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HAL Authorization

1 **Running head:** age-dependent breeding performances

2

3 **Age-related breeding success in little penguins: a result of selection and ontogenetic**
4 **changes in foraging and phenology**

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6

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13 following address: <https://doi.org/10.5061/dryad.m37pvmd2h>.

14 **Abstract**

15 Reproductive performance typically improves with age, reaching a plateau at middle age and
16 subsequently declining in older age classes (senescing individuals). Three potential non-
17 exclusive mechanisms can explain the improvement in reproductive performance with age: (1)
18 selection (poor quality individuals are removed from the population with increasing age), (2)
19 constraint (individual efficiency increases through experience) and (3) restraint (reproductive
20 investment increases with age as the residual reproductive value decreases). While all three
21 mechanisms received strong empirical support, few studies have aimed at teasing apart those
22 hypotheses and understanding their underlying functioning. In little penguins (*Eudyptula minor*),
23 we used a 19-year longitudinal dataset on breeding and foraging of more than 450 individuals to
24 investigate the effect of age on breeding success. We separated within- from among-individual
25 age-effects using state-of-the-art statistical methods (within-subject centering and population
26 change decomposition). We then assessed whether within-individual changes in breeding
27 resulted from ontogenetic changes in foraging performances, breeding phenology or access to
28 mates and nest sites. Fidelity and assortative pairing explained the high correlation in male and
29 female ages within a pair. Breeding performances followed a typical bell-shaped curve with
30 performance increasing up to 8 years-old, before reaching a plateau and subsequently declining
31 after age 16. Both selection and within-individual processes occurred, although within-individual
32 changes dominated differences in age-dependent breeding success. The selective appearance had
33 almost no effect (apart from ages 2 to 3), and selective disappearance mostly affected changes at
34 old ages (above 16), although they were also responsible for the slight increase in reproductive
35 performances from ages 5 to 8. Focusing on within-individual changes, birds exhibited higher
36 performances at middle ages, with birds foraging better, laying earlier and changing partner and
37 nest less often. Their reproductive investment did not vary with age for females and slightly
38 decreased for males. This supports the constraint hypothesis but not the restraint one. Finally, the

39 increase in breeding performances at young ages was explained by the age-related increase in
40 foraging performances during chick-rearing and advancement of laying. In contrast, reproductive
41 senescence was defined by a general decrease in bird performances.

42 **Keywords: assortative pairing, constraint, experience, restraint, seabirds, selective**
43 **disappearance, senescence**

44

45 **Introduction**

46 In vertebrates, a population's reproductive performance typically improves with age until it
47 reaches a plateau at middle ages (Clutton-Brock 1988, Forslund and Pärt 1995, Kirkwood and
48 Austad 2000, Jones et al. 2014). How reproductive performance varies with age in animals
49 closer to the end of life is more debated. There is a traditional view that breeding success
50 decreases with age due to senescence (Nussey et al. 2013). However, there is growing evidence
51 that terminal investment could also occur due to fewer future breeding prospects, resulting in
52 very high terminal reproductive performance (Clutton-Brock 1984, Duffield et al. 2017). Three
53 hypotheses have been proposed to explain the age-related change in reproductive performance
54 (Forslund and Pärt 1995): (1) the selection hypothesis; the progressive disappearance of low-
55 quality phenotypes in the population (Vaupel and Yashin 1985), (2) the constraint hypothesis;
56 gained experience results in an increased individual breeding performance with age (Curio 1983)
57 and (3) the restraint hypothesis; reproductive effort and allocation increase with age according to
58 life-history trade-offs as future breeding prospects decrease (Williams 1966). These three
59 hypotheses are not mutually exclusive, and it is often challenging to distinguish them separately
60 (Forslund and Pärt 1995). The **selection hypothesis** attributes differences to interindividual
61 intrinsic characteristics present at or developed soon after birth, also known as fixed
62 heterogeneity (Wilson and Nussey 2010, Bergeron et al. 2011). In more detail, within a
63 population, different phenotypes might cause specific individuals to have higher reproductive
64 quality than others (Vaupel and Yashin 1985). If individuals of varying quality also have
65 intrinsically different survival probabilities, i.e. lower quality individuals having a lower chance
66 of survival (Nur 1988), the apparent increase in reproductive performance with age in a
67 population might result from the progressive disappearance of poorer quality phenotypes in older
68 age classes (Forslund and Pärt 1995). An increasing number of studies support selective

69 phenotypic disappearance of lower capability individuals (Mauck et al. 2004, Reid et al. 2008,
70 McCleery et al. 2008, Lescroël et al. 2009, Rebke et al. 2010).

71 On the other hand, the constraint and restraint hypotheses result from within-individual changes
72 over time, also known as dynamic-heterogeneity (Tuljapurkar et al. 2009). The **constraint**
73 **hypothesis** (Curio 1983) states that the lack of accumulated skills limits younger individuals'
74 success (Balbontin et al. 2007). As individuals age, they gain experience and become more
75 competent at providing for their offspring (Part 1995). Therefore, increased experience allows
76 greater parental output per unit cost. There is widespread support for the effect of experience on
77 performance, particularly in birds (e.g. Hatch and Westneat, 2007), mammals (Broussard et al.
78 2003, Bowen et al. 2006) and reptiles (Schwartz et al. 2007). Still, the mechanisms through
79 which breeding performance increases remain unclear. Several parameters are known to affect
80 reproductive performances. For instance, access to mates (or mates of better quality) might be
81 reserved to more territorial individuals, a characteristic that often varies with age (see for
82 instance, species with dominance-rank-based mating tactics, e.g. (Coltman et al. 2002, Spong et
83 al. 2008)). Similarly, age can affect an individual's access to a higher quality breeding territory
84 (Ferrer and Bisson 2003), which in return has important consequences on reproductive success
85 (Catchpole and Phillips 1992, Siikamäki 1995). Breeding phenology also affects breeding
86 success, primarily due to the match of the energetically costly reproductive period with prey
87 abundance (Durant et al. 2007, Reed et al. 2013). Indeed, reproduction is an energetically
88 expensive event, and the acquisition of food and energy is thus expected to be one of the most
89 important drivers of breeding performance (Lescroël et al. 2010). Thus, previous studies have
90 proposed that the peak in middle-age breeding performances could result from improved
91 foraging performances at those ages (Cunningham et al. 2017). Foraging performance results
92 from the balance between foraging efficiency, i.e. the rate of energy gain, and foraging effort,
93 i.e. the total amount of energy spent foraging (Daunt et al. 2007). As such, this performance may

94 be improved by individuals learning more efficient hunting techniques minimizing energy
95 expenditure and time spent hunting for prey (Marchetti and Price 1989, Daunt et al. 2007). This
96 in turn may increase the dietary range available by providing older individuals with access to
97 better foraging territories (Pärt 2001) and more nutritionally valuable prey items (Rutz et al.
98 2006, Le Vaillant et al. 2013). Therefore, accumulated parental experience allows adults to
99 provide more for their chicks without increasing the associated costs, resulting in parents
100 becoming more competent foragers with age (Curio 1983, Galbraith et al. 1999). A decrease in
101 foraging performance associated with other aspects of senescence could also explain patterns of
102 decrease in breeding success towards the end of an individual's life (Nussey et al. 2008, Reed et
103 al. 2008, Rebke et al. 2010).

104 While foraging performances represent the energy available for an individual, the next question
105 is to assess how individuals allocate this energy to either self-maintaining their body condition or
106 reproducing (Levins 1968, Stearns 1989). The **restraint hypothesis** explains the change in
107 resource allocation with age between adults and their offspring due to the change in residual
108 reproductive value with age (Williams 1966). Residual reproductive value is defined as the
109 average future reproductive success for individuals of that age and sex in the population
110 (Williams 1966). Young long-lived individuals are predicted to favour their survival over the
111 current breeding attempt so they preferentially allocate resources to the maintenance of body
112 condition rather than to reproduction (Drent and Daan 1980), as they have a high residual
113 reproductive value. In theory, with increasing age and fewer breeding attempts left, energy
114 should then be preferentially allocated to reproduction and chick provisioning rather than self-
115 maintenance so that reproductive effort increases with age (Williams 1966, Trivers 1972, Pianka
116 and Parker 1975). However, only a few studies have shown an age-related increase in the
117 reproductive effort using proxies such as territory defence or breeding frequency (Descamps et
118 al. 2007). Thus, rather than a continuous increase in breeding effort, another possible

119 consequence of the restraint hypothesis would be a sudden increase in breeding effort past a
120 certain age or ageing threshold, when the residual reproductive value would subsequently
121 become very small (Duffield et al. 2017). Such an increase observed in several species is often
122 named terminal investment (Clutton-Brock 1984, Part et al. 1992, Velando et al. 2006, Froy et
123 al. 2013).

124 Although age-specific reproductive success changes have been shown in a large number of
125 studies, the three hypotheses are usually investigated separately (but see Mauck, Huntington, &
126 Doherty Jr, 2012; Orgeret, Weimerskirch, & Bost, 2016). Longitudinal data studies are required
127 to separate within- and among-individual effects and reveal the underlying processes leading to
128 population-level changes (van de Pol and Verhulst 2006, Nussey et al. 2008, Rebke et al. 2010).
129 Further, methods to distinguish between constraint (reproductive quality) and restraint
130 (reproductive effort) need to be developed to understand better the ontogenetic changes
131 occurring within individuals.

132 Seabirds' long life spans and slow ageing rates for their body size make them ideal models to
133 study the effect of age on life-history traits (Holmes and Austad 1995). Furthermore, seabirds'
134 highly stochastic environments place strong selection on coping with an unpredictable food
135 supply, perhaps enhancing individual differences in performance capabilities (Saraux et al.
136 2011a). The average lifespan of a little penguin, *Eudyptula minor*, is estimated to be 6.5 years
137 (Reilly and Cullen 1979), but this is due to a highly skewed age-specific survival probability
138 (substantial juvenile mortality of 83% within the first year; Sidhu, Catchpole, & Dann, 2007).
139 Conversely, adult mortality is rather low (17%; (Sidhu et al. 2007)) and the oldest little penguin
140 found to date was 25 years old (Dann et al. 2005). Although this might appear relatively young
141 for a seabird, it would still relate as long-lived for a vertebrate. Therefore, a large part of the
142 population is made up of old birds that could significantly influence population dynamics.
143 Further, previous studies on the little penguin have shown age-dependent foraging performances

144 (Zimmer et al. 2011), age-segregation in foraging areas (Pelletier et al. 2014) and an increase in
145 breeding performances in the first years (Nisbet and Dann 2009). Individual foraging
146 performance is crucial in little penguins, as they have one of the shortest known foraging ranges
147 of seabirds (<30km: Collins, Cullen, & Dann, 1999) and are limited by the need to return to land
148 to feed their chicks. Thus, we expected the constraint hypotheses to play an essential role in
149 increasing breeding performances with age. Yet, little penguins show a trade-off between chick
150 provisioning and body maintenance, exhibiting a bimodal pattern of foraging trip duration
151 (Saraux et al. 2011b) similar to other seabirds (Chaurand and Weimerskirch 1994, Ropert-
152 Coudert et al. 2004, Kato et al. 2008). This behaviour suggests that parents might modulate their
153 effort and thus show potential for the restraint hypothesis. Finally, we showed previously that
154 some individuals performed consistently better by making more foraging trips than others to
155 feed the chicks, which could be related to their intrinsic quality (Saraux et al. 2011a). If such
156 intrinsic quality is linked to reproduction and survival, it might lead to selective disappearance
157 that affects population performance.

158 In this study, we investigated the effect of age on breeding performances of little penguins at
159 Phillip Island using an automatic monitoring system from 2001 to 2018 on more than 450 birds.
160 We proposed a framework to test for all 3 hypotheses: constraint, restraint and selection. First,
161 we examined the age-dependence in breeding performance and, more specifically, its
162 improvement from early life onwards, the decrease late in life due to senescence processes or the
163 increase at the very end due to terminal investment. Second, using mixed modelling (van de Pol
164 and Verhulst 2006, Fay et al. 2020) and decomposition of population change in a trait (Rebke et
165 al. 2010), we distinguished between within- and among-individual variability in breeding
166 performances. Third, we constructed performance and investment indices to separate between
167 the restraint and constraint hypotheses. Finally, we focused on ontogenetic changes in
168 reproduction (i.e. within individual age-related changes) and analyzed whether these were

169 related to improved foraging performances, breeding timing, or access to better partners or
170 breeding territories.

