are centered and scaled.

882   ¶: predictors reflecting the relationship between LRS and AFR, see Table 1 and the Indices and

883   estimates section of Materials and methods.

884 **Table 4.** Relative importance of predictors included in the full model for the analysis of Delay Index

885 variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging

886 estimates (based on 28 models with Δ AICc (AICc $_{focal\ model}$ – AICc $_{best\ model}$) ≤ 5, see Table S10).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.42	(-0.34, 1.18)
ln(body mass)	0.57	1.00	0.36	(-0.23, 0.95)
sex	0.57	1.00	Both: 0.00	Na
			Female: -0.67	(-1.43, 0.09)
			Male: -0.35	(-1.11, 0.42)
Choice Index ¶	0.57	1.00	0.35	(0.17, 0.52)
Lifespan Effect Index ¶	0.57	1.00	0.54	(0.37, 0.72)
After Variation Index ¶	0.38	0.66	-0.20	(-0.56, -0.05)
helper presence	0.26	0.46	NO: 0.00	Na
			YES: 0.56	(0.03, 2.40)
family-living	0.24	0.42	NO: 0.00	Na
			YES: -0.32	(-1.59, 0.08)
mean lifespan	0.23	0.41	0.20	(-0.01, 0.98)
chick development mode	0.10	0.17	Altricial: 0.00	Na
			Precocial: -0.11	(-1.28, 0.04)
nest predation risk	0.10	0.17	0.06	(-0.08, 0.74)
latitude	0.07	0.13	0.02	(-0.32, 0.56)
Choice Index: family-living	0.04	0.07	NO: 0.00	Na
			YES: 0.03	(-0.14, 0.87)
Choice Index: helper presence	0.04	0.07	NO: 0.00	Na
			YES: 0.03	(-0.18, 1.07)
Before Variation Index ¶	0.03	0.06	0.01	(-0.16, 0.35)

887 *: sum of model weights from Table S10 including the focal predictor. na – not applicable;
888 †: predictor weight relative to the highest weighted predictor.
889 ‡: model averaging estimates according to full model averaging approach since the best AIC$_c$ model
890 is not strongly weighted (weight = 0.10) (Symonds and Moussalli 2011).
891 §: reference levels of categorical variables have an estimate of 0; estimates reflect difference in
892 slope between the reference level and focal level.
893 Note: The relative importance of body mass and sex is due to their inclusion by default in each
894 model to control for allometry and sex differences. All continuous variables are centered and scaled.
895 ¶: predictors reflecting relationship between LRS or survival and AFR, see Table 1 and the Indices
896 and estimates section of Materials and methods.

Figure legends

Figure 1. Mean AFR (years) and standard deviation for all 36 populations (34 species) (both sexes combined). Mean AFR ranged from 1 to 12.8 years (mean ± SD = 3.0 ± 2.6, N = 36), and standard deviation from 0 to 2.31 (mean ± SD = 0.80 ± 0.58, N = 36). A number after the name of a species indicates different populations.

Figure 2. Relationship between AFR (years) and the associated mean lifespan within species and sexes (years, N = 22 populations (21 species) for which detailed data on mean lifespan per AFR category were available). Each point is the mean lifespan of individuals within each AFR category. A number after the name of a species indicates different populations. Regression lines are based on the raw data and were drawn for all cases independent of whether the correlation was significant or not.

Figure 3. Variation in AFR and consequences on fitness - Relationship between standardized LRS and AFR for the 36 populations of the 34 species, separated by sex where possible (a point is the mean LRS (centred and scaled) over all individuals that started to reproduce at a specific AFR). Curves represent quadratic fit of the relationship between standardized LRS and AFR independent of whether the relationship was significant or not.

Figure 4. Species-specific Optimal AFR presented relative to the species age at maturity (left y-axis) with species ordered by mean lifespan (both sexes combined). Mean lifespan values are represented by the grey line and the right y-axis. A number after the name of a species indicates the different populations included in the study.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the

publisher's website:

Table S1. Information on the source and the type of LRS data for each study

Table S2. Model without weighting – Variation in AFR analysis

Table S3. Model without weighting – Fitness consequence of AFR analysis

Table S4. Model without weighting – Delay Index analysis excluding Lifespan Effect Index

Table S5. Model without weighting – Delay Index analysis including Lifespan Effect Index

Table S6. Model without weighting – Model selection output for the analysis of Delay Index

variation excluding Lifespan Effect Index

Table S7. Model without weighting – Model selection output for the analysis of Delay Index

variation including Lifespan Effect Index

Table S8. Justification for the interactions used in the analysis of the Delay Index

Table S9. Model selection output for the analysis of Delay Index variation excluding Lifespan

Effect Index

Table S10. Model selection output for the analysis of Delay Index variation including

Lifespan Effect Index

Table S11. Fitness consequence of AFR analysis

Table S12. Correlation between Optimal AFR vs. modal AFR and mean AFR for different sest

of species

Table S13. Model with 90CI Indices – Delay Index analysis excluding Lifespan Effect Index

Table S14. Model with 90CI Indices – Delay Index analysis including Lifespan Effect Index

Lifespan and reproductive cost explain interspecific variation in the optimal onset of reproduction

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Table S1. Information on the source and the type of LRS data for each study.

Species	Scientific name	Location	LRS type	Sample size*	Reference
alpine swift	*Apus melba*	North-Western Switzerland	fledglings	F: 157; M: 121	**Pierre Bize**
azure-winged magpie	*Cyanopica cyanus*	Valdesequera, Spain	fledglings	F: 200; M: 104	**Juliana Valencia & Carlos de la Cruz**
barn swallow	*Hirundo rustica*	Kraghede, Denmark	fledglings	F: 1394; M: 1360	**Anders Pape Møller**
black-browed albatross	*Thalassarche melanophris*	Bird Island, UK	fledglings	B: 76	**Richard Phillips & Andrew G. Wood**
blue Tit 1	*Cyanistes caeruleus*	Oxford, UK	recruits	F: 1177; M: 972	**Sandra Bouwhuis & Ben Sheldon**
blue Tit 2	*Cyanistes caeruleus*	Vienna, Austria	recruits	F: 261; M: 211	**Bart Kempenaers & Emmi Schlicht**
blue-footed booby	*Sula nebouxii*	Isla Isabela, Mexico	fledglings	F: 222; M: 246	Kim et al. (2011)
collared flycatcher	*Ficedula albicollis*	Budapest, Hungary	recruits	F: 453; M: 481	**Márton Herényi & János Török**
common barn owl	*Tyto alba*	Payerne, Switzerland	fledglings	F: 170; M: 174	**Alexandre Roulin**
common buzzard	*Buteo buteo*	Eastern Westphalia, Germany	fledglings	F: 239	**Olivier Krüger**
Eurasian sparrowhawk	*Accipiter nisus*	Annandale, Eskdale, Scotland	fledglings	F: 52	McGraw & Caswell (1996)
Eurasian oystercatcher	*Haematopus ostralegus*	Schiermonnikoog, Netherlands	fledglings	F: 19; M: 33	**Martijn Van de Pol**
Florida scrub-jay	*Aphelocoma coerulescens*	Archbold, USA	fledglings	F: 37; M: 43	Fitzpatrick & Woolfenden (1988)
goshawk	*Accipiter gentilis*	Bissendorf, Spenge, Germany	fledglings	F: 74	Krüger (2005)
great tit	*Parus major*	Oxford, UK	recruits	F: 4935; M: 4370	**Sandra Bouwhuis & Ben Sheldon**
green woodhoopoe	*Phoeniculus purpureus*	Eastern Cape, South Africa	fledglings	F: 59; M: 62	**Andrew Radford**
grey-headed albatross	*Thalassarche chrysostoma*	Bird Island, UK	fledglings	B: 74	**Richard Phillips & Andrew G. Wood**
house sparrow	*Passer domesticus*	Lundy Island, UK	fledglings	F: 287; M: 265	**Terry Burke & colleagues**
indigo bunting	*Passerina cyanea*	Southern Michigan, USA	fledglings	F: 360; M: 357	Payne (1989)
lesser snow goose	*Chen caerulescens*	La Perouse Bay, Canada	1st 4 years of life	F: 2616	Viallefont et al. (1995)
long-tailed tit	*Aegithalos caudatus*	Sheffield, UK	recruits	F: 119; M: 109	**Ben Hatchwell**
meadow pipit	*Anthus pratensis*	North-west Germany	fledglings	F: 33; M: 49	**Hermann Hötker**
merlin	*Falco columbarius*	Saskatoon, Canada	fledglings	F: 26; M: 68	**Richard Espie & Ian G. Warkentin**
mute swan	*Cygnus olor*	Abbotsbury, UK	recruits	F: 252; M: 277	**Anne Charmantier,** Ben Sheldon & Chris Perrins
osprey	*Pandion haliaetus*	Michigan, USA	fledglings	B: 40	Postupalsky (1989)
pied flycatcher	*Ficedula hypoleuca*	Wolfsburg, Germany	fledglings	F: 1411; M: 1135	Sternberg (1989)
pinyon jay	*Gymnorhinus cyanocephalus*	Flagstaff, USA	yearlings	F: 39; M: 41	**John Marzluff**
Seychelles warbler	*Acrocephalus sechellensis*	Cousin Island, Seychelles	fledglings	F: 41; M: 37	Komdeur (1996)
short-tailed shearwater	*Puffinus tenuirostris*	Fisher Island, Australia	fledglings	B: 186	Wooller et al. (1989)
Siberian jay	*Perisoreus infaustus*	Arvidsjaur, Sweden	fledglings	F: 44; M: 56	Ekman & Griesser (2016)
tawny owl	*Strix aluco*	Kielder Forest, UK	fledglings	F: 83; M: 51	Millon et al. (2010)
ural owl	*Strix uralensis*	Päijät-Häme, Finland	fledglings	F: 57	Brommer et al. (1998)
wandering albatross	*Diomedea exulans*	Bird Island, UK	fledglings	F: 1819; M: 1519	**Richard Phillips & Andrew G. Wood**
western gull 1	*Larus occidentalis*	Farallon Island, USA	fledglings	F: 163; M: 108	Pyle et al. (1997)
western gull 2	*Larus occidentalis*	Farallon Island, USA	fledglings	F: 66; M: 93	**Russell Bradley**
wood duck	*Aix sponsa*	South Carolina, USA	fledglings	F: 90	Oli et al. (2002)

Bold reference indicates unpublished data provided directly by researchers.* number of individuals of F: female, M: male, B: both sexes

Table S2. Model without weighting (see Table 2 for output model with weighting) - Effect of sex, mean lifespan of species, family-living and presence of helpers on mean AFR within a species (N = 26 populations, 24 species for which data were available for both sexes). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

	Standard deviation	Estimate	95% CI	Δ AIC$_c$
Fixed effects:				
intercept		0.10	(-0.14, 0.34)	-
sex: Females		0.00	na	1.99
sex: Male		0.02	(-0.03, 0.07)	
mean lifespan $_{species}$*		0.82	(0.67, 0.96)	-58.68†
family-living: NO		0.00	na	2.60
family-living: YES		-0.11	(-0.87, 0.66)	
helper presence: NO		0.00	na	2.07
helper presence: YES		-0.34	(-1.18, 0.50)	
Random effects:				
species	0.52		(0.40, 0.70)	
residuals	0.09		(0.07, 0.12)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table S3. **Model without weighting** (see Table S11 for output model with weighting). Results from models testing the within- and among-species effect of AFR on LRS (N = 36 populations, 34 species). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