171

172 **Materials and methods**

173 **Little penguin monitoring**

174 In this study, the little penguin breeding colony is located at Summerland Peninsula on the
175 western tip of Phillip Island (33° 31'S, 145° 09'E), Victoria, Australia. This megacolony consists
176 of approximately 32,000 little penguin breeding adults (Sutherland and Dann 2014). All
177 penguins included in this study nested in 100 artificial burrows (nest boxes) established behind
178 the Penguin Parade® area with an annual occupation between 43 and 77 boxes (Chiaradia and
179 Kerry 1999). This study covers 19 breeding seasons from 2000 to 2018 (inclusive), where each
180 breeding season spans from August to March the year after (the austral summer). The penguin
181 population on Phillip Island has been monitored since 1967 (Reilly and Cullen 1979, 1981, Dann
182 and Cullen 1990). Between 1968 and 2000, individuals were marked and identified by flipper
183 bands, and since 2000, all monitored birds have been implanted with subcutaneous passive
184 transponder tags (Allflex, Capalaba, Australia) between the scapulae (shoulder blades; Chiaradia
185 & Kerry, 1999). This intensive monitoring of the population means that the colony consists
186 primarily of known-age individuals, with most penguins marked as chicks. Sex was determined
187 by bill measurements when the birds were first found in the colony as adults (Arnould et al.
188 2004). The artificial nest boxes were monitored three times a week during the breeding season to
189 assess breeding phenology and success of each pair. Individuals with transponders were detected
190 in the nest using a purpose-built handheld transponder reader (Kean Electronics, Australia). This
191 monitoring ensured a recapture probability close to one and informed us about laying date, the
192 number of clutches per season (1 to 3), as well as the number of fledglings per breeding event (0

193 to 2). Chicks were considered fledged when they had all their adult feathers and were older than
194 40 days when last seen. Fledging success was estimated as the number of chicks that survived to
195 fledging per breeding event. Based on this monitoring, breeding was also divided in three
196 consecutive phases: i) incubation of the eggs, ii) guard of the chicks, a period when chicks are
197 always guarded by one of the two parents and iii) post-guard, when both parents are out at sea
198 foraging during the day and only return a few hours at night (but not always every night) to feed
199 the chicks.

200 **Foraging variables**

201 Attendance data were recorded by an Automatic Penguin Monitoring System (APMS) located
202 along the main path into the Penguin Parade study site, and were used to calculate three foraging
203 parameters: foraging trip duration, change in adult body mass, and chick meal size (Kerry et al.
204 1993, Chiaradia and Kerry 1999, Saraux et al. 2011a). Note that the APMS records started in
205 June 2001, and foraging variables are thus absent in the 2000 season. The APMS consists of an
206 electronic transponder reader and a weighing platform that records the transponder
207 identification, mass, and time of a penguin crossing the weighbridge (Robinson et al. 2005).
208 APMS is calibrated weekly to account for tare drifts, and deviance is considered for weight
209 assessment (Salton et al. 2015). However, automatic weighing can sometimes provide
210 inconsistent data due to multiple birds crossing at once. Only individual masses ranging between
211 700 and 1700g were considered, based on field observation of body mass range (Salton et al.
212 2015). Only penguins with a breeding record (i.e. for which at least one egg was laid) were
213 included in the foraging dataset so that changes in foraging performance could be directly related
214 to reproductive success ($N_{\text{penguins}}=465$).

215 Foraging trip duration was calculated as the number of days at sea between colony visits.
216 Foraging duration was measured in days, as little penguins depart before sunrise and return after
217 sunset (Chiaradia and Kerry 1999, Daniel et al. 2007). Only trips that lasted between 1 and 16

218 days were considered for incubation and post-guard, and trips up to 3 days in guard (longer trips
219 were classed as false negatives or abandonment and end of breeding; (Chiaradia and Kerry 1999,
220 Kato et al. 2008, Saraux et al. 2011b)). Short trips were defined as those lasting less than or
221 equal to 2 days (≤ 2 days) whereas long trips lasted more than 2 days (≥ 3 days; (Saraux et al.
222 2011b)).

223 Two mass parameters were determined for each trip: parental body mass change and chick meal
224 size (Saraux et al. 2011a). Adult body mass change was the amount of mass change per foraging
225 trip and was calculated as the difference in body mass between when a penguin goes out and
226 when it returns from the foraging trip. Based on the manual weighing of individuals in the
227 colony, changes in body mass outside of the 0 to 600g range during chick-rearing (guard and
228 post guard) and -75 to 500g range during incubation were considered inconsistent and discarded.
229 Chick meal size was the amount of food given to the chick(s) and was assumed to be the mass
230 difference between the penguin arriving at the colony after the foraging trip and returning once
231 again to sea. Chick meal size could solely be estimated during post-guard, when little penguins
232 only spend a few hours in the colony (Daniel et al. 2007), the mass loss while in the colony
233 assumed to be due to feeding their chicks rather than their metabolism. Only chick meal sizes
234 smaller than 550g were included in data analysis following previous direct observations
235 (Chiaradia and Nisbet 2006).

236 **Performance and investment indices**

237 To distinguish between the restraint and constraint hypotheses, we built five indices related to
238 performance or investment. First, performances were evaluated through 4 indices all translating
239 a different aspect: i) phenology based on a bird's laying date, ii) propensity to keep the same
240 nest, iii) propensity to keep the same partner and iv) foraging performances. The foraging
241 performance index was based on a bird's mass gain during its foraging trip. Because body mass
242 change varied according to breeding stage and foraging trip duration, we applied a correction to

243 this parameter. During incubation, mass change increased with trip duration (LMM: $t = 19.291$,
244 $P < 0.001$, $n = 3849$, $N = 278$; Appendix S1: Fig. S1), so that we used the residuals of this
245 regression as an index of foraging performances during incubation. During guard, as mass
246 change was not related to trip duration (LMM: $t = -1.493$, $P = 0.135$, $n = 7000$, $N = 263$,
247 Appendix S1: Fig. S1), we used body mass change directly to indicate foraging performance.
248 Finally, during post-guard, mass change was better explained by the short/long trip binary
249 variable than by the actual foraging trip duration ($\Delta AIC = -31$; Appendix S1: Fig. S1).
250 Therefore, we used the model's residual, which explained mass change by the binary short-long
251 trip variable (LMM: $t = 8.599$, $P < 0.001$, $n = 15656$, $N = 247$) as an index of foraging
252 performance during post-guard.

253 To quantify parental investment into chicks, we needed to account for the trade-off between
254 reproduction and maintenance and use the proportion of energy that is allocated to reproduction
255 (represented here by chick meal size) compared to the total amount of energy (assessed here by
256 the change in adult body mass during a foraging trip) (Viblanco et al. 2016). Because chick meal
257 size is likely to depend on the birds' performance, we corrected this by the body mass gained
258 during a given trip. To estimate the total investment over the breeding event rather than the
259 immediate investment associated to each trip, we averaged chick meal size and the birds'
260 performance over the entire breeding event. These data were only available over the post-guard
261 stage, which is the only time we have access to chick meal size. Thus, the investment index was
262 estimated as the residual of the regression of average chick meal size on average body mass
263 change (see Fig. 1). Positive residuals indicate a higher investment towards reproduction than
264 the average population, while negative ones represent a lower investment towards reproduction
265 than the average, i.e., a higher investment towards soma than the average population investment
266 towards soma.

267 **Statistical analysis**

268 All statistical analyses were carried out in the R 3.5.0 statistical program (R Development Core
269 Team, 2018). Variables were considered significant at $P < 0.05$. All results are represented as
270 mean \pm standard error.

271 *Removing inter-annual variations: year centering*

272 Because environmental fluctuations can generate significant year-to-year variations in little
273 penguin phenology and breeding success, we worked on relative indices rather than absolute
274 ones. Relative indices indicate how an individual behaves compared to the average population
275 behaviour in that year. To do so, we centered (i.e. subtracted the annual means to) all our
276 variables (as suggested in Rebke et al., 2010). This procedure removed year-to-year variation
277 and removed any potential bias linked to covariation between age and year (e.g. very old birds
278 usually only present at the end of datasets). All analyses were then performed on relative
279 fledging success, relative laying dates, relative probability to change nest or partner, relative
280 investment and relative foraging performances (for which the year-centering was applied per
281 breeding stage). For instance, a positive relative laying date indicated that a bird reproduced later
282 than the average population in a given year.

283 *Age-dependent breeding performances*

284 As age effects are usually non-linear (bell-shaped or reaching a plateau), we first described age-
285 effects on relative fledging success (number of chicks fledged per breeding event relative to the
286 mean of the year) using generalized additive mixed models (GAMM). Because breeding success
287 is the same for the male and female of a pair, data were not independent and we ran separate
288 analyses for both sexes. The penguins' identification number was entered as a random effect in
289 all models, to account for the repeated recordings of the same individual in the longitudinal
290 dataset.

291 *Within- versus among-individual changes in breeding performances*

292 To separate the selection hypothesis from the constraint or restraint hypotheses, we applied two
 293 different approaches. First, based on an adaptation of the within-individual centering method
 294 (van de Pol and Wright 2009) and quadratic effects (Fay et al. 2020), we separated within- and
 295 among-individual age-related changes in breeding performances. Briefly, within-individual
 296 centering was performed by subtracting an individual's mean age from its age in different years.
 297 The centered age and the mean age were then used as independent variables representing within
 298 and among-individual variation, respectively. Only individuals known during their entire
 299 lifetime were included, i.e. individuals that had not been seen at the colony after 2016,
 300 corresponding to 301 penguins, and not including those 172 penguins that were still alive at the
 301 end of the study period. The same procedure was conducted using the squared age variable (age^2
 302 - $mean(age^2)$) (more details in Fay et al., 2020). Again, this model was run separately on males
 303 and females. The model thus read:

$$Nb\ of\ fledglings_{rel} \sim age_{centered} + age_{centered}^2 + meanage + mean(age^2) + (1|ID)$$

304 A stepwise backward model selection was applied to this model until the AIC stopped
 305 decreasing. Note that the same model including higher-order linearity of age (i.e. cubic effects or
 306 age^4) displayed higher AIC (not presented here), so that quadratic effects seemed to better
 307 explain changes in relative number of fledglings.

308 Second, we used a decomposition method (Rebke et al. 2010) that focuses on change in a given
 309 variable from one age to the next. It decomposes the change into 1) those that occurred within
 310 individuals and 2) changes occurring as new individuals appear in the breeding population and
 311 old ones disappear. The method is based on the fact that the change in a parameter at the
 312 population scale is the sum of three processes, which can be expressed by the following
 313 equation:

$$P_{a+1} - P_a = (P_{a+1} - p_{a+1}) + (p_{a+1} - p_a) + (p_a - P_a)$$

314 Where P_a is the average of a trait at the population scale at age a , p_a the average trait at age a of
315 individuals that were present at both ages a and $a+1$. The first term represents the difference
316 between the population average at age $a+1$ and the average at $a+1$ over birds that were already
317 present at age a (selective appearance). The second term is the difference between age $a+1$ and
318 age a for birds that were present at both ages (within-individual ontogenetic changes) and the
319 last term the difference between the average at age a over birds that will also be present at age
320 $a+1$ and the population average at age a (selective disappearance). Because this method
321 investigates changes from one age to the next, we averaged relative fledgling success over the
322 breeding season rather than a breeding event (i.e average over all clutches). Age-related changes
323 in relative fledging success were thus decomposed following this method and age classes were
324 then regrouped according to their similarities in population trends and the importance of the 3
325 different processes. Again, this method was applied only on a subset of the data comprising just
326 penguins that were monitored during their entire lifetime, i.e. that died over the study period.

327 *Constraint and restraint hypothesis: Age-dependent changes in performances and investment*

328 To test the constraint and restraint hypotheses, we first investigated age-effects on the 4
329 performance indices (foraging performances, laying date, access to better breeding territory or
330 partners) as well as the reproductive investment index described above using generalized
331 additive mixed models. Note that foraging performances were averaged over a breeding event
332 (or over breeding stages) rather than keep it at the trip scale to avoid individuals for which more
333 trips were monitored to be overrepresented and bias the results. Because laying date and divorce
334 are the same for the male and female of a pair (if an individual divorces, its partner does as well
335 by definition), we ran separate models for males and females for these two parameters. For the
336 other three parameters, sex was included as a covariate in the model as well as an interaction of
337 sex and age, to test whether age effects differed between the sexes, while the penguins'
338 identification number was entered as a random effect to account for the repeated recordings of

339 the same individual in the longitudinal dataset. Second, for those parameters that did vary with
340 age, we investigated within- versus among-individual age-related changes in the performance
341 and investment parameters using Rebke's decomposition method including only individuals
342 known all their life. Once again separate analyses were run for males and females for laying
343 date, divorce rates and those parameters for which the sex*age interaction was significant in the
344 GAMM. Relative foraging parameters as well as relative propension to change nest or divorce
345 were averaged over the breeding season rather than a breeding event (i.e. over all clutches) in
346 this analysis as it investigates changes from one age to the next. However, only first clutches
347 were considered to estimate the laying date of the breeding season so that a bird that laid more
348 than one clutch would not be considered as late because of that. Because this analysis was done
349 to explain changes in breeding performances, results are presented grouped per the same age
350 class defined by the decomposition of relative fledging success.

351 *Influence of parameters to explain ontogenetic changes in breeding performances*

352 Finally, to understand ontogenetic changes in breeding success, we used linear mixed models
353 (LMM) for each age class where important ontogenetic changes had been observed in breeding
354 success to link relative fledging success with relative foraging performances, laying date, access
355 to better breeding territory or partners and investment. Here, again, two separate analyses were
356 run: one for males and one for females, while the individual's identity was added as a random
357 factor in each model to account for repeated measurements. Whenever the individual explained a
358 trivial amount of variance, it was removed and a linear model was run instead to avoid problem
359 of linear mixed model singularity and convergence.

360 Similarly, we used linear models to investigate the link between ontogenetic changes in relative
361 fledging success with ontogenetic changes in these 5 parameters (foraging performances, laying
362 date, nest or partner changes, and reproductive investment). Ontogenetic changes were assessed
363 by estimating the slopes of linear relationships of age on the studied parameter for each

364 individual that was present in the given age class. Because sample sizes varied strongly between
365 the studied parameters, models were run with a unique explanative variable each time so as to
366 maximize statistical power.

367 **Results**

368 A total of 465 known-age individuals and 2752 breeding records (note that this corresponds to
369 1376 breeding events, as one breeding event is associated with 2 parents: the male and female)
370 were recorded between 2000 and 2018. Fledging success varied between 0 and 2 fledged chicks
371 per breeding event (average 0.99 ± 0.02). It varied strongly among years (range: 0.31 ± 0.05 in
372 2018 - 1.56 ± 0.07 in 2002), justifying the year centering we used for further analyses. The ages
373 of breeding individuals varied between 2 and 21 years. Male and female ages were positively
374 related (Fig. 2A; LM: $t = 24.159$, $P < 0.001$, $R^2 = 0.30$, $n = 1348$ breeding events). Little
375 penguins had a low divorce rate (27% of cases where the previous partner was still alive). This
376 means that birds remained with the same partner in 70% of the cases (the remaining 3%
377 corresponding to widowers), a high fidelity that could explain the positive relationship between
378 male and female age, as individuals of a pair would grow old together. Yet, focusing on breeding
379 events where birds had to choose a partner (i.e. first recorded breeding events or new partner),
380 male and female ages were still positively related (Fig. 2B; LM: $t = 9.945$, $P < 0.001$, $R^2 = 0.17$, n
381 $= 479$), suggesting some assortative pairing. Further, birds changed burrows from one breeding
382 event to another 46% of the time. Laying in this species is relatively asynchronous and varies
383 from year to year, as shown by the wide range of laying dates in this study from the 19th of May
384 to the 16th of January, with a peak in mid-October (annual means: 16th of August – 21st of
385 November).

386 Finally, a total of 42,473 trips was monitored, but because the mass was not always recorded,
387 foraging performances were known for only 26,705 trips (15% in incubation, 26% in guard and
388 59% in post-guard).

389 *Age-dependent breeding performances*

390 The relative number of chicks fledged (per breeding event) was significantly affected by age in
391 both males and females (GAMM♂: $F = 11.51$, $P < 0.001$, $n = 1346$, $N = 229$, $R^2 = 0.03$ and
392 $\Delta AIC = -29$ with the null model, GAMM♀: $F = 11.53$, $P < 0.001$, $n = 1348$, $N = 232$, $R^2 = 0.03$
393 and $\Delta AIC = -30$ with the null model, Fig.3A). Briefly, it strongly increased from age 2 to 8
394 (predicted values from -0.38 ± 0.08 in females and -0.36 ± 0.08 in males to 0.15 ± 0.04 in both
395 males and females) before levelling-off. It remained above 0 until age 13 before decreasing quite
396 strongly (-0.44 ± 0.23 for females and -0.41 ± 0.22 in males at age 21). Similarly, the relative
397 number of clutches per season varied significantly with age in both males and females (GAMM
398 ♂: $F = 7.06$, $P < 0.001$, $n = 1093$, $N = 229$, $R^2 = 0.02$, $\Delta AIC = -12$ with the null model. GAMM♀
399 : $F = 3.63$, $P = 0.010$, $n = 1095$, $N = 232$, $R^2 = 0.01$ $\Delta AIC = -2$ with the null model, Fig.3B). The
400 relative number of clutches increased until age 8 before decreasing again in males, while the
401 increase in young females was slower but lasted until age 11, before decreasing again, a decrease
402 occurring at a faster pace after 15 (Fig. 3B).

403 *Selection hypothesis: Within- or among-individual differences*

404 Using the within-subject centering for a linear and quadratic age effect showed that the age
405 effect observed on breeding performance resulted from both within- and among-individual
406 effects in both males and females (see Table 1). Selection by AIC retained all 4 variables (mean
407 age, centered age and their squares) in females, while mean age² was not selected in males. A

408 quadratic effect of age was observed within individual in both males and females, showing an
409 increase of breeding performance with age before decreasing again (Fig. 4). The peak in
410 reproductive performances changed depending on the mean age of an individual from after mid-
411 life for individuals that disappear young (centered age = 4) to before mid-life for individuals of
412 high longevity (centered age = -2), suggesting a common age of maximal performances around
413 age 9-10 for both males and females. Further, individuals with a lower mean age (i.e. that
414 disappeared from the population earlier), had a lower breeding performance (Fig. 4). This was
415 translated in the model by a quadratic effect of mean individual age in females and a positive
416 linear effect in males (i.e. among-individual variation due to selective disappearance). Breeding
417 performances at a given age increased with individual mean age (i.e., longevity), although this
418 increase was more important at lower mean age than at higher ones, where it levelled off for
419 females (Fig. 4). Finally, within-individual age effects explained more deviance in breeding
420 performances than among-individual age effects (16.23 vs. 5.4, i.e. 75 vs. 25% of the age effects
421 respectively in males and 20.06 vs. 15.17, i.e. 57% vs. 43% in females).

422 Second, we applied a decomposition of age changes that revealed both ontogenetic changes and
423 population changes. Age-dependent breeding performances were explained mainly by
424 ontogenetic changes (median of the proportion of population changes explained by ontogenetic
425 changes = 102% and 107% for males and females respectively vs. 2% and 3% for selective
426 disappearance and 0% for selective appearance; Fig. 5A&C). The selective appearance had a
427 negative effect on relative reproduction changes between age 2 and 3 in both males and females
428 (though more strongly in females) but almost no impact afterwards (Fig. 5A&C, Appendix S1:
429 Fig. S2). In other words, individuals breeding for the first time at age 3 had a lower breeding
430 success at age 3 than individuals that had already bred the previous year. Further, breeding
431 performances increased due to ontogenetic development until age 5 in females and age 6 in
432 males and decreased after age 16 due to ontogenetic senescence. Finally, selective disappearance

433 had a small positive effect on breeding performances at the population level, i.e. individuals that
434 died earlier had lower breeding performances, an effect mainly occurring between age 5 and 8 or
435 after age 16 in both males and females (Fig. 5A&C, Appendix S1: Fig. S2). Thus, we defined 4
436 age categories: i) from ages 2 to 5, when breeding performances increased at the population level
437 (0.24 and 0.40 fledgling per age year in males and females respectively) primarily due to
438 ontogenetic development despite the selective appearance of lower breeding quality individuals
439 at age 3, ii) from ages 5 to 8, when breeding performances continued to increase in males
440 (although 2.5 times less than in the first age category) and remained stable in females at the
441 population level due to selective disappearance, while within-individual performances had
442 levelled-off or started to slightly decrease, iii) from ages 8 to 16 when breeding performances
443 were stable (very slight decrease) at the population level, and iv) from ages 16 to 20, when
444 breeding performances decreased at the population level (-0.13 and -0.28 per age year in males
445 and females respectively) due to ontogenetic changes but despite selective disappearance of
446 lower breeding quality individuals (Fig. 5C & D).

447 *Constraint hypothesis: Age-dependent changes in performance*

448 We studied the constraint hypothesis through age-dependent changes in 4 different indicators of
449 performance (Fig. 6). First, foraging performances at the population level were significantly
450 affected by age, albeit slightly differently in males and females (GAMM: $F = 15.58$, $P < 0.001$
451 for the interaction age*sex and $F = 11.36$, $P < 0.001$ for age $n = 3462$, $N = 288$; $R^2 = 0.02$, Fig.
452 6A). For both sexes, foraging performances increased until age 10 before decreasing until age
453 20. While the increase in early ages was slightly stronger in females, the decrease at old ages
454 was stronger in males (Fig. 6A). Note that similar trends were observed when looking at
455 foraging performances during guard or post-guard separately but not during incubation, when
456 foraging performances did not vary consistently with age (Appendix S1: Fig. S3 A, B & C).
457 Second, laying date was significantly affected by age in both males and females (GAMM♂: $F =$

458 22.05, $P < 0.001$, $n = 1071$, $N = 227$; $R^2 = 0.10$, $\Delta AIC = -92$ with the null model; GAMM♀: $F =$
459 19.24, $P < 0.001$, $n = 1067$, $N = 231$, $R^2 = 0.09$, $\Delta AIC = -81$ with the null model). Briefly, it
460 decreased until age 6 or 7 for females and males respectively (age-7 males laid eggs on average
461 35 days earlier than age-2 males and age-6 females 33 days earlier than age-2 females),
462 remained relatively stable until age 14 or 16 in females and males before increasing, older birds
463 laying ~ 20 days later than intermediate birds (Fig. 6B). Further, the proportion of birds that
464 changed nests decreased with age (GAMM: $F = 6.57$, $P = 0.003$, $n = 1692$, $N = 333$, $R^2 = 0.01$,
465 $\Delta AIC = -6$ with the null model, Fig. 6C), regardless of sex ($F = 1.18$, $P = 0.308$), with a rapid
466 decrease from 3 to 8. From age 8 onwards, the proportion of birds changing nests did not show
467 any trend, although the variability increased at old ages (Fig. 6C). Finally, the propensity of
468 birds to divorce was significantly affected by age in males (GAMM ♂: $F = 8.23$, $P < 0.001$, $n =$
469 715, $N = 156$, $R^2 = 0.03$, $\Delta AIC = -12$ with the null model) and tended to be affected by age in
470 females (GAMM ♀: $F = 3.03$, $P = 0.033$, $n = 718$, $N = 157$, $R^2 = 0.01$, $\Delta AIC = 0$ with the null
471 model). Birds decreased their divorce rates from ages 3 to 9, especially males (Fig. 6D). From
472 age 9 onwards, the proportion of males changing partners increased while the proportion of
473 females changing partners was stable until age 16 before it slightly increased again at older ages
474 (Fig. 6D).

475 Because these changes occurred at the population level and could be unrelated to within-
476 individual changes, we decomposed age changes according to ontogenetic changes, selective
477 appearance and disappearance (Fig. 6E-H). We found that age changes in foraging
478 performances, laying date and the probability of changing nest burrow were primarily due to
479 within-individual ontogenetic changes. However, females appearing later in the breeding
480 population tended to lay their eggs later and exhibit high foraging performances (Fig. 6 E&F).

481 The importance of ontogenetic changes compared to selective appearance or disappearance was
482 also observed when looking at foraging performances in guard or post-guard (Appendix S1: Fig.
483 S3 D, E & F). Age changes in the probability to change partners resulted from a combination of
484 selective disappearance and ontogenetic changes in males (Fig 6H): from ages 2 to 5 the
485 important decrease in divorce rates was due to the disappearance of birds divorcing, while from
486 ages 5 to 8, it was due to individuals divorcing less. Finally, the increase of divorce rates after
487 age 16 was due to individuals increasing their divorce rate (Fig. 6H).

488 *Restraint hypothesis: changes in investment*

489 We used the residuals of the average meal size given to the chicks over the average mass gained
490 at sea for an individual per breeding event as a proxy of its investment into reproduction. This
491 index did not exhibit any trend with age in females but decreased linearly with age in males (Fig.
492 7A, GAMM: edf = 1, F = 0.06, P = 0.809 and edf = 1, F = 5.40, P = 0.020, for females and males
493 respectively, n = 984, N = 238, Δ AIC = -6 with the null model). In the absence of age-related
494 changes in females, the age decomposition was performed only in males. Population changes
495 mainly reflected ontogenetic changes within males (Fig. 7B).

496 *Influence of parameters to explain ontogenetic changes in breeding performances*

497 According to previous results, ontogenetic changes in fledging success occurred mainly at young
498 ages with an important increase in fledging success between ages 2 to 5 and at old ages when
499 fledging success decreased strongly between ages 16 to 20. To explain these ontogenetic
500 changes, we investigated whether the different parameters of performances and investment
501 affected fledging success in these two groups of birds: young and old birds.

502 First, relative fledging success in young birds (ages 2 to 5) was linked to relative laying dates
503 (LMM♂: -0.006 ± 0.001 , t = -4.50, P < 0.001, n = 404, N=191, Δ AIC = -6 with the null model
504 and LMM♀: -0.010 ± 0.001 , t = -6.42, P < 0.001, n = 384, N=193, Δ AIC = -26 with the null

505 model; Appendix S1: Fig. S4 A) and relative foraging performances (LMM♂: 0.002 ± 0.001 , $t =$
506 2.95 , $P = 0.003$, $n = 260$, $N=119$, $\Delta AIC = -6$ with the null model; LMM♀: 0.004 ± 0.001 , $t =$
507 4.50 , $P = 0.003$, $n = 225$, $N=104$, $\Delta AIC = -5$ with the null model; Appendix S1: Fig. S4 B). That
508 is breeding events of earlier laying or/and with better foraging resulted in more chicks fledged.
509 The relationship with foraging performance held true when looking at foraging performances
510 during guard (LMM♂: 0.003 ± 0.001 , $t = 4.52$, $P < 0.001$, $n = 219$, $N=106$, $\Delta AIC = -5$ with the
511 null model; LMM♀: 0.003 ± 0.001 , $t = 4.36$, $P < 0.001$, $n = 211$, $N=103$, $\Delta AIC = -4$ with the
512 null model) and post-guard (LM♂: 0.002 ± 0.001 , $t = 2.16$, $P = 0.032$, $n = 193$; LM♀: $0.003 \pm$
513 0.001 , $t = 2.57$, $P = 0.011$, $n = 179$, individual identity random effect removed due to trivial
514 explained variance), but not in incubation (LMM♂: 0.001 ± 0.001 , $t = 1.39$, $P = 0.165$, $n = 216$,
515 $N=103$, $\Delta AIC = 13$ with the null model; LMM♀: 0.001 ± 0.001 , $t = 1.04$, $P = 0.301$, $n = 216$,
516 $N=103$, $\Delta AIC = 14$ with the null model). Reproductive investment, the chance to switch nest or
517 partners was not related to relative fledging success in young birds, neither in males nor females
518 (LMMs: all $P > 0.05$ and all $\Delta AIC > 0$; Appendix S1: Fig. S4 C-D-E), although there was a
519 tendency of higher fledging success for females that divorced less (LMM♀: -0.272 ± 0.143 , $t = -$
520 1.90 , $P = 0.059$, $n = 166$, $N = 111$, $\Delta AIC = 0.5$ with the null model; Appendix S1: Fig. S4E).
521 When focusing on old birds (i.e. ≥ 16 yr-old), the individual identity random effect on the
522 relative number of fledged chicks was trivial and was thus removed, resulting in the use of linear
523 models. Relative fledging success in old birds was explained by foraging performances (LM♂:
524 0.005 ± 0.002 , $t = 2.04$, $P = 0.048$, $n = 41$; LM♀: 0.007 ± 0.003 , $t = 2.39$, $P = 0.022$, $n = 39$;

525 Appendix S1: Fig. S5 B), which held true in post-guard (LM♂: 0.008 ± 0.003 , $t = 2.89$, $P =$
526 0.007 , $n = 29$; LM♀: 0.006 ± 0.003 , $t = 1.79$, $P = 0.085$, $n = 30$) but not in incubation (LM♂:
527 0.001 ± 0.002 , $t = 0.75$, $P = 0.458$, $n = 39$; LM♀: 0.002 ± 0.002 , $t = 1.32$, $P = 0.196$, $n = 40$) or
528 guard (LM♂: 0.002 ± 0.001 , $t = 1.66$, $P = 0.106$, $n = 40$; LM♀: 0.003 ± 0.002 , $t = 1.39$, $P =$
529 0.175 , $n = 36$). Laying date, reproductive investment or the propensity to change nest or partner
530 did not explain the relative number of fledglings in old birds. However, the relationships with
531 the propensity to change nest, partner and the laying date were close to significance in females,
532 suggesting that females changing less partners or nests or laying earlier tended to produce more
533 fledglings (Appendix S1: Fig. S5).