	Standard deviation	Estimate	95% CI	Δ AIC$_c$
Fixed effects:				
intercept		0.00	(-0.36, 0.37)	-
ln(body mass)*		-0.01	(-0.17, 0.14)	2.10
sex: Both		0.00	na	
sex: Female		0.12	(-0.28, 0.54)	3.76
sex: Male		0.14	(-0.26, 0.54)	
within-species AFR*		-0.38	(-0.56, -0.20)	-14.97†
within-species AFR^2*		-0.30	(-0.51, -0.10)	-6.36†
between-species AFR		0.03	(-0.16, 0.22)	2.03
Random effects:				
species	0.00		(0.00, 0.13)	
residuals	0.86		(0.79, 0.93)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table S4. Model without weighting (see Table 3 for output model with weighting). Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 58 models with Δ AICc (AICc $_{focal\ model}$ – AICc $_{best\ model}$) ≤ 5, see Table S6).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.07	(-0.78, 0.92)
ln(body mass)	0.49	1.00	0.36	(0.08, 0.64)
sex	0.49	1.00	Both: 0.00	na
			Female: -0.01	(-0.92, 0.89)
			Male: -0.05	(-0.97, 0.87)
Choice Index ¶	0.49	1.00	0.59	(0.34, 0.85)
Before Variation Index ¶	0.48	0.98	0.30	(0.08, 0.52)
Before Variation Index: Choice Index	0.34	0.70	0.25	(0.01, 0.71)
latitude	0.17	0.35	-0.06	(-0.42, 0.06)
After Variation Index ¶	0.12	0.25	-0.03	(-0.31, 0.09)
mean lifespan	0.10	0.20	0.04	(-0.16, 0.54)
family-living	0.08	0.16	NO: 0.00	na
			YES: -0.03	(-0.65, 0.31)
nest predation risk	0.07	0.14	0.01	(-0.20, 0.31)
helper presence	0.06	0.12	NO: 0.00	na
			YES: -0.00	(-0.69, 0.66)
chick development mode	0.05	0.11	Altricial: 0.00	na
			Precocial: 0.00	(-0.75, 0.76)
Choice Index: family-living	0.01	0.03	NO: 0.00	na
			YES: 0.02	(-0.42, 1.38)
After Variation Index: Choice Index	0.01	0.02	0.00	(-0.15, 0.34)
Before Variation Index: After Variation Index	0.01	0.02	-0.00	(-0.17, 0.11)
mean lifespan: helper presence	0.00	0.01	0.01	(-0.26, 2.12)
Choice Index: helper presence	0.00	0.01	NO: 0.00	na
			YES: -0.01	(-1.99, -0.14)

*: sum of model weights from Table S6 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC$_c$ model is not strongly weighted (weight = 0.04) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

<u>Note</u>: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S5. Model without weighting (see Table 4 for output model with weighting). Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 28 models with Δ AICc (AICc $_{focal\ model}$ − AICc $_{best\ model}$) ≤ 5, see Table S7).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.16	(-0.67, 0.99)
ln(body mass)	0.51	1.00	0.24	(-0.44, 0.92)
sex	0.51	1.00	Both: 0.00	na
			Female: -0.26	(-1.17, 0.65)
			Male: -0.03	(-0.92, 0.87)
Lifespan Effect Index ¶	0.51	1.00	0.54	(0.32, 0.77)
Choice Index ¶	0.49	0.96	0.32	(0.07, 0.60)
mean lifespan	0.30	0.59	0.33	(0.02, 0.10)
After Variation Index ¶	0.25	0.48	-0.13	(-0.51, -0.03)
helper presence	0.24	0.47	NO: 0.00	na
			YES: 0.47	(-0.10, 2.06)
family-living	0.18	0.35	NO: 0.00	na
			YES: -0.26	(-1.57, 0.08)
latitude	0.08	0.15	-0.04	(-0.60, 0.06)
mean lifespan: helper presence	0.05	0.10	0.15	(0.21, 2.82)
Choice Index: family-living	0.05	0.09	NO: 0.00	na
			YES: 0.04	(-0.01, 0.95)
Choice Index: helper presence	0.04	0.08	NO: 0.00	na
			YES: 0.04	(-0.04, 1.04)
Before Variation Index ¶	0.03	0.05	0.01	(-0.16, 0.34)
chick development mode	0.03	0.05	Altricial: 0.00	na
			Precocial: -0.02	(-1.00, 0.22)
nest predation risk	0.02	0.03	0.00	(-0.32, 0.34)

*: sum of model weights from Table S7 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC$_c$ model is not strongly weighted (weight = 0.08) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

<u>Note:</u> The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS or survival and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S6. Model without weighting (see Table S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.20	0.42	+	-	-	-	-	-	-	0.63	0.30	-	-	-	0.34	-	-	-	-	-	-	9	-68.56	158.58	0.00	0.04
-0.06	0.37	+	-0.17	-	-	-	-	-	0.64	0.34	-	-	-	0.35	-	-	-	-	-	-	10	-67.44	159.19	0.61	0.03
0.14	0.40	+	-	-	-	-	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	8	-70.52	159.75	1.17	0.02
0.05	0.28	+	-	-	-	-	0.20	-	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	10	-67.80	159.91	1.33	0.02
0.25	0.40	+	-	-	-	-	-	-	0.62	0.31	-0.10	-	-	0.35	-	-	-	-	-	-	10	-68.07	160.45	1.87	0.02
-0.12	0.35	+	-0.17	-	-	-	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	9	-69.52	160.49	1.92	0.02
0.19	0.35	+	-	0.12	-	-	-	-	0.64	0.32	-	-	-	0.41	-	-	-	-	-	-	10	-68.10	160.52	1.94	0.02
-0.03	0.34	+	-0.19	-	-	-	-	-	0.63	0.35	-0.11	-	-	0.36	-	-	-	-	-	-	11	-66.71	160.70	2.12	0.01
0.20	0.42	+	-	-	+	-	-	-	0.62	0.29	-	-	-	0.35	-	-	-	-	-	-	10	-68.29	160.90	2.32	0.01
-0.02	0.25	+	-	-	-	-	0.20	-	0.52	0.25	-	-	-	-	-	-	-	-	-	-	9	-69.77	161.00	2.42	0.01
-0.09	0.37	+	-0.19	-	+	-	-	-	0.63	0.33	-	-	-	0.36	-	-	-	-	-	-	11	-66.94	161.15	2.57	0.01
0.08	0.22	+	-	-	-	-	0.24	-	0.64	0.33	-0.12	-	-	0.35	-	-	-	-	-	-	11	-67.00	161.29	2.71	0.01
0.22	0.41	+	-	-	-	-	-	+	0.63	0.30	-	-	-	0.36	-	-	-	-	-	-	10	-68.54	161.39	2.81	0.01
0.20	0.42	+	-	-	-	+	-	-	0.63	0.30	-	-	-	0.34	-	-	-	-	-	-	10	-68.56	161.43	2.85	0.01
-0.10	0.34	+	-0.21	-	-	+	-	-	0.63	0.33	-	-	-	0.35	-	-	-	-	-	-	11	-67.18	161.64	3.07	0.01
-0.03	0.32	+	-0.19	-	-	-	-	+	0.66	0.34	-	-	-	0.41	-	-	-	-	-	-	11	-67.21	161.70	3.12	0.01
-0.04	0.33	+	-0.15	0.08	-	-	-	-	0.64	0.35	-	-	-	0.39	-	-	-	-	-	-	11	-67.25	161.78	3.20	0.01
0.25	0.29	+	-	0.16	-	-	-	-	0.64	0.35	-0.13	-	-	0.44	-	-	-	-	-	-	11	-67.25	161.78	3.20	0.01
0.17	0.38	+	-	-	-	-	-	-	0.50	0.24	-0.08	-	-	-	-	-	-	-	-	-	9	-70.17	161.81	3.23	0.01
-0.08	0.31	+	-0.13	-	-	-	0.10	-	0.64	0.33	-	-	-	0.35	-	-	-	-	-	-	11	-67.29	161.86	3.28	0.01
-0.01	0.48	+	-	-	-	-	-	-	0.49	-	-	-	-	-	-	-	-	-	-	-	7	-72.98	162.03	3.45	0.01
0.09	0.44	+	-	-	-	-	-	+	0.50	0.24	-	-	-	-	-	-	-	-	-	-	9	-70.30	162.05	3.47	0.01
0.18	0.43	+	-	-	+	-	-	-	0.54	0.28	-	-	-	0.34	-	+	-	-	-	-	11	-67.39	162.06	3.48	0.01
0.13	0.40	+	-	-	+	-	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	9	-70.34	162.15	3.57	0.01

Table S6 following. Model without weighting (see Table S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

Covariate			Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
-0.10	0.32	+	-0.18	-	-	-	-	-	0.50	0.28	-0.10	-	-	-	-	-	-	-	-	-	10	-68.99	162.29	3.71	0.01
0.13	0.39	+	-	0.02	-	-	-	-	0.50	0.24	-	-	-	-	-	-	-	-	-	-	9	-70.50	162.47	3.89	0.01
0.13	0.40	+	-	-	-	+	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	9	-70.51	162.49	3.91	0.01
0.06	0.29	+	-	-	+	-	0.18	-	0.64	0.30	-	-	-	0.35	-	-	-	-	-	-	11	-67.64	162.56	3.98	0.01
-0.15	0.35	+	-0.18	-	+	-	-	-	0.50	0.26	-	-	-	-	-	-	-	-	-	-	10	-69.16	162.64	4.06	0.01
0.01	0.20	+	-	-	-	-	0.24	-	0.52	0.26	-0.11	-	-	-	-	-	-	-	-	-	10	-69.17	162.66	4.08	0.01
-0.06	0.34	+	-0.21	-	+	-	-	-	0.63	0.35	-0.11	-	-	0.37	-	-	-	-	-	-	12	-66.20	162.77	4.19	0.01
0.08	0.28	+	-	0.05	-	-	0.16	-	0.65	0.32	-	-	-	0.37	-	-	-	-	-	-	11	-67.75	162.77	4.20	0.01
-0.08	0.29	+	-0.24	-	-	+	-	-	0.63	0.35	-0.13	-	-	0.37	-	-	-	-	-	-	12	-66.23	162.82	4.24	0.01
0.26	0.40	+	-	-	-	-	-	-	0.62	0.31	-0.12	-	0.10	0.39	-	-	-	-	-	-	11	-67.77	162.83	4.25	0.01
0.06	0.27	+	-	-	-	+	0.20	-	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	11	-67.79	162.87	4.29	0.00
0.05	0.28	+	-	-	-	-	0.20	+	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	11	-67.80	162.87	4.29	0.00
0.01	0.27	+	-0.16	0.12	-	-	-	-	0.64	0.38	-0.14	-	-	0.43	-	-	-	-	-	-	12	-66.25	162.88	4.30	0.00
0.24	0.40	+	-	-	+	-	-	-	0.62	0.30	-0.09	-	-	0.36	-	-	-	-	-	-	11	-67.82	162.91	4.33	0.00
0.16	0.46	+	-	-	+	+	-	-	0.62	0.30	-	-	-	0.35	-	-	-	-	-	-	11	-67.85	162.98	4.40	0.00
-0.15	0.33	+	-0.20	-	-	+	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.34	162.99	4.41	0.00
-0.14	0.28	+	-0.13	-	-	-	0.11	-	0.52	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.35	163.01	4.43	0.00
0.19	0.36	+	-	0.11	+	-	-	-	0.64	0.32	-	-	-	0.41	-	-	-	-	-	-	11	-67.87	163.01	4.44	0.00
-0.10	0.29	+	-	-	-	-	0.22	+	0.52	0.26	-	-	-	-	-	-	-	-	-	-	10	-69.39	163.08	4.51	0.00
0.11	0.41	+	-	-	+	-	-	-	0.41	0.21	-	-	-	-	-	-	-	+	-	-	10	-69.39	163.09	4.51	0.00
-0.13	0.37	+	-0.16	-	-	-	-	+	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.46	163.24	4.66	0.00
-0.05	0.25	+	-0.14	-	-	-	0.14	-	0.64	0.35	-0.12	-	-	0.36	-	-	-	-	-	-	12	-66.44	163.25	4.67	0.00
0.25	0.40	+	-	-	-	-	-	-	0.63	0.33	-0.09	-0.03	-	0.35	-	-	-	-	-	-	11	-67.98	163.25	4.67	0.00
-0.01	0.35	+	-0.19	-	-	-	-	-	0.63	0.35	-0.14	-	0.09	0.39	-	-	-	-	-	-	12	-66.44	163.25	4.67	0.00