534 Second, ontogenetic changes in a parameter at young and old ages were assessed for each
535 individual by the slopes of the linear relationships between this parameter and age in the given
536 age groups. Using these slopes as indicators of ontogenetic changes, we explored how
537 ontogenetic changes in fledging success could be explained by ontogenetic changes in different
538 performance indicators or investment. In young birds, ontogenetic changes in relative fledging
539 success were linked to ontogenetic changes in laying date, foraging performances during guard
540 and investment but not by ontogenetic changes in foraging performances during incubation or
541 post-guard nor by ontogenetic changes in divorce rates and nest changes. Indeed, the increase of
542 relative fledging success with age was related to a decrease of laying date with age (i.e. birds
543 laying earlier with age, LM: -0.004 ± 0.002 , $P = 0.021$, $n = 254$; Fig. 8A), by an increase in
544 foraging performances during guard with age (LM: 0.002 ± 0.000 , $P = 0.026$, $n = 118$; Fig 8B)
545 and by an increase in investment with age (LM: 0.005 ± 0.002 , $P = 0.005$, $n = 84$; Fig. 8C). At
546 old ages, the ontogenetic decrease in relative fledging success was only explained by an increase
547 in relative laying dates (i.e. birds laying later as they aged, LM: -0.007 ± 0.003 , $P = 0.030$, $n =$

548 28; Fig. 8D). Note however that the number of birds available in this age category was much
549 lower (28 birds at maximum and down to 12 birds for some parameters due to absence of
550 information on their foraging trips).

551

552 **Discussion**

553 *Age-related changes in breeding performances and the relative contribution of within- versus*
554 *among-individual changes*

555 Using an extensive dataset of more than 450 birds monitored over a 19-yr period, we confirmed
556 that little penguins displayed classical bell-shaped age-related changes in breeding performances
557 (Dann and Cullen 1990, Nisbet and Dann 2009). Breeding success increased until age 8 then
558 remained relatively stable before decreasing from age 16. The number of clutches laid per year
559 also followed a similar age-related pattern. These changes were explained by a combination of
560 within-individual ontogenetic changes and among-individual selective mechanisms, as
561 highlighted by two statistical analyses (i.e. the within-individual centering method (van de Pol
562 and Wright 2009) and the decomposition method (Rebke et al. 2010)). While within-individual
563 ontogenetic changes seemed to play a more significant role than selection mechanisms overall,
564 their relative importance depended on age classes. Indeed, ontogenetic changes were mostly
565 observed from ages 2 to 5 when individual performances increased at a speedy rate. These
566 changes were again detected after age 16 when individual performances quickly declined.
567 Selective disappearance had a small but mostly positive effect from 2 to 8, and became quite
568 crucial after age 16. Thus, young and older birds that displayed lower breeding performances
569 also disappeared earlier, coinciding with the highest adult mortality. A previous study performed
570 at the same location on age-dependent mortality has indeed shown that mortality was higher at
571 young ages (< age 4) but also started to increase continuously after age 9 (Sidhu et al. 2007). As

572 such, the older the birds the lower is the survival. Still, Sidhu and colleagues (2007) only studied
573 data until age 17 with small sample sizes after age 15. As survival declines are usually restricted
574 to the most advanced age groups in seabirds (actuarial senescence), one might expect the
575 decrease in survival to be even higher on our last age class (≥ 16).

576 What is usually considered a unique increase of breeding performances early in life (here from
577 age 2 to 8) actually resulted from the first phase of critical ontogenetic changes from ages 2 to 5
578 followed by selective disappearance of individuals from ages 5 to 8. Conversely, within-
579 individual changes and selective mechanisms acted in opposite directions at old ages, when
580 selective disappearance partly buffered the strong within-individual changes. Indeed, while
581 breeding performances decreased as birds aged, only high-quality birds survived at old ages so
582 that the apparent decrease in performance at the population scale was lowered. Decreases in
583 breeding performance often observed at old ages can result from the senescent reduction in bird
584 capability (Nussey et al. 2013). Senescence (or ageing) processes are defined as "progressive and
585 irreversible changes that impair rather than improve performances" (Monaghan et al. 2008) and
586 usually result from an accumulation of cellular damage (see Monaghan et al. (2008) for a
587 review). While seabirds might be specially adapted to prevent age-related tissue damage caused
588 by reactive oxygen species and prevention of formation of harmful by-products of oxidative
589 metabolism (Holmes et al. 2001), reproductive senescence has been reported in several seabird
590 species (e.g. Weimerskirch (1992), Tompkins and Anderson (2019)), but not in others (Berman
591 et al. 2009, Nisbet et al. 2020)). We concluded that the importance of a decrease in reproductive
592 performances due to senescence might be partially masked by selective disappearance when
593 working at the population scale. This highlights that senescence needs to be studied using
594 longitudinal data and focused on within-individual changes (Nussey et al. 2013). Also, focusing
595 on very old birds to investigate senescence mechanisms would mean to study only high quality
596 birds that might display different physiological capacities from birds having died earlier.

597

598 *Male, female or pair age?*

599 Age-dependent patterns in breeding performances were displayed by both males and females, in
600 contrast with (Nisbet and Dann 2009), who did not find significant age changes in females.
601 Whether this is due to a different study period, different sample sizes or other factors is
602 unknown. Still, we found a positive correlation between male and female ages within a pair
603 indicating that the age effects on individual breeding success might at least partly be due to their
604 partner's age. This correlation was related to a combination of fidelity (birds growing old
605 together) and assortative pairing. Such assortative pairing might result from different processes
606 that will need further studies: pairing with birds of the same cohort or similar size, similar age
607 spatio-temporal patterns (similar arrival dates at the breeding grounds or similar habitat; (Ferrer
608 and Penteriani 2003)), active mate choice (Cézilly et al. 1997, Schull et al. 2018), or a
609 combination of the two (Jouventin et al. 1999). Still, we showed that laying dates differed
610 according to age, suggesting that birds breeding timing might influence mate association and
611 thus explain assortative pairing.

612 Similarly, age-related changes in laying dates, foraging performances or the tendencies to
613 change nest or partner were very alike in males and females, suggesting analogous mechanisms
614 in both sexes. The only real difference observed was a slight decrease in reproductive investment
615 with age in males, while it did not vary depending on age in females (see below).

616

617 *Population selective mechanisms*

618 While selective disappearance explained part of what was observed at the population scale,
619 selective appearance played a minor role and was virtually trivial apart from changes from age 2
620 to 3. Indeed, birds breeding for the first time at age 3 had a lower breeding success than birds
621 that had already bred at age 2 that may have benefited from the previous year's experience

622 (Limmer and Becker 2010). For instance, in other penguin species, unpaired young birds return
623 to the colony during the mating period, possibly as a learning behaviour (Barrat 1976, Saraux et
624 al. 2011c). Furthermore, the higher the number of times a bird returned to the colony, the more
625 likely it was to engage in reproduction at a young age (Saraux et al. 2011c). Here, we found
626 birds that bred at age 2 laid earlier in the season at age 3 than birds that had not bred at 2.
627 However, these young but experienced birds displayed lower foraging performances in females,
628 suggesting that females that did not reproduce and spent more time at sea might have gained
629 more foraging experience (Ramírez et al. 2015), while males did not benefit from their extra
630 time at sea.

631

632 *Constraint versus restraint hypothesis?*

633 Within-individual changes seemed to follow the constraint hypothesis, as breeding performances
634 are thought to increase due to experience and development at young ages and decrease due to
635 senescence at old ages. By contrast, the restraint hypothesis predicts that investment should
636 increase with age (Descamps et al. 2007) either all along with an individual's life or brutally at
637 old ages due to terminal investment (Duffield et al. 2017), leading to an increase in breeding
638 performances. Our investment index showed no relation with age in females and a slight
639 decrease in males. Further, no sign of terminal investment or increase in reproductive success at
640 old ages was present, although we cannot exclude that this could be due to a sharp decrease in
641 our sample sizes for very old birds (>18 yr-old). Thus, our results tend to refute the restraint
642 hypothesis or at least indicate that the constraint hypothesis had a much higher impact. This
643 finding on little penguins aligns with several studies that supported constraints rather than
644 restraints in other birds (Forslund and Pärt 1995, Martin 1995) and mammals (Broussard et al.
645 2008).

646

647 *Main factors explaining ontogenetic changes*

648 In the constraint hypothesis, young breeders often perform poorly due to a lack of experience
649 and capability to find sufficient resources in breeding territories or nests or food (Curio 1983).
650 Reproduction being energetically costly, most studies have focused on the acquisition of food as
651 a critically important influence on breeding performance (Lescroël et al. 2010). As individuals
652 get older, they might learn more efficient foraging techniques and improve chick provisioning
653 (Curio 1983, Galbraith et al. 1999). Yet, other studies showed that the breeding phenology is the
654 main factor affected by age, which affects breeding performances (e.g. Blums et al. (1997) in
655 which the age effect on breeding performances disappeared after controlling for phenology). As
656 several factors may affect breeding performance, we investigated how breeding phenology,
657 foraging performance and nest and partner choice varied with age and whether age-related
658 changes in these factors might explain age-related differences in breeding performance. We
659 found that from the age of 2 to 5, birds were able to advance their laying date (~1.5 months),
660 increase their foraging performances by gaining more weight at sea, and decrease their
661 probability of changing nests (10% points). The increase in foraging performance could be
662 related to increased diving efficiency as seen in this and other penguin species (Zimmer et al.
663 2011, Le Vaillant et al. 2012, 2013) or a change in foraging areas (Pelletier et al. 2014). As part
664 of the learning process, young birds could sample different nests to assess nest quality before
665 settling. They might also have limited access to high-quality nests (Sherry and Holmes 1989).
666 Birds laying earlier and exhibiting greater foraging performances had a higher breeding success.
667 The age-related increase in bird breeding performances was explained by both an age-related
668 increase in foraging performances and an age-related decrease in laying dates, confirming the
669 two main hypotheses behind the constraint theory. Reproducing earlier might give them access
670 to better partners, nesting sites or even better match prey abundance, while higher foraging
671 performances enabled little penguins to gain more mass at sea. When looking at each breeding

672 stage separately, we found an effect of foraging performances on breeding success during chick-
673 rearing (guard and post-guard) but not during egg incubation, confirming that chick-rearing is
674 the most critical phase of breeding (Saraux et al. 2016).

675 Although the constraint hypothesis is often used to explain ontogenetic developmental changes
676 in young birds, it also applies to the decreases in breeding performance at old ages due to the
677 senescent decrease in bird capability (Nussey et al. 2013). While reproductive senescence has
678 been described in birds and mammals, little is known on other biological parameters (in
679 particular life-history traits, physiology or behaviour; Gaillard and Lemaître 2020). In this study,
680 birds older than 16 started to lay later, had lower foraging performances, and changed nest and
681 partner often, suggesting an overall decrease in bird breeding capability at these older ages. Yet,
682 the ontogenetic decrease in reproductive performances at old ages (i.e., reproductive senescence)
683 was directly related to birds laying later, but no other age-related changes in any of the
684 parameters. While these two results might seem contradictory, it actually translates into two
685 different processes. Reproductive senescence might be explained by a general ontogenetic
686 decrease in bird capability (in keeping the same mate and burrow, in foraging and in matching
687 their phenology with the optimal period). However, when comparing the strength of the
688 reproductive senescence among individuals, birds with the largest delay in their phenology
689 displayed the highest decrease in reproductive success, while other parameters did not affect the
690 level of reproductive senescence. However, only a few individuals (28) were monitored above
691 age 16 in our study and the absence of foraging data for some of them might explain why we did
692 not find statistically significant relationships between reproductive senescence and an age-
693 related decrease in foraging performance. The later laying for older birds might result from
694 carry-over effects of body mass from winter to breeding, as individuals with a higher body mass
695 in winter are more likely to breed early in the season (Salton et al. 2015). As birds older than 16
696 years exhibited lower foraging performance during reproduction, they may also suffer from the

697 same lower performance during winter taking them longer to reach a body mass needed for the
698 onset of the breeding season.