Table S6 following. Model without weighting (see Table S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
-0.12	0.36	+	-0.17	-0.02	-	-	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.50	163.32	4.74	0.00
0.25	0.39	+	-	-	-	+	-	-	0.62	0.31	-0.10	-	-	0.36	-	-	-	-	-	-	11	-68.06	163.40	4.82	0.00
0.26	0.39	+	-	-	-	-	-	+	0.63	0.31	-0.09	-	-	0.36	-	-	-	-	-	-	11	-68.06	163.41	4.83	0.00
0.00	0.29	+	-0.21	-	-	-	-	+	0.65	0.36	-0.11	-	-	0.41	-	-	-	-	-	-	12	-66.53	163.43	4.85	0.00
0.18	0.36	+	-	0.13	-	-	-	+	0.64	0.33	-	-	-	0.40	-	-	-	-	-	-	11	-68.09	163.46	4.88	0.00
0.19	0.35	+	-	0.12	-	+	-	-	0.64	0.33	-	-	-	0.41	-	-	-	-	-	-	11	-68.10	163.48	4.90	0.00
-0.03	0.34	+	-0.19	-	-	-	-	-	0.64	0.37	-0.10	-0.04	-	0.36	-	-	-	-	-	-	12	-66.57	163.50	4.92	0.00
0.11	0.28	+	-	-	-	+	0.16	-	0.60	0.29	-	-	-	0.33	-	-	+	-	-	-	12	-66.58	163.52	4.94	0.00
-0.04	0.26	+	-	-0.08	-	-	0.26	-	0.53	0.24	-	-	-	-	-	-	-	-	-	-	10	-69.61	163.53	4.95	0.00
0.02	0.48	+	-	-	+	+	-	-	0.42	0.20	-	-	-	-	-	-	+	+	-	-	12	-66.59	163.54	4.96	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AICc" represents the Akaike's information criterion corrected for sample size. "Δ AICc" is the difference in AICc between the focal model and the model with the lowest AICc. "weight" represents the relative probability of a model within the full set of models.

Table S7. Model without weighting (see Table S10 for output model with weighting). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	logLikelihood	AICc	Δ AICc	weight
0.11	-0.07	+	-	-	-	-	0.66	-	0.36	-	-0.27	0.54	-	-	-	-	-	-	10	-30.40	89.61	0.00	0.08
0.31	0.65	+	-	-	+	+	-	-	0.35	-	-	0.57	-	-	-	-	-	-	10	-31.00	90.79	1.19	0.05
0.31	0.60	+	-	-	+	+	-	-	0.20	-	-	0.52	-	-	+	-	-	-	11	-29.15	91.29	1.69	0.04
0.08	0.17	+	-	-	-	-	0.47	-	0.40	-	-	0.56	-	-	-	-	-	-	9	-33.33	91.59	1.99	0.03
0.36	0.56	+	-	-	+	+	-	-	0.22	-	-	0.57	-	+	-	-	-	-	11	-29.38	91.76	2.15	0.03
-0.08	0.43	+	-0.31	-	-	-	-	-	0.40	-	-	0.54	-	-	-	-	-	-	9	-33.56	92.04	2.44	0.02
0.03	-0.03	+	-	-	-	-	0.70	+	0.36	-	-0.33	0.52	-	-	-	-	-	-	11	-29.56	92.12	2.52	0.02
-0.12	-0.03	+	-0.19	-	-	-	0.54	-	0.37	-	-0.27	0.53	-	-	-	-	-	-	11	-29.58	92.16	2.56	0.02
0.18	-0.06	+	-	-	-	+	0.59	-	0.28	-	-0.28	0.51	-	-	-	+	-	-	12	-27.39	92.36	2.75	0.02
0.09	0.01	+	-	-	-	+	0.62	-	0.39	-	-0.27	0.52	-	-	-	-	-	-	11	-29.71	92.41	2.81	0.02
0.45	0.52	+	-	-	-	-	-	-	0.38	-	-	0.56	-	-	-	-	-	-	8	-35.72	92.77	3.16	0.02
0.15	-0.12	+	-	-	-	+	0.64	-	0.25	-	-0.30	0.53	-	+	-	-	-	-	12	-27.68	92.92	3.31	0.02
-0.01	0.36	+	-0.33	-	-	-	-	-	0.37	-	-0.17	0.53	-	-	-	-	-	-	10	-32.30	93.39	3.79	0.01
0.09	-0.09	+	-	-	+	-	0.69	-	0.38	-	-0.29	0.53	-	-	-	-	-	-	11	-30.33	93.65	4.05	0.01
-0.18	0.21	+	-0.21	-	-	-	0.34	-	0.40	-	-	0.54	-	-	-	-	-	-	10	-32.46	93.73	4.12	0.01
0.35	0.42	+	-	-	+	+	0.04	-	-	-	-	0.57	-	-	-	+	-	-	11	-30.36	93.73	4.12	0.01
0.10	-0.08	+	-	0.05	-	-	0.64	-	0.37	-	-0.27	0.56	-	-	-	-	-	-	11	-30.37	93.75	4.14	0.01
0.11	-0.07	+	-	-	-	-	0.66	-	0.36	0.02	-0.27	0.54	-	-	-	-	-	-	11	-30.39	93.77	4.16	0.01
0.34	0.63	+	-	-	+	+	-	-	0.36	0.12	-	0.52	-	-	-	-	-	-	11	-30.43	93.86	4.25	0.01
0.25	-0.19	+	-	-	-	+	0.58	-	-	-	-0.32	0.53	-	-	-	+	-	-	11	-30.46	93.92	4.32	0.01
0.26	0.44	+	-	-	+	+	0.14	-	0.25	-	-	0.55	-	-	-	+	-	-	12	-28.19	93.95	4.34	0.01
0.42	0.46	+	-	-	+	-	-	-	0.14	-	-	0.52	-	-	+	-	-	-	10	-32.59	93.97	4.36	0.01
0.06	0.25	+	-	-	-	+	0.43	-	0.43	-	-	0.53	-	-	-	-	-	-	10	-32.63	94.06	4.45	0.01
0.17	0.48	+	-	-	+	+	0.21	-	0.37	-	-	0.56	-	-	-	-	-	-	11	-30.55	94.09	4.49	0.01

Table S7 following. Model without weighting (see Table S10 for output model with weighting). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

(Intercept)	Covariate: ln(body mass)	sex	Ecological factors: latitude	nest predation risk	Social lifestyle factors: family-living	helper presence	Life-history factors: mean lifespan	chick development mode	Indices: Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.39	0.59	+	-	-	-	+	-	-	0.42	-	-	0.53	-	-	-	-	-	-	9	-34.70	94.33	4.72	0.01
0.25	0.56	+	-	0.13	+	+	-	-	0.37	-	-	0.60	-	-	-	-	-	-	11	-30.73	94.46	4.85	0.01
-0.15	0.37	+	-0.37	-	-	-	-	-	0.42	0.14	-	0.48	-	-	-	-	-	-	10	-32.85	94.50	4.90	0.01
0.37	0.62	+	-	-	+	+	-	-	0.34	-	-0.07	0.56	-	-	-	-	-	-	11	-30.76	94.53	4.92	0.01

Model set with Δ AICc ≤ 5. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AICc" represents the Akaike's information criterion corrected for sample size. "Δ AICc" is the difference in AICc between the focal model and the model with the lowest AICc. "weight" represents the relative probability of a model within the full set of models.

Table S8. Justification for the interactions used in the analysis of the Delay Index.

Interaction	Reason for inclusion in the model
Before Variation Index *x* After Variation Index	To test if the relative timing of the Optimal AFR over reproductive lifespan (Delay Index) was influenced simultaneously by a LRS cost from initiating reproduction both before the optimal timing (Before Variation Index) and after the optimal timing (After Variation Index).
Choice Index *x* Before Variation Index	To test if Delay Index was influenced simultaneously by the level of probability to adopt an AFR leading to the highest fitness return (i.e. the span of "beneficial AFR" within the observed range of AFR) and a LRS cost from initiating reproduction before Optimal AFR. *We expect species with a large span of "beneficial AFR" and a low LRS cost of early reproduction to benefit from a late AFR.*
Choice Index *x* After Variation Index	To test if Delay Index was influenced simultaneously by the level of probability to adopt an AFR leading to the highest fitness return (i.e. the span of "beneficial AFR" within the observed range of AFR) and a LRS cost from initiating reproduction after Optimal AFR. *We expect species with a small span of "beneficial AFR" and a high LRS cost of late reproduction to benefit from an early AFR.*
Mean lifespan *x* Family-living	For each of these interactions we tested whether sociality influenced the effect of the focal predictors on Delay Index based on the idea that living in a kin group (Family living) or breeding cooperatively (Helper presence) might buffer costs associated with the timing of the AFR within the reproductive lifespan.
Mean lifespan *x* Helper presence	
Nest predation risk *x* Family-living	*For instance, species with a high risk of nest predation need to get experience to successfully defend their nest and have a greater reproductive output. Consequently, they might benefit*
Nest predation risk *x* Helper presence	*from a later AFR. However, if the presence of helpers provides anti-predator protection, it might allow less experienced individuals to still achieve a good reproductive output.*
Choice Index *x* Family-living	*Therefore, we expect species with a high risk of nest predation breeding cooperatively to benefit more from an earlier AFR than species with a high risk of nest predation but*
Choice Index *x* Helper presence	*breeding as a pair without helpers.*

The variables included in the interactions are explained in the manuscript as well as in Table 1 for the indices.

Table S9. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.14	0.46	+	-	-	+	+	-	-	0.36	0.22	-	-	-	-	+	+	-	-	-	-	12	-60.84	152.05	0.00	0.05
0.06	0.30	+	-	-0.03	+	+	0.19	-	0.36	0.28	-	-	-	-	-	-	+	+	+	+	16	-54.44	152.97	0.92	0.03
0.06	0.33	+	-	-0.03	+	+	0.17	-	0.37	0.28	-	-	-	-	+	-	+	+	-	+	16	-54.74	153.56	1.51	0.02
0.22	0.47	+	-	-	+	+	-	-	0.47	0.29	-	-	-	0.22	+	+	-	-	-	-	13	-60.14	153.86	1.81	0.02
0.23	0.27	+	-	0.28	-	-	-	-	0.67	0.43	-	-	-	0.52	-	-	-	-	-	-	10	-64.84	153.99	1.94	0.02
0.10	0.22	+	-	-0.04	+	+	0.25	-	0.35	0.30	-0.16	-	-	-	-	-	+	+	+	+	17	-53.12	154.16	2.11	0.02
0.19	0.44	+	-	-	+	+	-	-	0.36	0.22	-0.11	-	-	-	+	+	-	-	-	-	13	-60.30	154.19	2.14	0.02
0.33	0.43	+	-	-	-	-	-	-	0.62	0.39	-	-	-	0.42	-	-	-	-	-	-	9	-66.41	154.29	2.24	0.02
0.10	0.25	+	-	-0.04	+	+	0.24	-	0.37	0.29	-0.17	-	-	-	+	-	+	+	-	+	17	-53.28	154.48	2.43	0.01
0.07	0.36	+	-	-0.02	+	+	0.12	-	0.34	0.27	-	-	-	-	-	-	+	+	-	+	15	-57.10	154.64	2.59	0.01
0.10	0.49	+	-	-	+	+	-	+	0.37	0.23	-	-	-	-	+	+	-	-	-	-	13	-60.60	154.79	2.74	0.01
-0.02	0.40	+	-0.10	-	+	+	-	-	0.38	0.24	-	-	-	-	+	+	-	-	-	-	13	-60.61	154.81	2.76	0.01
0.09	0.50	+	-	-	+	+	-	-	0.35	-	-	-	-	-	+	+	-	-	-	-	11	-63.77	154.82	2.77	0.01
0.08	0.39	+	-	-	+	+	0.09	-	0.37	0.23	-	-	-	-	+	+	-	-	-	-	13	-60.73	155.03	2.98	0.01
0.30	0.22	+	-	0.32	-	-	-	-	0.69	0.46	-0.15	-	-	0.57	-	-	-	-	-	-	11	-63.89	155.06	3.01	0.01
0.06	0.32	+	-	-0.03	+	+	0.17	-	0.37	0.29	-	-	-	-	-	-	+	+	+	+	16	-55.49	155.06	3.01	0.01
0.13	0.45	+	-	0.02	+	+	-	-	0.37	0.22	-	-	-	-	+	+	-	-	-	-	13	-60.83	155.25	3.20	0.01
0.15	0.29	+	-	0.03	+	+	0.14	-	0.46	0.35	-	-	-	0.23	-	-	+	+	+	+	17	-53.73	155.38	3.33	0.01
0.05	0.23	+	-	0.03	+	+	0.22	+	0.36	0.33	-0.22	-	-	-	-	-	+	+	+	+	18	-51.82	155.55	3.50	0.01
0.05	0.28	+	-	-0.03	+	+	0.21	-	0.38	0.29	-	-	-	-	-	-	+	+	+	+	17	-53.84	155.60	3.55	0.01
0.30	0.44	+	-	-	+	+	-	-	0.47	0.31	-0.13	-	-	0.25	+	+	-	-	-	-	14	-59.38	155.69	3.64	0.01
0.10	0.23	+	-	-0.04	+	+	0.25	-	0.37	0.30	-0.17	-	-	-	+	-	+	+	-	+	17	-54.01	155.92	3.87	0.01
0.22	0.20	+	-	0.04	+	+	0.21	-	0.48	0.38	-0.18	-	-	0.28	-	-	+	+	+	+	18	-52.01	155.93	3.88	0.01
0.06	0.30	+	-	-0.03	+	+	0.19	-	0.37	0.28	-	-	-	-	-	-	+	-	+	+	17	-54.04	155.99	3.94	0.01
0.11	0.29	+	-	-0.03	+	+	0.19	-	0.33	0.28	-0.15	-	-	-	-	-	+	+	-	+	16	-55.97	156.03	3.98	0.01

Table S9 following. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	ΔAICc	weight
0.02	0.32	+	-	0.01	+	+	0.16	+	0.36	0.30	-	-	-	-	-	-	+	+	+	+	17	-54.06	156.03	3.98	0.01
0.44	0.35	+	-	-	-	-	-	+	0.65	0.40	-	-	-	0.48	-	-	-	-	-	-	10	-65.86	156.04	3.99	0.01
0.15	0.32	+	-	0.03	+	+	0.12	-	0.47	0.35	-	-	-	0.22	+	-	+	+	-	+	17	-54.07	156.05	4.00	0.01
0.10	0.39	+	-	-	+	+	0.07	-	0.37	0.22	-	-	-	-	+	+	+	-	-	-	14	-59.66	156.25	4.20	0.01
0.39	0.42	+	-	-	-	-	-	-	0.63	0.40	-0.11	-	-	0.44	-	-	-	-	-	-	10	-65.98	156.27	4.22	0.01
0.22	0.22	+	-	0.03	+	+	0.19	-	0.49	0.38	-0.19	-	-	0.28	+	-	+	+	-	+	18	-52.21	156.33	4.28	0.01
0.06	0.26	+	-	0.02	+	+	0.21	+	0.37	0.33	-0.22	-	-	-	+	-	+	+	-	+	18	-52.22	156.34	4.29	0.01
0.10	0.39	+	-0.13	-	-	-	-	-	0.63	0.41	-	-	-	0.42	-	-	-	-	-	-	10	-66.04	156.38	4.33	0.01
0.18	0.35	+	-	0.05	+	+	0.07	-	0.46	0.35	-	-	-	0.27	-	-	+	+	-	+	16	-56.16	156.41	4.36	0.01
0.16	0.48	+	-	-	+	+	-	+	0.36	0.24	-0.14	-	-	-	+	+	-	-	-	-	14	-59.74	156.42	4.37	0.01
0.25	0.20	+	-	0.05	+	+	0.20	-	0.53	0.42	-0.20	-	-	0.35	-	+	+	+	-	+	18	-52.32	156.54	4.49	0.01
-0.02	0.34	+	-0.15	-	+	+	-	-	0.38	0.25	-0.14	-	-	-	+	+	-	-	-	-	14	-59.81	156.57	4.52	0.01
0.09	0.20	+	-	-0.04	+	+	0.28	-	0.37	0.31	-0.17	-	-	-	-	+	+	+	+	+	18	-52.33	156.58	4.53	0.00
0.05	0.40	+	-0.11	-	+	+	-	-	0.48	0.31	-	-	-	0.22	+	-	-	-	-	-	14	-59.86	156.66	4.61	0.00
0.18	0.30	+	-	0.05	+	+	0.12	-	0.50	0.38	-	-	-	0.29	-	+	+	+	-	+	17	-54.38	156.67	4.62	0.00
0.30	0.24	+	-	0.25	-	-	-	+	0.68	0.43	-	-	-	0.55	-	-	-	-	-	-	11	-64.70	156.67	4.62	0.00
0.18	0.42	+	-	-	-	-	-	-	0.43	0.25	-	-	-	-	-	-	-	-	-	-	8	-68.98	156.67	4.62	0.00
0.20	0.41	+	-	0.10	+	+	-	-	0.49	0.32	-	-	-	0.27	+	+	-	-	-	-	14	-59.91	156.76	4.71	0.00
0.09	0.30	+	0.03	-0.03	+	+	0.20	-	0.36	0.28	-	-	-	-	-	-	+	+	+	+	17	-54.43	156.76	4.71	0.00
0.30	0.31	+	-	0.32	-	-	-0.09	-	0.66	0.44	-	-	-	0.53	-	-	-	-	-	-	11	-64.74	156.77	4.72	0.00
0.13	0.26	+	-0.06	0.26	-	-	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.75	156.77	4.72	0.00
0.19	0.44	+	-	-	+	+	-	-	0.36	0.17	-0.14	0.06	-	-	+	+	-	-	-	-	14	-59.94	156.82	4.77	0.00

Table S9 following. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.04	0.35	+	-	0.00	+	+	0.15	+	0.37	0.29	-	-	-	-	+	-	+	+	-	+	17	-54.49	156.89	4.84	0.00
0.16	0.38	+	-	-	+	+	0.10	-	0.48	0.30	-	-	-	0.22	+	+	-	-	-	-	14	-59.98	156.90	4.85	0.00
0.25	0.37	+	-	-	-	-	0.09	-	0.63	0.39	-	-	-	0.42	-	-	-	-	-	-	10	-66.30	156.91	4.86	0.00
0.23	0.27	+	-	0.28	-	+	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.83	156.93	4.88	0.00
0.24	0.27	+	-	0.28	+	-	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.83	156.95	4.90	0.00
0.11	0.32	+	-	-	+	+	0.14	-	0.37	0.23	-0.13	-	-	-	+	+	-	-	-	-	14	-60.03	157.00	4.95	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AICc" represents the Akaike's information criterion corrected for sample size. "Δ AICc" is the difference in AICc between the focal model and the model with the lowest AICc. "weight" represents the relative probability of a model within the full set of models.

Table S10. Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.36	0.05	+	-	-	-	-	0.53	-	0.36	-	-0.33	0.53	-	-	-	-	-	-	10	-24.97	78.73	0.00	0.10
0.42	0.61	+	-	-	+	+	-	-	0.35	-	-	0.53	-	-	-	-	-	-	10	-25.55	79.90	1.17	0.06
0.35	0.30	+	-	0.39	-	-	-	+	0.38	-	-0.36	0.61	-	-	-	-	-	-	11	-23.91	80.82	2.09	0.04
0.51	0.58	+	-	-	+	+	-	-	0.33	-	-0.19	0.52	-	-	-	-	-	-	11	-23.91	80.82	2.09	0.04
0.35	0.08	+	-	-	-	+	0.53	-	0.38	-	-0.32	0.51	-	-	-	-	-	-	11	-24.30	81.61	2.87	0.02
0.68	0.78	+	0.21	-	+	+	-	-	0.31	-	-	0.54	-	-	-	-	-	-	11	-24.39	81.78	3.05	0.02
0.41	0.16	+	-	-	-	-	0.43	+	0.35	-	-0.36	0.52	-	-	-	-	-	-	11	-24.42	81.85	3.11	0.02
0.28	0.00	+	-	0.18	-	-	0.46	-	0.38	-	-0.33	0.57	-	-	-	-	-	-	11	-24.48	81.97	3.23	0.02
0.60	0.55	+	-	-	-	-	-	+	0.32	-	-0.33	0.54	-	-	-	-	-	-	10	-26.64	82.09	3.36	0.02
0.41	0.59	+	-	-	+	+	-	-	0.31	-	-	0.51	-	-	+	-	-	-	11	-24.69	82.38	3.65	0.02
0.42	0.59	+	-	-	+	+	-	-	0.31	-	-	0.52	-	+	-	-	-	-	11	-24.70	82.41	3.68	0.02
0.29	0.24	+	-	-	-	-	0.37	-	0.38	-	-	0.56	-	-	-	-	-	-	9	-28.90	82.72	3.98	0.01
0.33	-0.01	+	-	-	+	-	0.60	-	0.37	-	-0.35	0.52	-	-	-	-	-	-	11	-24.88	82.76	4.03	0.01
0.33	0.37	+	-0.21	-	-	-	-	-	0.35	-	-0.28	0.55	-	-	-	-	-	-	10	-27.02	82.83	4.10	0.01
0.35	0.04	+	-	-	-	-	0.54	-	0.36	0.02	-0.33	0.52	-	-	-	-	-	-	11	-24.95	82.90	4.17	0.01
0.37	0.04	+	0.02	-	-	-	0.56	-	0.36	-	-0.33	0.53	-	-	-	-	-	-	11	-24.96	82.91	4.18	0.01
0.75	0.80	+	0.28	-	+	+	-	-	0.24	-	-	0.51	-	-	+	-	-	-	12	-22.69	82.94	4.20	0.01
0.41	0.61	+	-	-	+	+	-	-	0.35	0.11	-	0.52	-	-	-	-	-	-	11	-25.04	83.07	4.34	0.01
0.48	0.55	+	-	-	-	-	-	-	0.35	-	-	0.59	-	-	-	-	-	-	8	-30.90	83.14	4.41	0.01
0.33	0.33	+	-	0.40	-	+	-	+	0.41	-	-0.36	0.58	-	-	-	-	-	-	12	-22.80	83.17	4.44	0.01