699

700 *Conclusions*

701 Reproductive performance followed a typical age-related pattern in little penguins, rapidly
702 increasing at young ages then remaining stable before decreasing at older ages. This pattern
703 resulted from both within- and among-individual processes, supporting the selection and
704 constraint hypothesis. The ontogenetic increase in performances stopped rapidly at age 5, so the
705 remaining age-related increase related to selective disappearance. This ontogenetic increase was
706 linked to an increase in foraging performances and an advancement of breeding phenology. By
707 contrast, the overall birds' performances decreased at old ages as they laid eggs later, had lower
708 foraging performances, and changed nest and partners more often. Still, the strength of
709 reproductive senescence was only related to the importance of the delay in bird phenology with
710 age. Finally, our results did not support the restraint hypothesis in the absence of a terminal
711 increase in reproductive performances and age-related changes in the investment index.

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Tables

978

979 Table 1. Within and among-individual age effects on the relative number of fledglings in little
 980 penguins. Main statistics associated with the 2 linear mixed models, one for males and one for
 981 females.

	Variable	Estimate \pm SE	t values	P values	Sum Squares	Sample size
Males	Intercept	-0.223 \pm 0.083	-2.68	0.008	-	n = 788, N = 142
	Age_center	0.119 \pm 0.036	3.27	0.001	6.69	
	Age_mean	0.030 \pm 0.010	2.94	0.004	5.40	
	Age ² _center	-0.007 \pm 0.002	-3.90	<0.001	9.54	
	Age ² _mean	not selected in the best model				
Females	Intercept	-0.767 \pm 0.211	-3.63	<0.001	-	n = 743, N = 141
	Age_center	0.149 \pm 0.038	3.88	<0.001	9.49	
	Age_mean	0.205 \pm 0.057	3.61	<0.001	8.23	
	Age ² _center	-0.008 \pm 0.002	-4.09	<0.001	10.57	
	Age ² _mean	-0.011 \pm 0.003	-3.32	0.001	6.94	

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984

Figure legends

985

986 **Fig 1.** Reproductive investment index calculation, as the residuals of the regression of average
987 chick meal size on average body mass change during a trip ($y = (0.95 \pm 0.03) x + (6.31 \pm 7.64)$,
988 $P < 0.001$, $n = 984$). Each point represents the average over a post-guard event. Points are
989 transparent so that darker areas represent higher densities of points.

990 **Fig 2.** Relationships between female and male age within a pair over A) all breeding attempts,
991 B) breeding attempts where new partners had to be found (i.e. first breeding attempts or when an
992 individual changed partners). The average prediction from the linear mixed model is indicated
993 with a black line on each panel.

994 **Fig 3.** Relative reproductive success according to age (mean \pm SE): A) relative number of
995 fledglings per breeding event and B) relative number of clutches per year. Males are indicated in
996 blue and females in red. Sample sizes are indicated at the bottom of the panels for each age
997 category. Further, the prediction and confidence interval of the GAMMs are drawn as blue and
998 red lines and ribbons for male and female, respectively.

999 **Fig 4.** Age effects on relative number of fledglings according to the within-subject method in A)
1000 females and B) males.

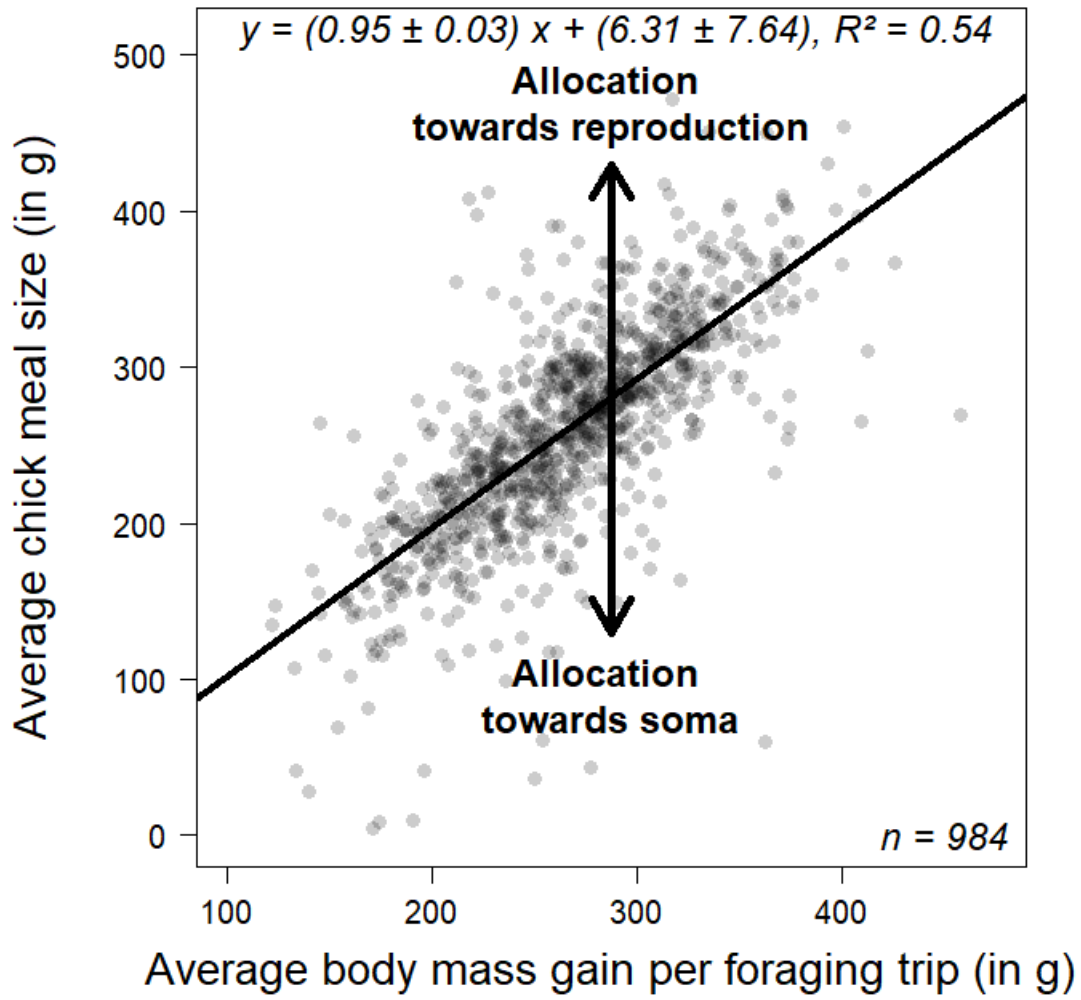
1001 **Fig 5.** Relative reproduction according to age. Panels A (males) and C (females) represent the
1002 observed population trend (in dark blue), as well as the age patterns we would have observed
1003 had only one process occurred in the population: light blue for ontogenetic development, red
1004 selective disappearance, and orange selective appearance. Note that age 21 was not represented
1005 for clarity purposes as only one male and one female of age 21 were present. Panels B (males)

1006 and D (females) summarise changes in relative reproduction from one age to the next by age
1007 categories according to the different processes.

1008 **Fig 6.** Test of the constraint hypothesis. Age-related changes (mean \pm SE) in A) foraging
1009 performances, B) laying date, C) proportion of birds that changed nest burrows and D)
1010 proportion of birds that changed partners. Sample sizes are indicated per age class at the top and
1011 bottom of the panels. Blue and red lines and ribbons indicate male and female prediction along
1012 with their confidence intervals from the GAMM, while a black line and grey ribbon indicate the
1013 predictions for all individuals pooled in the absence of sex effect. The bottom panels (E, F, G
1014 and H) represent the changes from one age to the next at the population level and according to
1015 ontogenetic changes, selective disappearance or selective appearance for each of the four
1016 parameters for the four different age classes highlighted in fledging success analyses. These are
1017 separated by sex for foraging performances (E), laying date (F) and divorce rates (H), while the
1018 decomposition was run on both sexes pooled for proportion of birds changing nests (G) in the
1019 absence of significant differences in the age-related changes of males and females. Note that
1020 selective appearance cannot be tested for the proportion of birds that changed nest or partners as
1021 these can be defined only compared to the previous year (so that birds cannot appear).

1022 **Fig. 7.** Test of the restraint hypothesis. A) Age-related changes in investment into reproduction
1023 for males in blue and females in red. Mean \pm SE. Sample sizes are indicated per age class and
1024 sex at the top and bottom of the plot for males and females respectively. The GAMM prediction
1025 and confidence interval are drawn as blue line and ribbon for male, while no prediction is
1026 displayed for female in the absence of significant age-related changes in reproductive
1027 investment. B) Changes in males only from one age to the next at the population level, according
1028 to ontogenetic changes, selective disappearance or selective appearance for the four different age
1029 classes highlighted in fledging success analyses.

1030 **Fig. 8** Relationships between ontogenetic changes in relative fledging success and A) relative
1031 laying dates, B) foraging performances during guard, C) reproductive investment in young birds
1032 (ages 2 to 5) and D) relative laying dates in old birds (≥ 16 yr-old).



1033

1034 **Figure 1.**

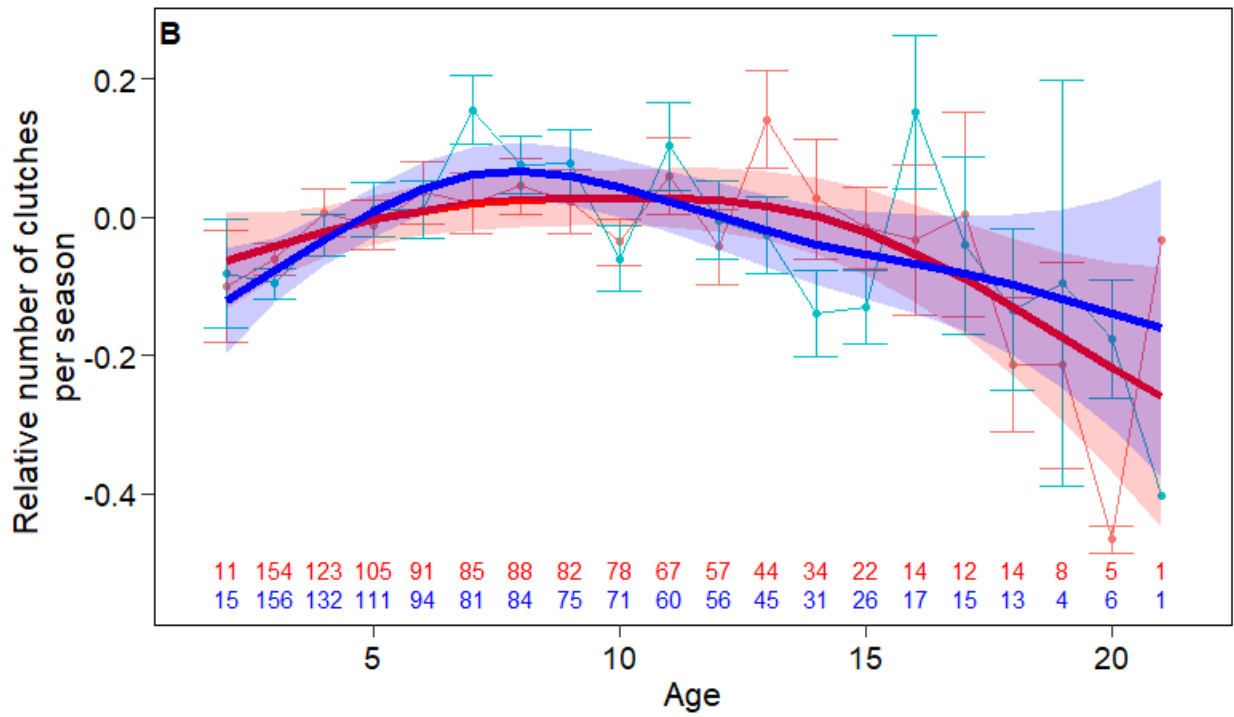
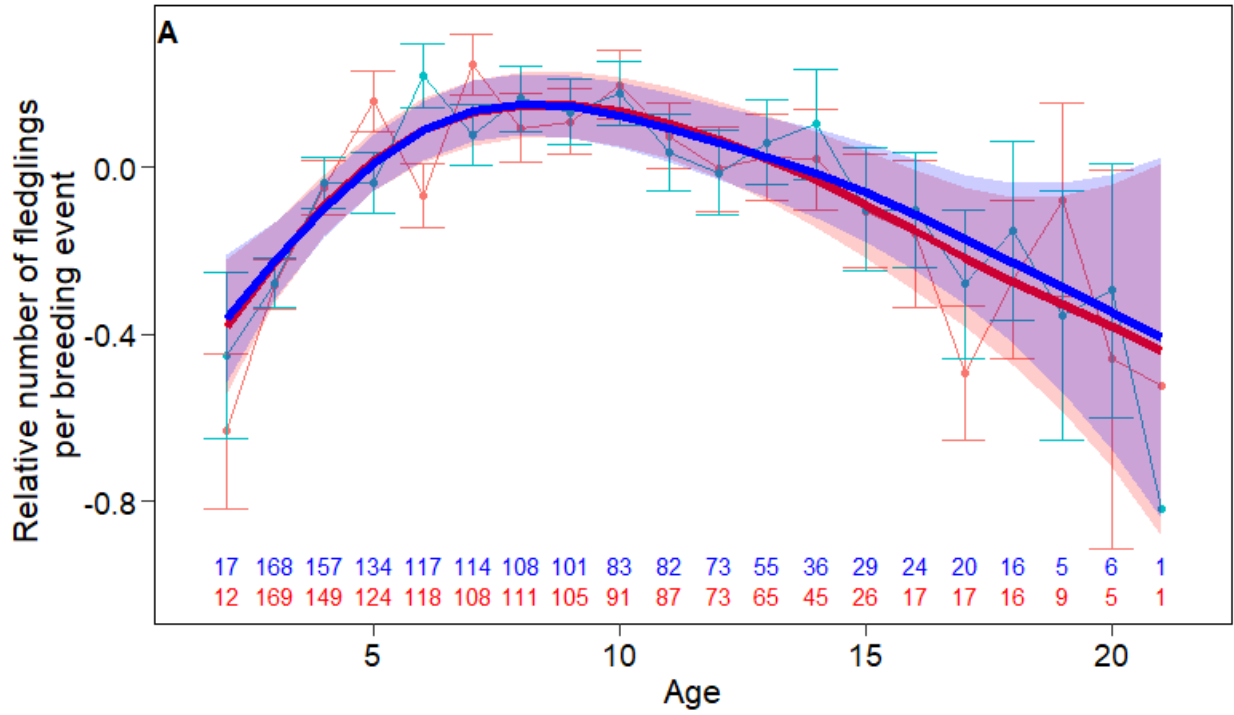
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1038 **Figure 2**