Table S10 following. Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

(Intercept)	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.50	0.56	+	-	-	+	+	-	-	0.29	-	-0.20	0.50	-	-	+	-	-	-	12	-22.84	83.24	4.51	0.01
0.29	0.26	+	-	0.45	-	-	-	+	0.39	0.17	-0.38	0.59	-	-	-	-	-	-	12	-22.84	83.25	4.52	0.01
0.75	0.78	+	0.27	-	+	+	-	-	0.25	-	-	0.53	-	+	-	-	-	-	12	-22.85	83.26	4.53	0.01
0.51	0.55	+	-	-	+	+	-	-	0.29	-	-0.19	0.52	-	+	-	-	-	-	12	-22.89	83.35	4.62	0.01
0.35	0.27	+	-	0.37	-	-	-	-	0.38	-	-0.24	0.65	-	-	-	-	-	-	10	-27.28	83.37	4.64	0.01
0.52	0.80	+	-	-	+	+	-0.21	-	0.33	-	-	0.54	-	-	-	-	-	-	11	-25.27	83.53	4.80	0.01
0.34	0.53	+	-	0.13	+	+	-	-	0.37	-	-	0.56	-	-	-	-	-	-	11	-25.31	83.61	4.88	0.01
0.58	0.52	+	-	-	-	-	-	-	0.33	-	-0.21	0.58	-	-	-	-	-	-	9	-29.39	83.69	4.96	0.01

Model set with Δ AICc ≤ 5. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AICc" represents the Akaike's information criterion corrected for sample size. "Δ AICc" is the difference in AICc between the focal model and the model with the lowest AICc. "weight" represents the relative probability of a model within the full set of models.

Table S11. Results from models testing the within- and among-species effect of AFR on LRS (N = 36 populations, 34 species). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

	Standard deviation	Estimate	95% CI	Δ AIC$_c$
Fixed effects:				
intercept		-0.12	(-0.87, 0.62)	-
ln(body mass)*		-0.11	(-0.29, 0.08)	0.91
sex: Both		0.00	na	
sex: Female		0.38	(-0.37, 1.14)	3.09
sex: Male		0.41	(-0.34, 1.16)	
within-species AFR*		-0.54	(-0.70, -0.39)	-43.83†
within-species AFR^2*		-0.26	(-0.43, -0.10)	-7.45†
between-species AFR		0.08	(-0.13, 0.29)	1.57
Random effects:				
species	0.00		(0.00, 0.16)	
residuals	19.64		(18.14, 21.35)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table S12. Correlation between Optimal AFR vs. modal AFR and Optimal AFR vs. mean AFR.

cases	Mean AFR vs. Optimal AFR			AFR mode vs. Optimal AFR		
	Correlation coefficient	P	Slope	Correlation coefficient	P	Slope
all (N=62)	0.84 (Spearman)	< 0.0001	0.95	0.80 (Spearman)	< 0.0001	0.98
with AFR range > 4 (N=29)	0.85 (Spearman)	< 0.0001	0.99	0.87 (Spearman)	< 0.0001	0.82
with AFR range > 6 (N=12)	0.96 (Pearson)	< 0.0001	1.13	0.92 (Pearson)	< 0.0001	1.06

Table S13. Model with 90CI indices (see Table 3 for comparison). Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 51 models with Δ AICc (AICc $_{focal\ model}$ – AICc $_{best\ model}$) ≤ 5, see Table S15).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.42	(-0.60, 1.44)
ln(body mass)	0.51	1.00	0.21	(-0.17, 0.59)
sex	0.51	1.00	Both: 0.00	na
			Female: -0.30	(-1.40, 0.79)
			Male: -0.54	(-1.64, 0.56)
Choice Index 90CI ¶	0.51	1.00	0.53	(0.29, 0.77)
Before Variation Index 90CI ¶	0.51	1.00	0.36	(-0.02, 0.74)
Before Variation Index 90CI: Choice Index 90CI	0.51	1.00	0.86	(0.35, 1.37)
nest predation risk	0.41	0.80	0.35	(0.03, 0.84)
After Variation Index 90CI ¶	0.35	0.69	-0.17	(-0.49, 0.01)
Before Variation Index 90CI: After Variation Index 90CI	0.17	0.33	-0.05	(-0.32, 0.01)
family-living	0.13	0.26	NO: 0.00	na
			YES: 0.15	(-0.95, 2.15)
chick development mode	0.12	0.24	Altricial: 0.00	na
			Precocial: 0.17	(-0.28, 1.69)
mean lifespan	0.10	0.20	-0.04	(-0.77, 0.35)
helper presence	0.10	0.19	NO: 0.00	na
			YES: -0.12	(-2.91, 1.63)
nest predation risk: family-living	0.05	0.09	NO: 0.00	na
			YES: 0.09	(-0.34, 2.21)
Choice Index: helper presence	0.04	0.08	NO: 0.00	na
			YES: -0.12	(-2.55, -0.30)
latitude	0.04	0.08	0.00	(-0.30, 0.42)
Choice Index: family-living	0.04	0.07	NO: 0.00	na
			YES: 0.11	(0.62, 2.44)
After Variation Index 90CI: Choice Index 90CI	0.02	0.04	-0.00	(-0.53, 0.48)
mean lifespan: helper presence	0.02	0.03	NO: 0.00	na
			YES: 0.13	(2.18, 7.04)
mean lifespan: family-living	0.02	0.03	NO: 0.00	na
			YES: -0.10	(-5.17, -1.96)
nest predation risk: helper presence	0.01	0.01	NO: 0.00	na
			YES: -0.01	(-3.41, 0.27)

*: sum of model weights from Table S15 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC$_c$ model is not strongly weighted (weight = 0.05) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S14. Model with 90CI indices (see Table 4 for comparison). Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 45 models with Δ AICc (AICc $_{focal\ model}$ – AICc $_{best\ model}$) ≤ 5, see Table S16).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.64	(-0.24, 1.52)
ln(body mass)	0.61	1.00	0.47	(-0.02, 0.96)
sex	0.61	1.00	Both: 0.00	na
			Female: -0.82	(-1.51, 0.34)
			Male: -0.59	(-1.52, 0.34)
Lifespan Effect Index ¶	0.61	1.00	0.47	(0.25, 0.69)
Choice Index 90CI ¶	0.58	0.96	0.34	(0.11, 0.61)
Before Variation Index 90CI ¶	0.32	0.52	0.12	(-0.09, 0.56)
Before Variation Index 90CI: Choice Index 90CI	0.31	0.51	0.25	(0.18, 0.83)
After Variation Index 90CI ¶	0.29	0.47	-0.12	(-0.51, -0.01)
family-living	0.16	0.27	NO: 0.00	na
			YES: -0.25	(-2.30, 0.45)
nest predation risk	0.15	0.25	0.10	(-0.01, 0.82)
helper presence	0.15	0.25	NO: 0.00	na
			YES: 0.42	(-1.19, 4.58)
chick development mode	0.09	0.15	Altricial: 0.00	na
			Precocial: -0.08	(-1.27, 0.18)
mean lifespan	0.08	0.14	-0.02	(-0.94, 0.71)
latitude	0.08	0.14	0.03	(-0.33, 0.70)
Mean lifespan: helper presence	0.04	0.06	NO: 0.00	na
			YES: 0.20	(-0.44, 7.34)
Choice Index: helper presence	0.01	0.02	NO: 0.00	na
			YES: -0.03	(-2.45, -0.28)
Choice Index: family-living	0.01	0.02	NO: 0.00	na
			YES: 0.01	(-0.11, 0.80)

*: sum of model weights from Table S16 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC$_c$ model is not strongly weighted (weight = 0.06) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

<u>Note:</u> The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS or survival and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S15. Model with 90CI indices (see Table S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.27	0.16	+	-	0.44	-	-	-	-	0.52	0.31	-0.25	-	-	0.81	-	-	-	-	-	-	11	-67.68	162.63	0.00	0.04
0.32	0.13	+	-	0.49	-	-	-	-	0.59	0.56	-0.25	-0.14	-	1.03	-	-	-	-	-	-	12	-66.22	162.80	0.17	0.04
0.22	0.25	+	-	0.35	-	-	-	-	0.47	0.23	-	-	-	0.71	-	-	-	-	-	-	10	-69.72	163.76	1.12	0.02
0.57	0.29	+	-	0.62	-	-	-0.33	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	13	-65.15	163.89	1.26	0.02
0.63	0.29	+	-	-	-	-	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	10	-69.83	163.98	1.34	0.02
0.47	0.18	+	-	0.27	-	-	-	+	0.51	0.21	-	-	-	0.80	-	-	-	-	-	-	11	-68.66	164.61	1.97	0.02
0.44	0.27	+	-	0.53	-	-	-0.23	-	0.52	0.30	-0.24	-	-	0.83	-	-	-	-	-	-	12	-67.19	164.74	2.11	0.02
0.50	0.09	+	-	0.36	+	-	-	-	0.55	0.29	-0.27	-	-	0.88	-	-	-	-	-	+	13	-65.61	164.81	2.17	0.01
0.42	0.12	+	-	0.37	-	-	-	+	0.53	0.29	-0.22	-	-	0.85	-	-	-	-	-	-	12	-67.26	164.88	2.24	0.01
0.48	0.09	+	-	0.41	-	-	-	+	0.61	0.54	-0.21	-0.15	-	1.09	-	-	-	-	-	-	13	-65.68	164.94	2.30	0.01
0.35	0.45	+	-	-	-	-	-	-	0.43	0.22	-	-	-	0.62	-	-	-	-	-	-	9	-71.77	165.01	2.37	0.01
0.46	0.17	+	0.11	0.48	-	-	-	-	0.53	0.31	-0.25	-	-	0.83	-	-	-	-	-	-	12	-67.46	165.29	2.65	0.01
0.43	0.38	+	-	0.46	-	-	-0.28	-	0.48	0.23	-	-	-	0.75	-	-	-	-	-	-	11	-69.01	165.29	2.66	0.01
0.29	0.14	+	-	0.45	+	-	-	-	0.53	0.32	-0.26	-	-	0.82	-	-	-	-	-	-	12	-67.49	165.34	2.71	0.01
0.53	0.07	+	-	0.41	+	-	-	-	0.61	0.53	-0.27	-0.14	-	1.09	-	-	-	-	-	+	14	-64.27	165.47	2.84	0.01
0.51	0.14	+	0.11	0.52	-	-	-	-	0.60	0.56	-0.25	-0.15	-	1.05	-	-	-	-	-	-	13	-65.97	165.52	2.89	0.01
0.29	0.15	+	-	0.44	-	+	-	-	0.52	0.31	-0.25	-	-	0.81	-	-	-	-	-	-	12	-67.60	165.56	2.93	0.01
0.34	0.11	+	-	0.50	+	-	-	-	0.60	0.57	-0.26	-0.14	-	1.05	-	-	-	-	-	-	13	-66.02	165.63	3.00	0.01
0.39	0.17	+	-	0.34	+	+	-	-	0.49	0.29	-0.26	-	-	0.77	+	+	-	-	-	-	15	-62.63	165.69	3.06	0.01
0.27	0.15	+	-	0.45	-	-	-	-	0.53	0.32	-0.25	-	-0.03	0.81	-	-	-	-	-	-	12	-67.67	165.71	3.07	0.01
0.33	0.12	+	-	0.49	-	+	-	-	0.59	0.56	-0.25	-0.14	-	1.04	-	-	-	-	-	-	13	-66.13	165.84	3.20	0.01
0.64	0.28	+	-	-	-	-	-	+	0.50	0.24	-0.13	-	-	0.78	-	-	-	-	-	-	11	-69.29	165.86	3.22	0.01

Table S15 following. Model with 90CI indices (see Table S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.41	0.42	+	-	-	-	-	-	-	0.45	0.27	-0.17	-	-	0.67	-	-	-	-	-	-	10	-70.84	166.00	3.36	0.01
0.32	0.13	+	-	0.49	-	-	-	-	0.59	0.56	-0.25	-0.14	-0.02	1.03	-	-	-	-	-	-	13	-66.22	166.01	3.38	0.01
0.37	0.45	+	-	-	+	+	-	-	0.39	0.19	-	-	-	0.57	+	+	-	-	-	-	13	-66.27	166.13	3.49	0.01
0.43	0.27	+	0.11	0.39	-	-	-	-	0.48	0.23	-	-	-	0.73	-	-	-	-	-	-	11	-69.48	166.24	3.61	0.01
0.43	0.14	+	-	0.38	+	+	-	-	0.56	0.53	-0.26	-0.14	-	0.99	+	+	-	-	-	-	16	-61.11	166.31	3.67	0.01
0.28	0.14	+	-	0.17	+	+	0.12	-	0.38	0.31	-0.28	-	-	0.55	-	-	+	+	-	+	17	-59.22	166.34	3.71	0.01
0.44	0.20	+	-	0.27	+	-	-	-	0.50	0.21	-	-	-	0.77	-	-	-	-	-	+	12	-68.02	166.41	3.78	0.01
0.45	0.24	+	-0.11	-	-	-	-	+	0.49	0.20	-	-	-	0.77	-	-	-	-	-	-	11	-69.59	166.47	3.83	0.01
0.24	0.25	+	-	0.35	-	+	-	-	0.47	0.23	-	-	-	0.71	-	-	-	-	-	-	11	-69.66	166.60	3.97	0.01
0.23	0.24	+	-	0.36	+	-	-	-	0.48	0.23	-	-	-	0.72	-	-	-	-	-	-	11	-69.67	166.62	3.98	0.01
0.66	0.24	+	-	0.55	-	-	-0.29	+	0.62	0.58	-0.20	-0.17	-	1.15	-	-	-	-	-	-	14	-64.87	166.68	4.04	0.01
0.42	0.04	+	-	0.47	+	+	-	-	0.56	0.32	-0.29	-	-	0.87	-	-	-	-	-	-	13	-66.60	166.78	4.15	0.01
0.71	0.27	+	-	-	-	-	-	+	0.56	0.45	-0.12	-0.12	-	0.98	-	-	-	-	-	-	12	-68.25	166.88	4.24	0.01
0.45	0.40	+	-	-	+	+	-	-	0.41	0.24	-0.19	-	-	0.62	+	+	-	-	-	-	14	-64.97	166.88	4.25	0.01
0.64	0.29	+	-	-	-	+	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.80	166.89	4.25	0.01
0.62	0.28	+	-	-	-	-	0.02	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.83	166.94	4.30	0.01
0.63	0.29	+	-	-	+	-	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.83	166.94	4.31	0.01
0.58	0.28	+	-	0.36	-	-	-0.20	+	0.51	0.21	-	-	-	0.81	-	-	-	-	-	-	12	-68.29	166.96	4.32	0.01
0.30	0.29	+	-	0.24	+	+	-	-	0.43	0.21	-	-	-	0.65	+	+	-	-	-	-	14	-65.01	166.96	4.33	0.01
0.46	0.01	+	-	0.51	+	+	-	-	0.63	0.57	-0.29	-0.15	-	1.10	-	-	-	-	-	-	14	-65.08	167.09	4.45	0.00
0.58	0.28	+	-	0.62	-	+	-0.33	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	14	-65.10	167.14	4.50	0.00
0.56	0.27	+	-	0.62	+	-	-0.32	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	14	-65.13	167.19	4.55	0.00

Table S15 following. Model with 90CI indices (see Table S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

(Intercept)	Covariate			Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information			
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Lik	AICc	Δ AICc	weight
0.55	0.29	+	-0.01	0.62	-	-	-0.34	-	0.61	0.60	-0.23	-0.18	-	1.11	-	-	-	-	-	-	14	-65.15	167.24	4.60	0.00
0.57	0.29	+	-	0.62	-	-	-0.33	-	0.61	0.60	-0.23	-0.17	-0.01	1.11	-	-	-	-	-	-	14	-65.15	167.24	4.61	0.00
0.54	0.37	+	-	-	+	+	-	+	0.43	0.17	-	-	-	0.68	+	+	-	-	-	-	14	-65.21	167.35	4.72	0.00
0.53	0.22	+	-	0.46	-	-	-0.19	+	0.53	0.29	-0.21	-	-	0.86	-	-	-	-	-	-	13	-66.93	167.44	4.81	0.00
0.26	0.09	+	-	0.16	+	+	0.17	-	0.38	0.31	-0.29	-	-	0.53	-	-	+	+	+	+	18	-57.77	167.45	4.82	0.00
0.45	0.41	+	-	-	-	-	-	-	0.50	0.45	-0.16	-0.11	-	0.83	-	-	-	-	-	-	11	-70.11	167.49	4.86	0.00
0.27	0.14	+	-	0.16	+	+	0.14	-	0.39	0.30	-0.26	-	-	0.52	+	-	+	+	-	+	18	-57.81	167.53	4.89	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AICc" represents the Akaike's information criterion corrected for sample size. "Δ AICc" is the difference in AICc between the focal model and the model with the lowest AICc. "weight" represents the relative probability of a model within the full set of models.

Table S16. Model with 90CI indices (see Table S10 for comparison). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

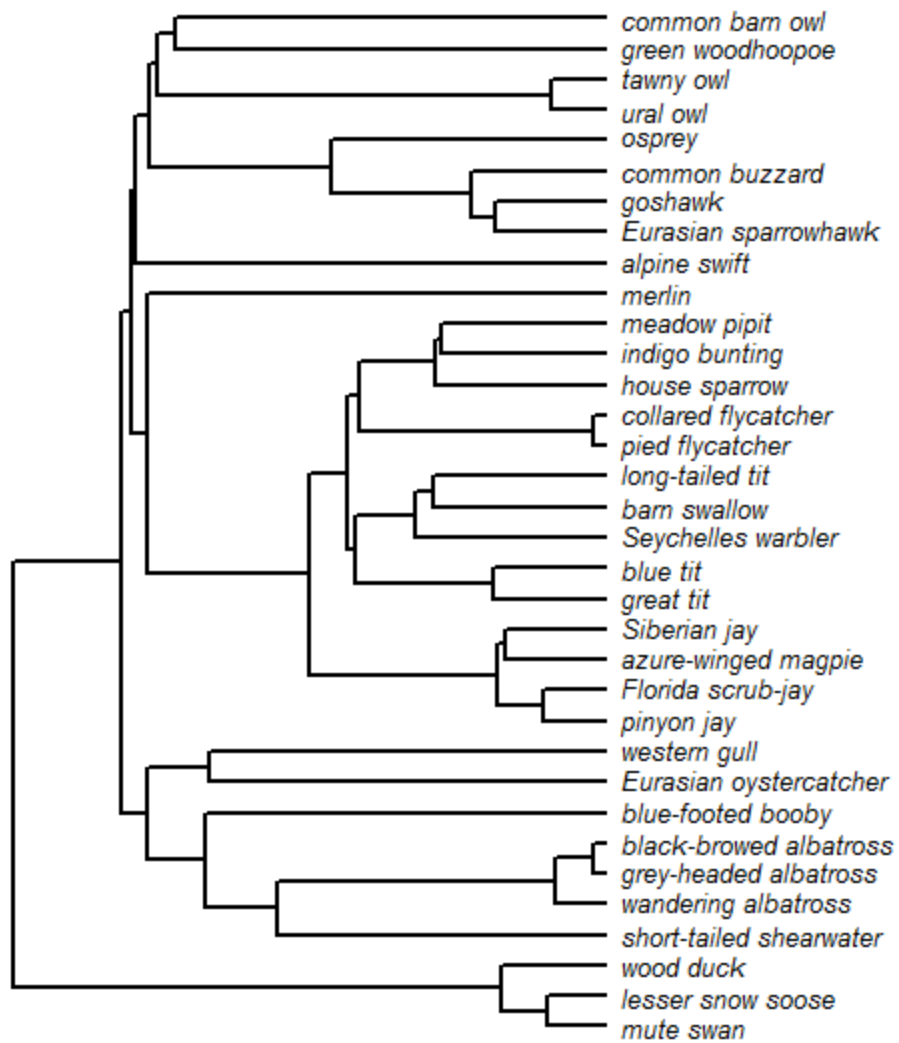| (Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	Lifespan Effect Index	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information			
0.59	0.22	+	-	0.42	-	-	-	-	0.47	0.32	-0.26	0.44	0.58	-	-	-	-	-	12	-24.05	85.66	0.00	0.06
0.82	0.53	+	-	-	-	-	-	-	0.42	0.17	-	0.40	0.47	-	-	-	-	-	10	-28.54	85.89	0.23	0.05
0.88	0.51	+	-	-	-	-	-	-	0.42	0.17	-0.21	0.41	0.48	-	-	-	-	-	11	-26.67	86.34	0.69	0.04
0.57	0.30	+	-	0.34	-	-	-	-	0.46	0.28	-	0.42	0.54	-	-	-	-	-	11	-27.01	87.02	1.37	0.03
0.51	0.48	+	-	-	-	-	-	-	0.30	-	-	0.55	-	-	-	-	-	-	8	-32.89	87.10	1.45	0.03
0.55	0.50	+	-	-	-	-	-	+	0.30	-	-0.31	0.53	-	-	-	-	-	-	10	-29.21	87.22	1.56	0.03
0.32	0.14	+	-	0.56	-	-	-	+	0.43	0.39	-0.37	0.46	0.47	-	-	-	-	-	13	-22.53	87.60	1.95	0.02
0.45	0.52	+	-	-	+	+	-	-	0.26	-	-	0.50	-	-	-	-	-	-	10	-29.40	87.61	1.95	0.02
0.80	0.76	+	0.29	-	+	+	-	-	0.23	-	-	0.51	-	-	-	-	-	-	11	-27.58	88.15	2.50	0.02
0.57	0.46	+	-	-	-	-	-	-	0.30	-	-0.20	0.56	-	-	-	-	-	-	9	-31.62	88.17	2.52	0.02
0.49	0.48	+	-	-	+	-	-	-	0.26	-	-	0.56	-	-	-	-	-	-	9	-31.64	88.21	2.55	0.02
1.00	0.95	+	0.42	-	+	+	-0.18	-	-	-	-	0.49	-	-	-	+	-	-	12	-25.36	88.29	2.63	0.02
0.50	0.50	+	-	-	+	+	-	-	0.26	-	-0.21	0.51	-	-	-	-	-	-	11	-27.75	88.50	2.84	0.01
0.39	0.13	+	-	-	-	-	0.36	-	0.28	-	-0.28	0.52	-	-	-	-	-	-	10	-29.97	88.74	3.08	0.01
0.68	0.99	+	-	-	+	+	-0.49	-	0.24	-	-	0.52	-	-	-	-	-	-	11	-27.95	88.90	3.25	0.01
0.49	0.51	+	-	-	-	-	-	+	0.30	-	-	0.53	-	-	-	-	-	-	9	-32.08	89.09	3.43	0.01
0.82	0.55	+	-	-	-	+	-	-	0.44	0.16	-	0.38	0.47	-	-	-	-	-	11	-28.06	89.12	3.46	0.01
0.55	0.46	+	-	-	+	-	-	-	0.26	-	-0.21	0.57	-	-	-	-	-	-	10	-30.17	89.14	3.49	0.01
0.40	0.34	+	-	0.24	-	-	-	+	0.32	-	-0.34	0.57	-	-	-	-	-	-	11	-28.28	89.56	3.90	0.01
0.40	0.30	+	-	-	-	-	0.20	-	0.29	-	-	0.53	-	-	-	-	-	-	9	-32.34	89.60	3.95	0.01
0.77	0.52	+	-	-	+	-	-	-	0.39	0.18	-	0.41	0.43	-	-	-	-	-	11	-28.33	89.65	4.00	0.01
0.79	0.52	+	-	-	-	-	-	+	0.40	0.19	-0.27	0.41	0.40	-	-	-	-	-	12	-26.07	89.70	4.04	0.01
0.59	0.24	+	-	0.41	-	+	-	-	0.48	0.31	-0.25	0.41	0.58	-	-	-	-	-	13	-23.60	89.74	4.08	0.01
1.01	1.07	+	0.37	-	+	+	-0.29	-	0.14	-	-	0.50	-	+	-	+	-	-	14	-20.90	89.80	4.14	0.01
0.46	0.46	+	-	-	+	-	-	-	0.20	-	-	0.52	-	-	+	-	-	-	10	-30.51	89.82	4.16	0.01