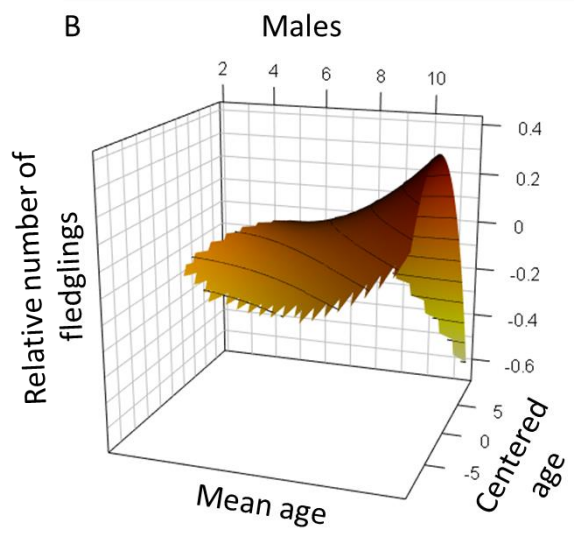
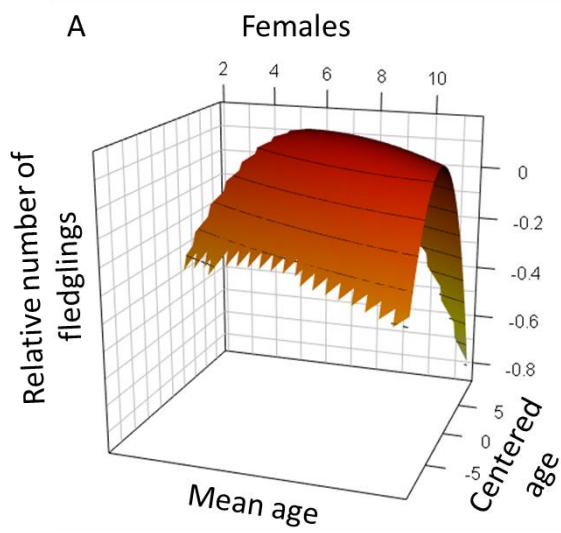


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1040 **Figure 3.**

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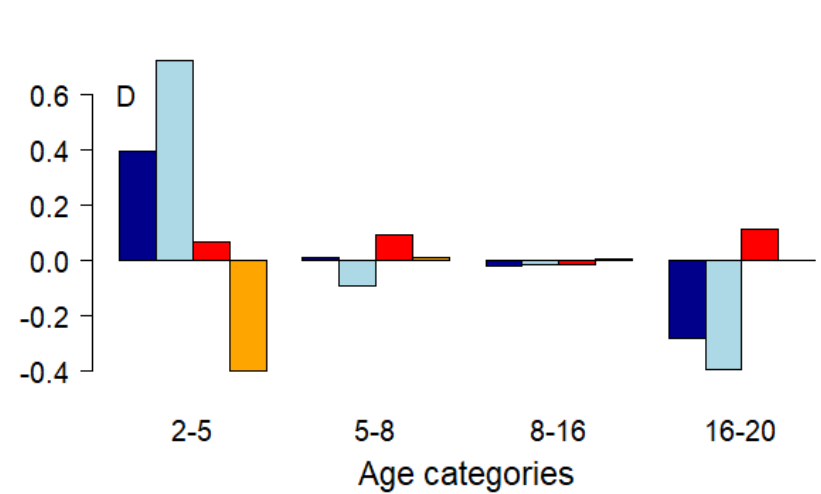
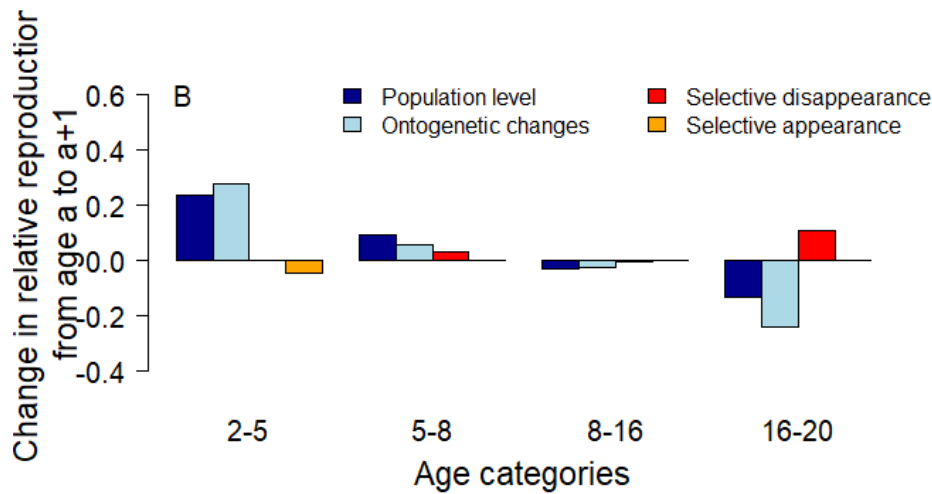
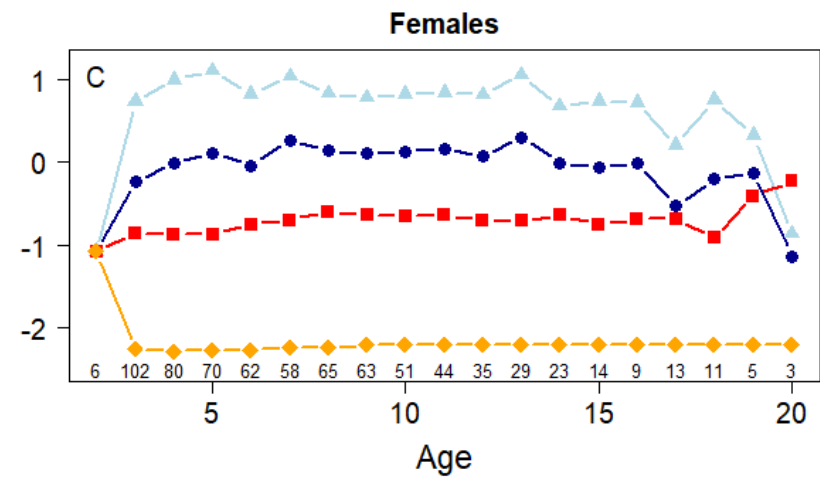
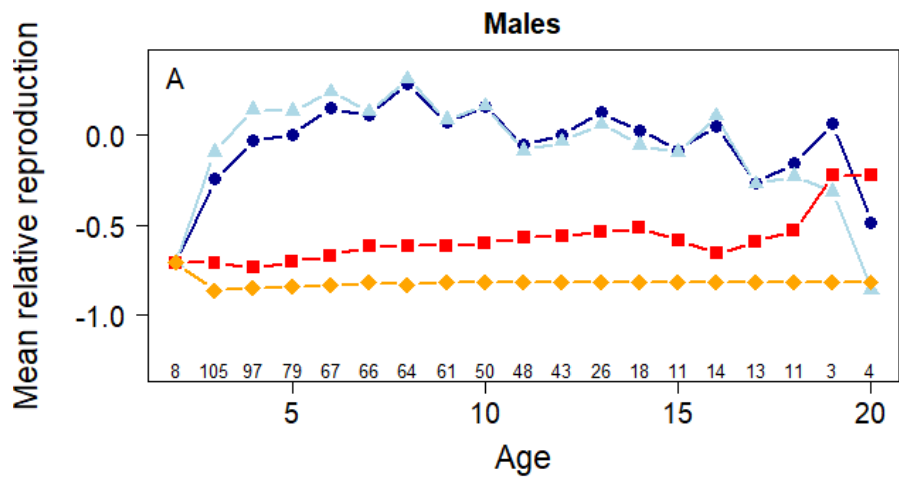


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1045 **Fig 4.**

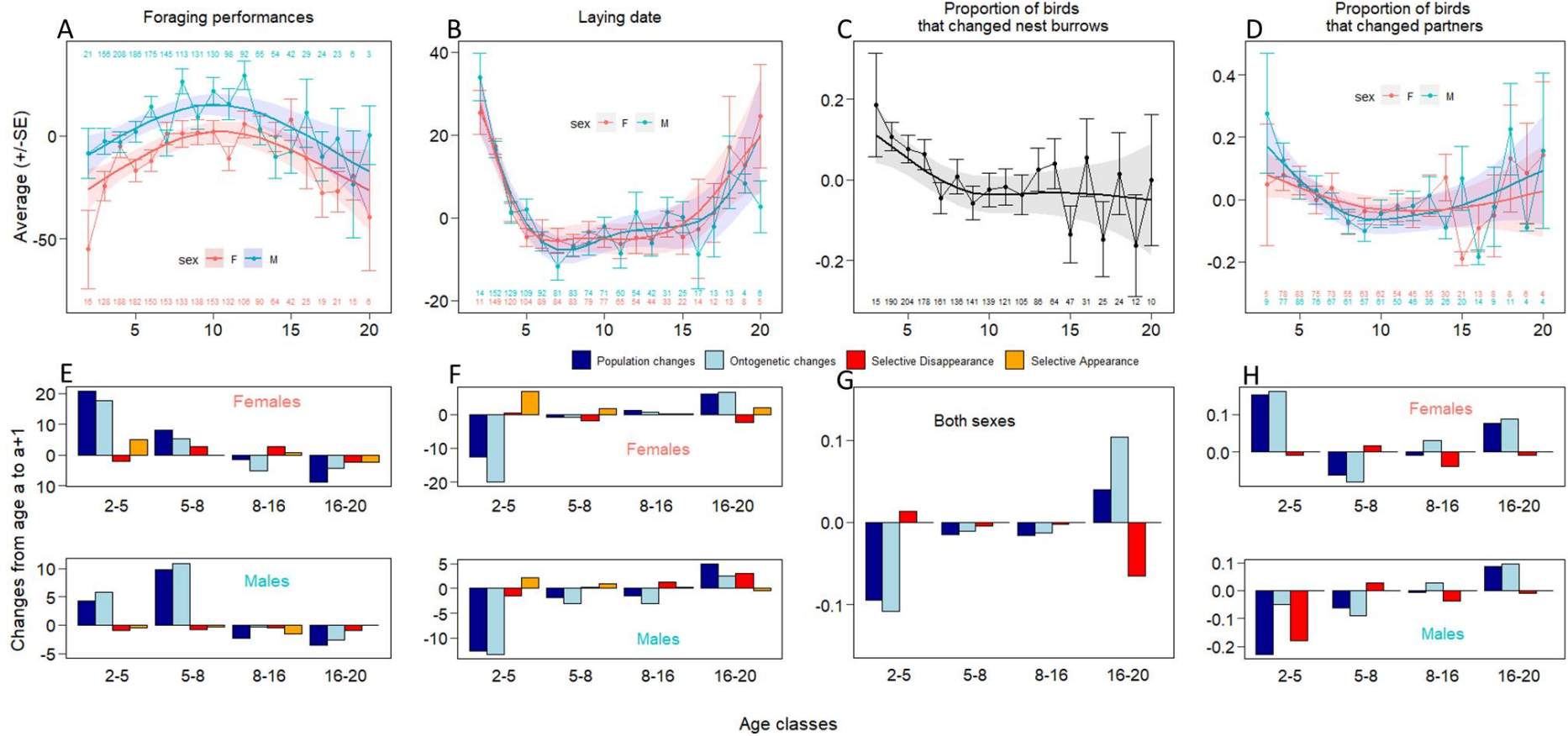
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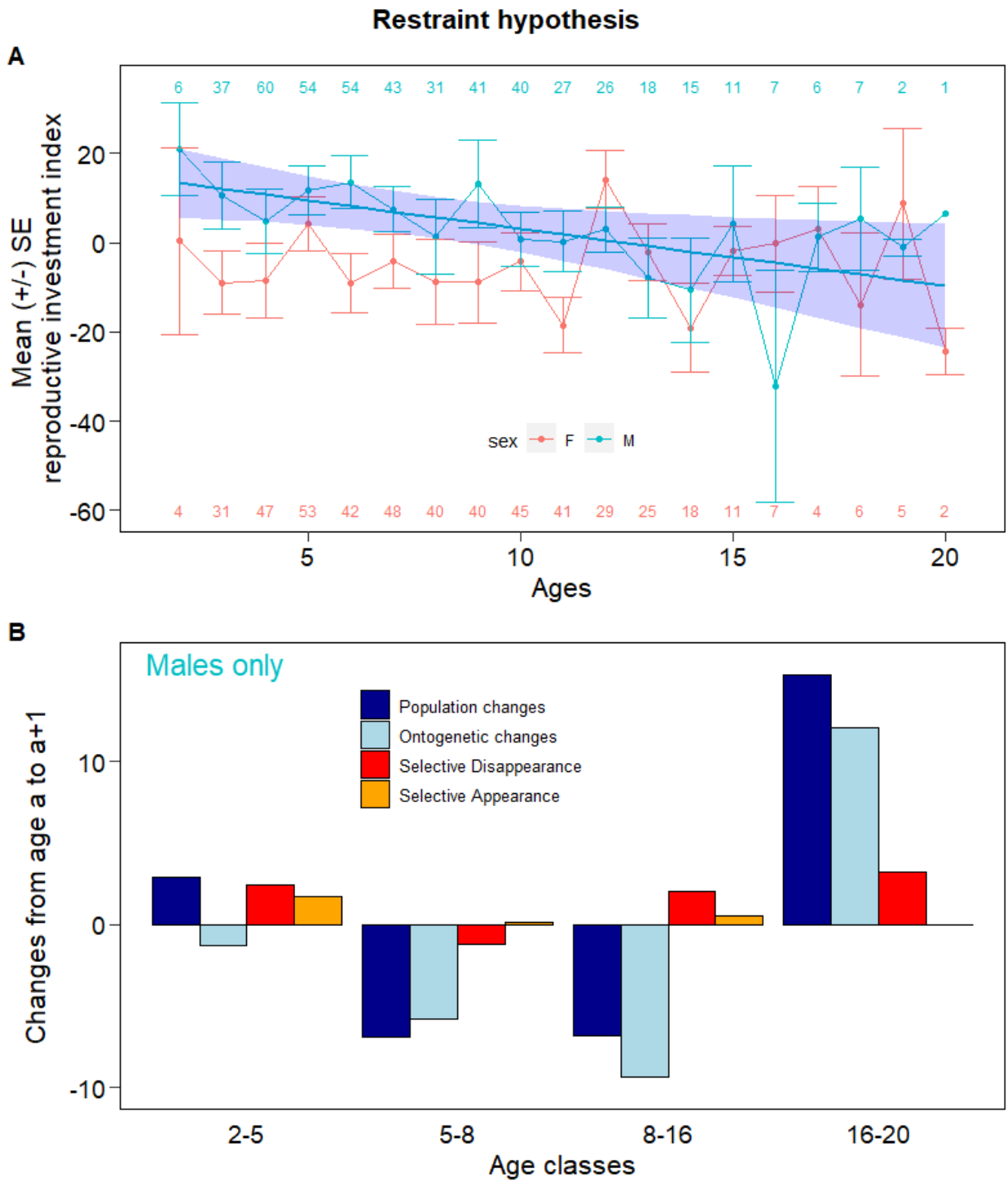
1048 **Figure 5.**

Constraint hypothesis



1049

1050 **Figure 6.**

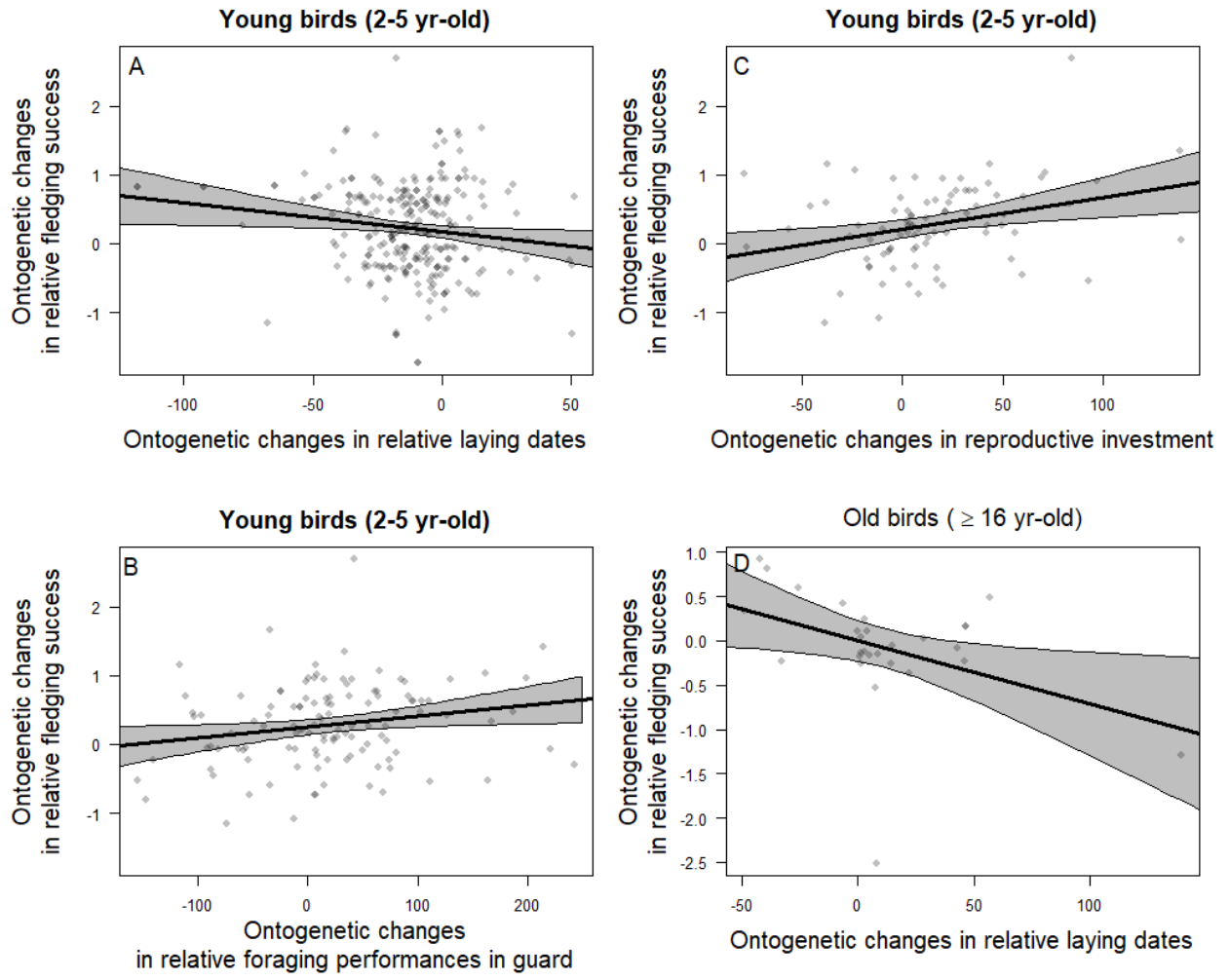


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1052 **Figure 7.**

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1056 **Figure 8.**

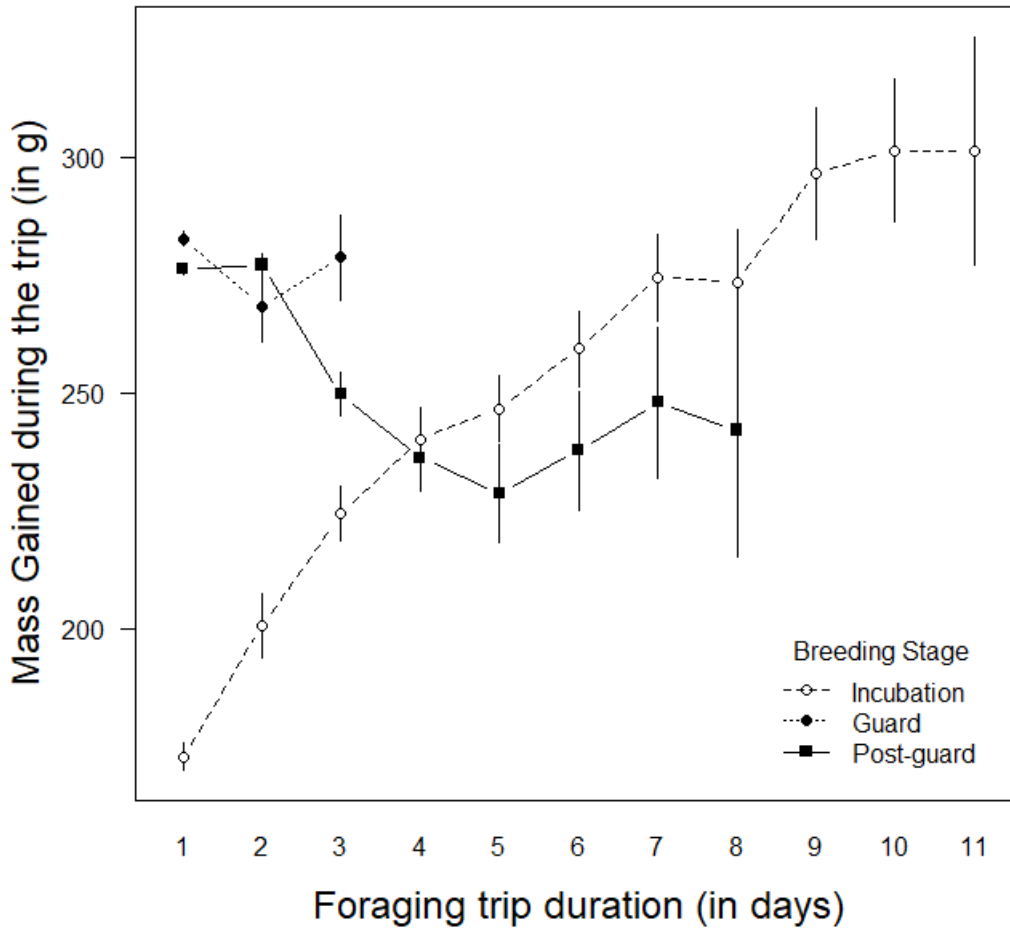
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1059 **Appendix S1**

1060 Saraux C., Chiaradia A. Age-related breeding success in little penguins: a result of selection and
1061 ontogenetic changes in foraging and phenology. *Ecological Monographs*