Table S16 following. Model with 90CI indices (see Table S10 for comparison). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

| (Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	Lifespan Effect Index	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.38	0.41	+	-0.10	-	-	-	-	-	0.30	-	-	0.53	-	-	-	-	-	-	9	-32.46	89.84	4.19	0.01
0.71	0.43	+	-0.10	-	-	-	-	-	0.41	0.20	-0.24	0.39	0.46	-	-	-	-	-	12	-26.15	89.86	4.20	0.01
0.72	0.31	+	-	-	-	-	0.20	-	0.40	0.19	-0.26	0.40	0.43	-	-	-	-	-	12	-26.15	89.86	4.20	0.01
0.74	0.49	+	-0.05	-	-	-	-	-	0.42	0.18	-	0.40	0.46	-	-	-	-	-	11	-28.44	89.87	4.22	0.01
0.88	0.53	+	-	-	-	+	-	-	0.43	0.17	-0.21	0.39	0.48	-	-	-	-	-	12	-26.19	89.94	4.28	0.01
0.40	0.37	+	-	0.17	-	-	-	-	0.31	-	-	0.58	-	-	-	-	-	-	9	-32.52	89.96	4.31	0.01
0.80	0.50	+	-	-	-	-	0.03	-	0.42	0.17	-	0.40	0.46	-	-	-	-	-	11	-28.53	90.06	4.41	0.01
0.82	0.53	+	-	-	-	-	-	+	0.42	0.17	-	0.40	0.46	-	-	-	-	-	11	-28.54	90.08	4.43	0.01
0.38	0.36	+	-0.14	-	-	-	-	-	0.29	-	-0.24	0.54	-	-	-	-	-	-	10	-30.66	90.12	4.46	0.01
0.51	0.50	+	-	-	-	+	-	-	0.31	-	-	0.53	-	-	-	-	-	-	9	-32.62	90.16	4.51	0.01
0.71	1.09	+	-	-	+	+	-0.61	-	0.20	-	-	0.50	-	+	-	+	-	-	13	-23.81	90.17	4.51	0.01
0.64	0.97	+	-	-	+	+	-0.58	-	-	-	-	0.48	-	-	-	+	-	-	11	-28.64	90.28	4.62	0.01
0.86	0.79	+	0.35	-	+	+	-	-	0.16	-	-	0.50	-	-	+	-	-	-	12	-26.36	90.28	4.63	0.01
0.83	0.50	+	-	-	+	-	-	-	0.39	0.18	-0.22	0.42	0.44	-	-	-	-	-	12	-26.38	90.33	4.67	0.01
0.52	0.19	+	-0.05	0.40	-	-	-	-	0.46	0.32	-0.27	0.43	0.56	-	-	-	-	-	13	-23.91	90.37	4.72	0.01
0.57	0.49	+	-	-	-	-	-	-	0.30	-0.06	-	0.56	-	-	-	-	-	-	9	-32.75	90.42	4.76	0.01
0.84	0.74	+	0.37	-	+	+	-	-	-	-	-	0.48	-	-	-	-	-	-	10	-30.87	90.53	4.88	0.01
0.60	0.23	+	-	0.43	-	-	-0.02	-	0.47	0.32	-0.25	0.44	0.58	-	-	-	-	-	13	-24.04	90.62	4.97	0.01
0.59	0.22	+	-	0.42	+	-	-	-	0.47	0.32	-0.26	0.44	0.57	-	-	-	-	-	13	-24.04	90.64	4.98	0.00
0.54	0.52	+	-	-	-	+	-	+	0.31	-	-0.31	0.51	-	-	-	-	-	-	11	-28.83	90.65	5.00	0.00

Model set with Δ AICc ≤ 5. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AICc" represents the Akaike's information criterion corrected for sample size. "Δ AICc" is the difference in AICc between the focal model and the model with the lowest AICc. "weight" represents the relative probability of a model within the full set of models.

Figure S1. Phylogenetic tree for the 34 species studied in this paper (based on the full tree from Jetz et al. 2012; Ericson backbone phylogeny).


- common barn owl
- green woodhoopoe
- tawny owl
- ural owl
- osprey
- common buzzard
- goshawk
- Eurasian sparrowhawk
- alpine swift
- merlin
- meadow pipit
- indigo bunting
- house sparrow
- collared flycatcher
- pied flycatcher
- long-tailed tit
- barn swallow
- Seychelles warbler
- blue tit
- great tit
- Siberian jay
- azure-winged magpie
- Florida scrub-jay
- pinyon jay
- western gull
- Eurasian oystercatcher
- blue-footed booby
- black-browed albatross
- grey-headed albatross
- wandering albatross
- short-tailed shearwater
- wood duck
- lesser snow soose
- mute swan

Figure S2. Variation in AFR and consequences for mean reproductive lifespan. Relationship between mean reproductive lifespan (mean lifespan (per AFR classes) minus AFR) and AFR for 22 populations (21 species) used to estimate the Lifespan Effect Index (Table 1); each point represents the mean value for individuals that start to reproduce at a specific AFR. B = both sexes, F = female, M = male.
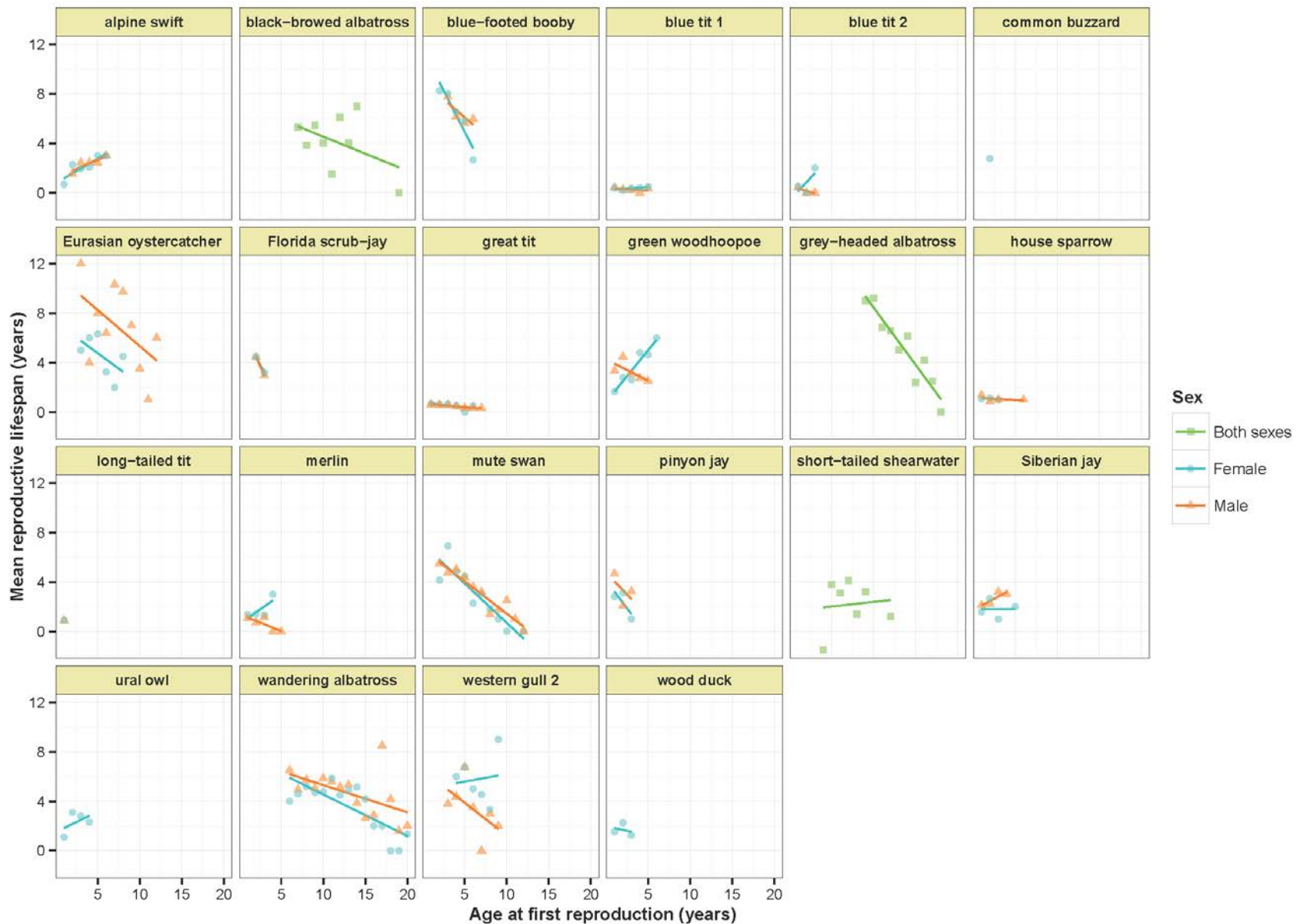
Figure S3. Variation in AFR. (**A**) Number of times the specific AFR corresponded to a species modal AFR (over 28 out of 34 species as we excluded 4 species with only 1 AFR age class and 2 species for which the sample size per AFR age class was missing). (**B**) Frequency of observation of a specific AFR age class across all 34 species (an AFR age-class was counted as being observed within a population when at least one individual initiated reproduction at the focal AFR – e.g. a values of about 20% for an AFR of 9 means that about 7 species (20% of 34) had individuals that initiated their reproduction at age 9).
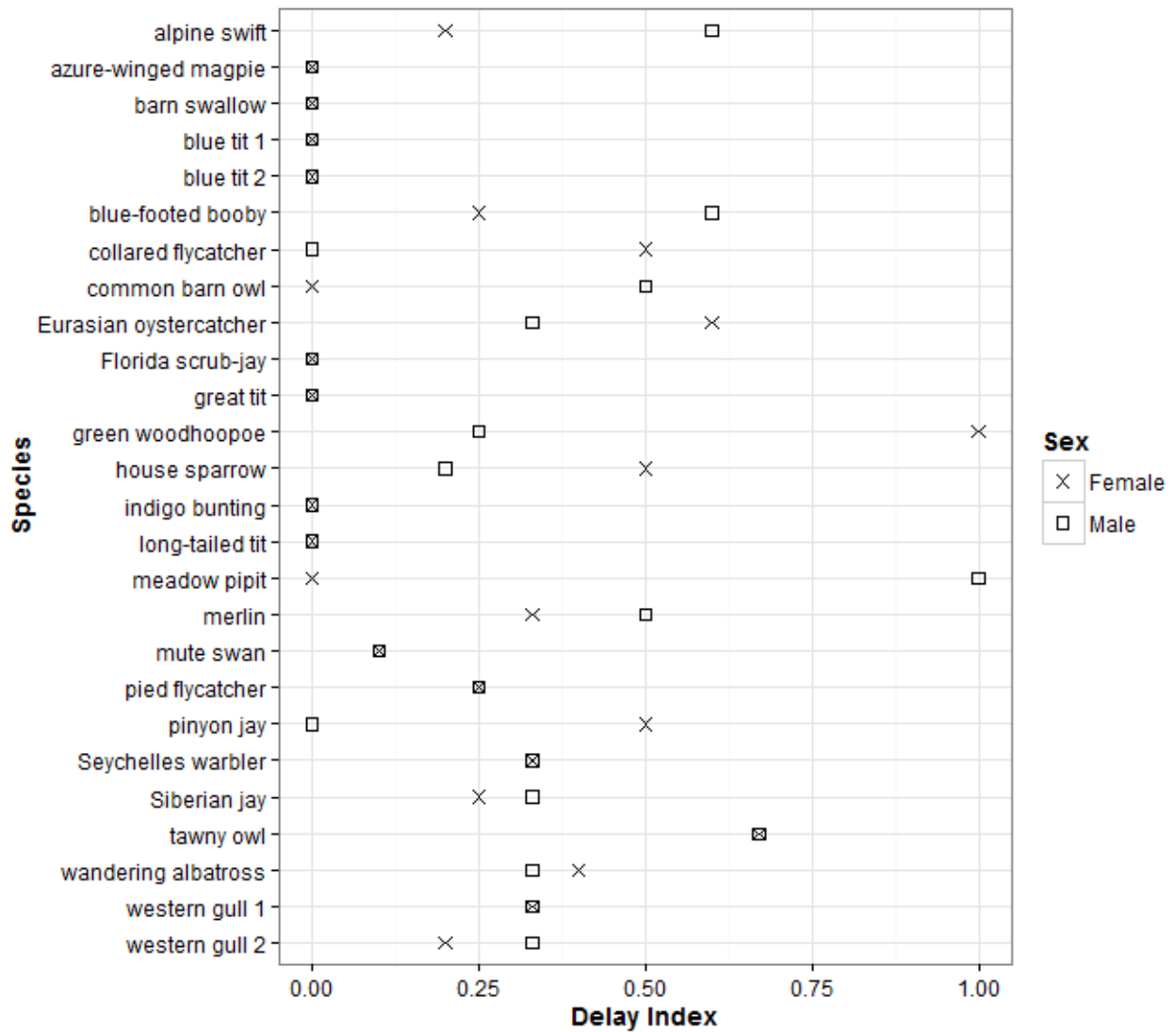
A
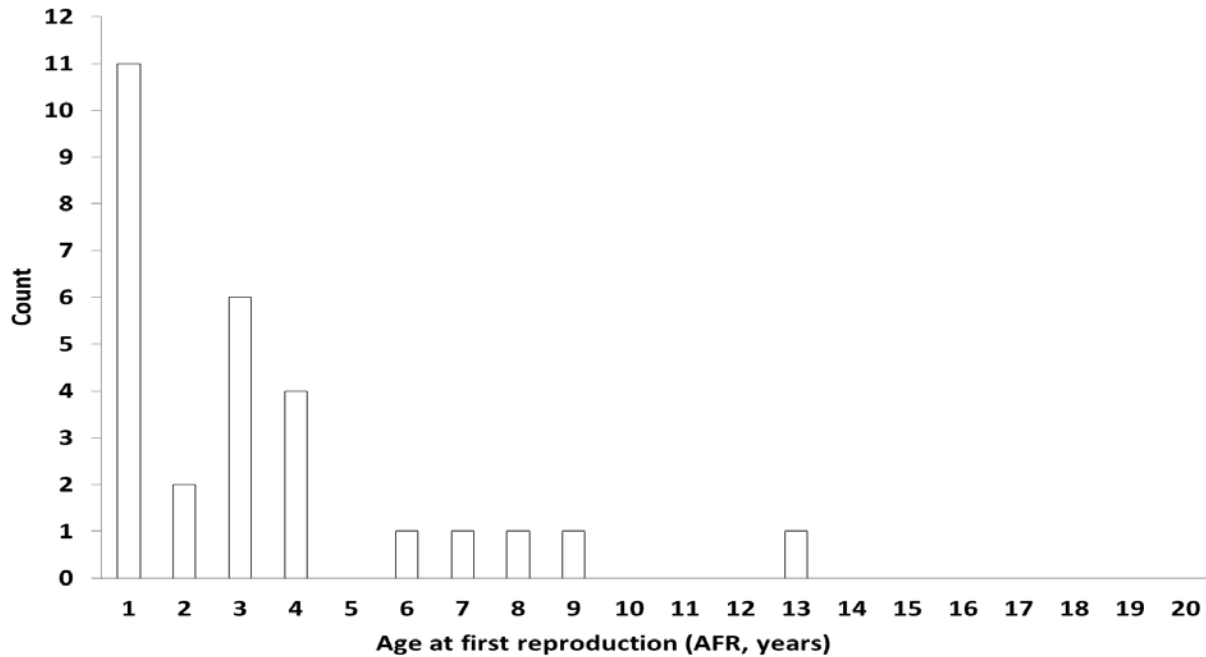
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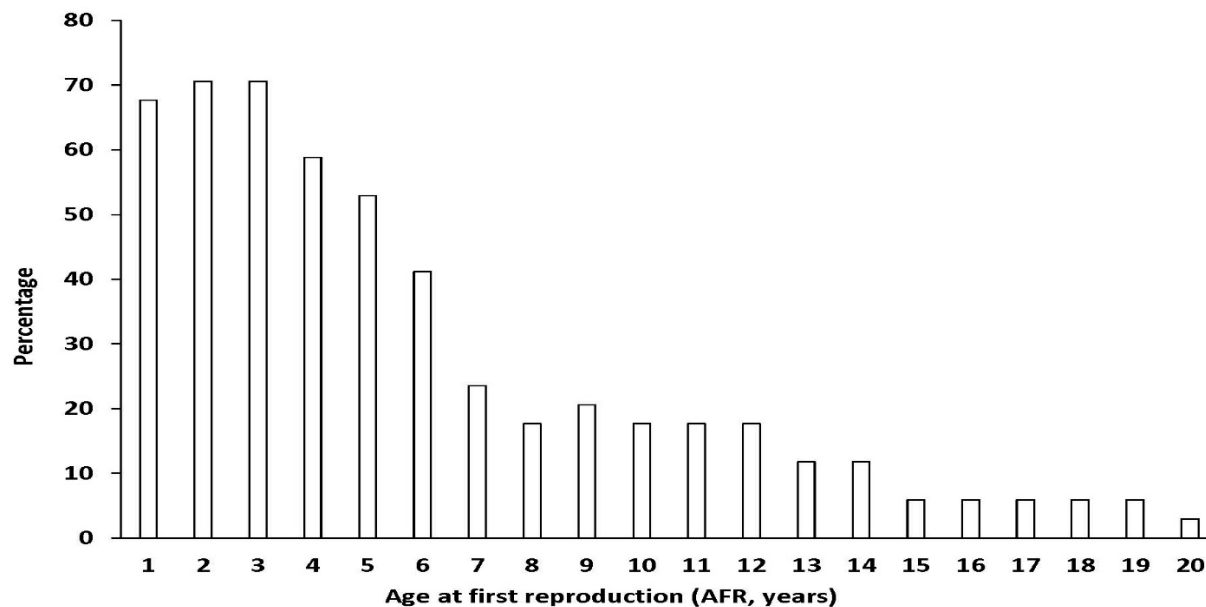
Figure S4. Sex differences in the Delay Index for the 26 populations (24 species) for which we had separate data for males (M, square symbols) and females (F, cross symbols). A number after the species indicates separate studies.

LITERATURE CITED

Brommer, J. E., H. Pietiainen, and H. Kolunen. 1998. The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. J. Anim. Ecol. 67:359-369.

Ekman, J. and M. Griesser. 2016. Siberian jays: delayed dispersal in absence of cooperative breeding. Pp. 6-18 *in* W. D. Koenig, and J. Dickinson, eds. Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior. . Cambridge University Press, Cambridge.

Fitzpatrick, J. W. and G. E. Woolfenden. 1988. Components of lifetime reproductive success in the Florida Scrub Jay. Pp. 305-319 *in* T. H. Clutton-Brock, ed. Reproductive Success. University of Chicago Press, Chicago.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444-448.

Kim, S. Y., A. Velando, R. Torres, and H. Drummond. 2011. Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird. Oecologia 166:615-626.

Komdeur, J. 1996. Influence of age on reproductive performance in the Seychelles warbler. Behav. Ecol. 7:417-425.

Krüger, O. 2005. Age at first breeding and fitness in goshawk *Accipiter gentilis*. J. Anim. Ecol. 74:266-273.

McGraw, J. B. and H. Caswell. 1996. Estimation of individual fitness from life-history data. Am. Nat. 147:47-64.

Millon, A., S. J. Petty, and X. Lambin. 2010. Pulsed resources affect the timing of first breeding and lifetime reproductive success of tawny owls. J. Anim. Ecol. 79:426-435.

Oli, M. K., G. R. Hepp, and R. A. Kennamer. 2002. Fitness consequences of delayed maturity in female wood ducks. Evol. Ecol. Res. 4:563-576.

Payne, R. B. 1989. Indigo Bunting. Pp. 153-172 *in* I. Newton, ed. Lifetime Reproductive Success. Academic Press.

Postupalsky, S. 1989. Osprey. Pp. 297-313 *in* I. Newton, ed. Lifetime Reproductive Success. Academic Press.

Pyle, P., N. Nur, W. J. Sydeman, and S. D. Emslie. 1997. Cost of reproduction and the evolution of deferred breeding in the western gull. Behav. Ecol. 8:140-147.

Strenberg, H. 1989. Pied Flycatcher. Pp. 55-73 *in* I. Newton, ed. Lifetime Reproductive Success. Academic Press.

Symonds, M. R. E. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65:13-21.

Viallefont, A., F. Cooke, and J. D. Lebreton. 1995. Age-specific costs of first-time breeding. Auk 112:67-76.

Wooller, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1989. Short-tailed Shearwater. Pp. 405-417 *in* I. Newton, ed. Lifetime Reproductive Success. Academic Press, London.