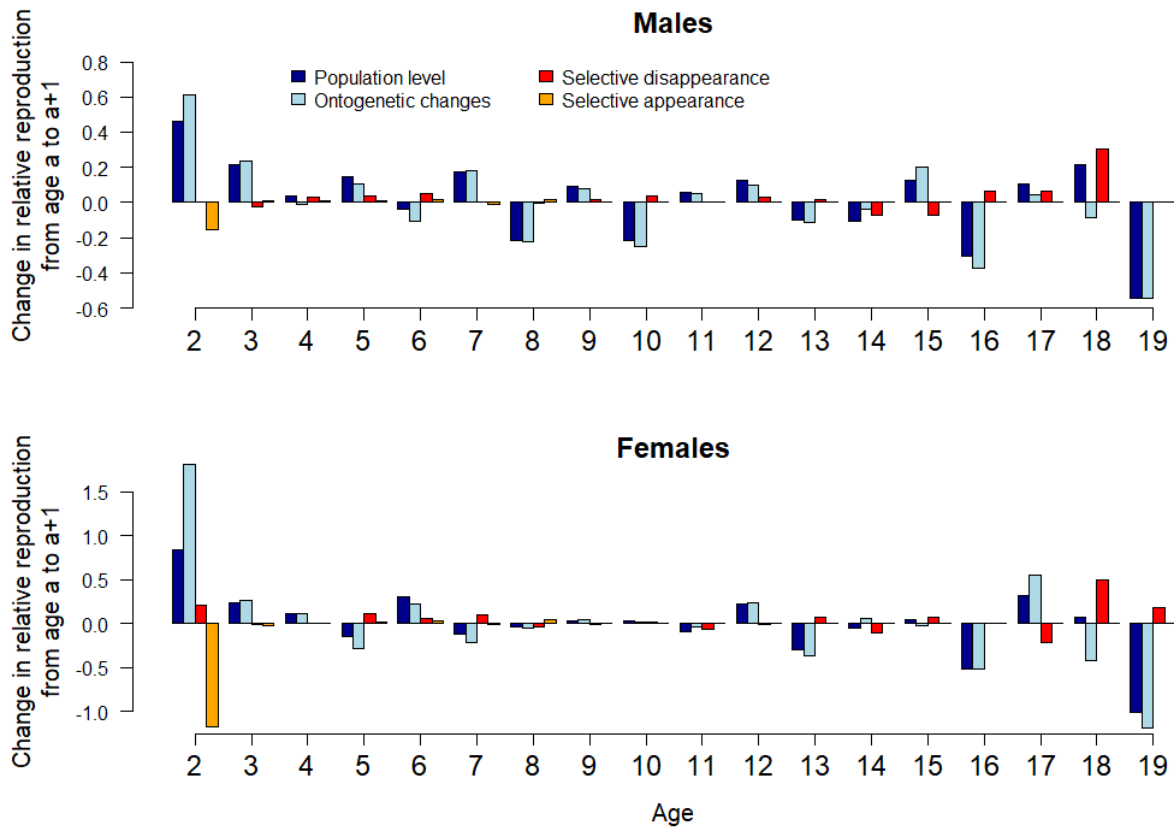
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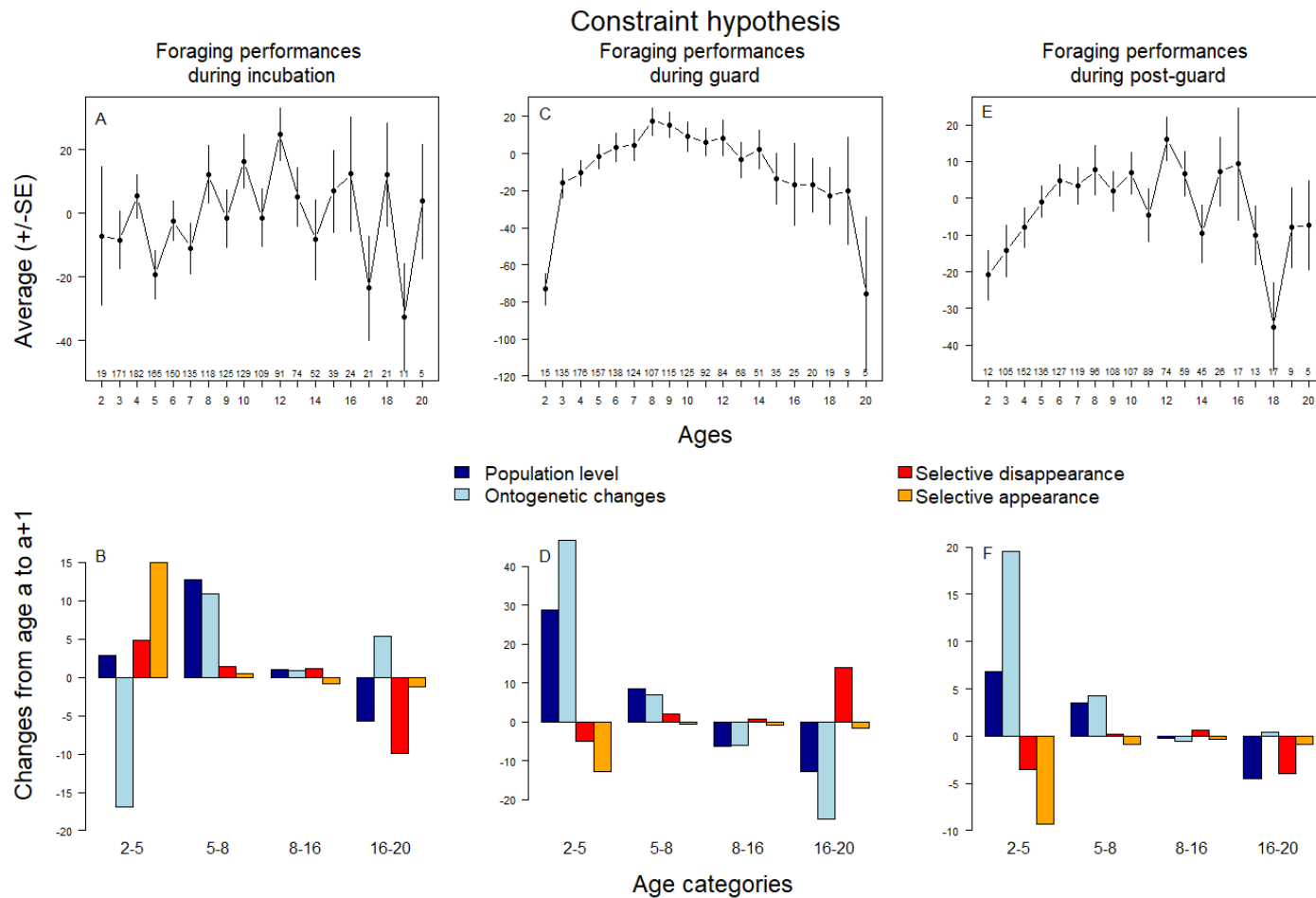
1064 **Figure S1:** Mean \pm SE mass gained during a foraging trip (in g) according to foraging trip
1065 duration (in days) for each breeding stage (incubation indicated with open circles and a dashed
1066 line, guard with black circles and a dotted line, and post-guard with black squares and a plain
1067 line).

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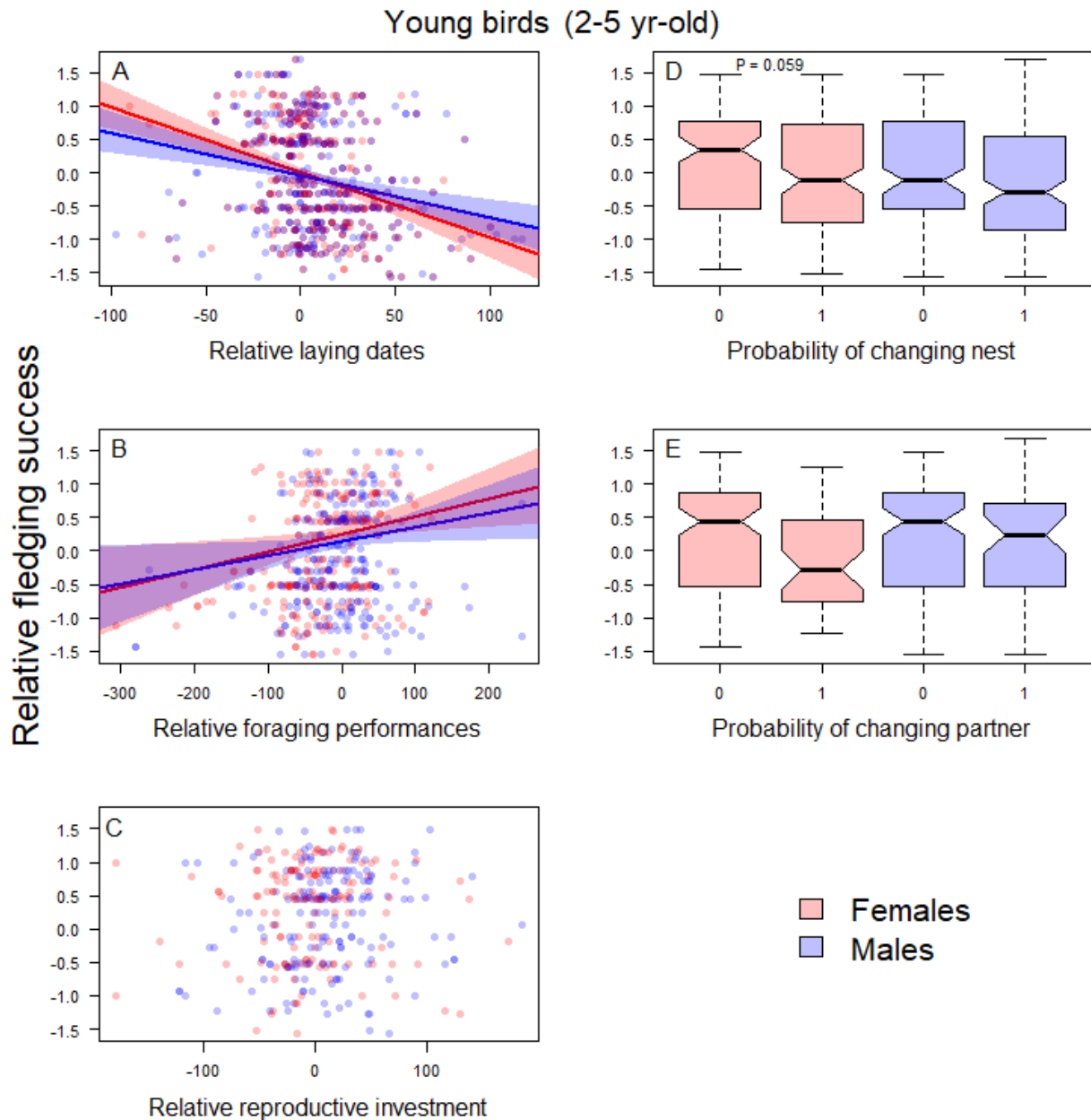
1070 **Figure S2.** Change in relative reproduction from one age to the next at the population level (dark
 1071 blue) and its decomposition in within-individual ontogenetic changes (light blue), selective
 1072 disappearance (red) and selective appearance (orange) in male and female little penguins.



1073

1074 **Figure S3.** Constraint hypothesis – Foraging performances according to age during incubation (A), guard (C), and post-guard (E) and changes in
 1075 foraging performances from one age to the next at the population level (dark blue) and their decomposition in ontogenetic changes (light blue),
 1076 selective disappearance (red) and selective appearance (orange) in incubation (B), guard (D) and post-guard (F).

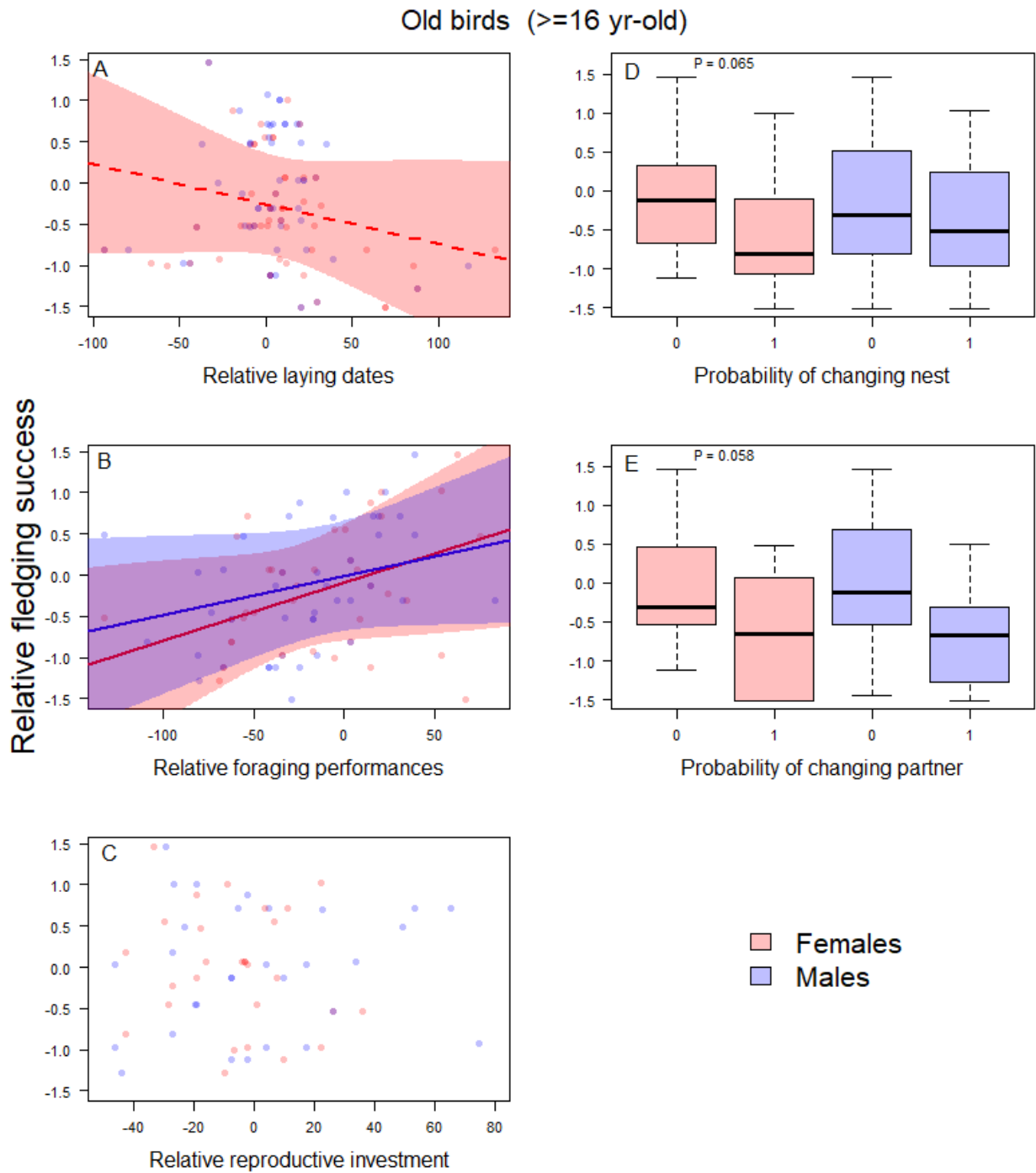
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1079 **Figure S4.** Relative fledging success according to relative laying dates (A), relative foraging
 1080 performances (B) relative reproductive investment (C), divorce rate (D) and change of partner
 1081 (E) in young birds (ages 2-5). Significant relationships are indicated with lines and confidence
 1082 intervals around. As one P-value was close to significant, it is given in panel D. Males are shown
 1083 in blue, while females are shown in red.

1084



1085

1086 **Figure S5.** Relative fledging success according to relative laying dates (A), relative foraging
 1087 performances (B) relative reproductive investment (C), divorce rate (D) and change of partner
 1088 (E) in old birds (≥ 16 years-old). Significant relationships are indicated with lines and confidence
 1089 intervals around. When P-values were close to significant, dotted lines are indicated or the P-
 1090 value written on the figure for boxplots. Males are shown in blue, while females are shown in
 1091 red.