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► To cite this version:

Nicolas Joly, Andre Chiaradia, Jean-Yves Georges, Claire Saraux. Unpacking the lifelong secrets of little penguins: individual quality, energy allocation, and stochasticity in defining fitness. *Evolution - International Journal of Organic Evolution*, 2023, 77 (9), pp.2056-2067. 10.1093/evolut/qpad126 . hal-04212025

HAL Id: hal-04212025

<https://hal.science/hal-04212025v1>

Submitted on 5 Feb 2024

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1 **Running head:** Fitness and individual heterogeneity

2 **Unpacking the Lifelong Secrets of Little Penguins: Individual Quality, Energy**
3 **Allocation, and Stochasticity in Defining Fitness**

4

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13 *Open research statement:* Data are available at <https://doi.org/10.17632/wnskdj8p5s.1>

14

15 *Author contributions and conflict of interest:* AC and CS conceived the ideas, designed
16 methodology and collected the data; NJ, JG and CS analyzed the data; NJ led the writing of
17 the manuscript. All authors contributed critically to the drafts and gave final approval for
18 publication. The authors of this manuscript have no conflict of interest to declare.

19 *Acknowledgements:* We thank Phillip Island Nature Parks for their continued support and
20 commitment to penguin research. The long-term dataset received several funding sources over
21 the years: the Penguin Foundation, Australian Academy of Science, Australian Research
22 Council, Australian Antarctic Division, Kean Electronics and ATT Kings. This research
23 project was funded by the Agence National de la Recherche APEX project (ANR-21-CE02-

24 0007). We also sincerely thank Paula Wasiak, Leanne Renwick, Marg Healy, Alona Charuvi,
25 Marjolein van Polaten Petel, Ross Holmberg, and several past students and volunteers for
26 their tireless support in collecting these data. Without them, this work would not be possible.
27 The study was conducted with research permits issued by the Department of Environment,
28 Land, Water and Planning, Victorian State Government, Australia, and ethics approvals from
29 the Animal Ethics Committee of Phillip Island Nature Parks. We sincerely thank the 2
30 anonymous reviewers for their helpful comments and suggestions.

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32

33 **Abstract**

34 While the heterogeneity among individuals of a population is more and more documented,
35 questions on the paths through which it arises, particularly whether it is linked to fixed
36 heterogeneity or chance alone, are still widely debated. Here, we tested how individual
37 quality, energy allocation trade-offs and environmental stochasticity define individual fitness.
38 To do so, we simultaneously investigated the contribution of 18 life-history traits to the fitness
39 of breeding little penguins (*Eudyptula minor*), using a structural equation model. Fitness was
40 highly variable amongst the 162 birds monitored over their entire lifespan. It increased with
41 the individual penguin's ability to increase i) the number of breeding events (i.e. living
42 longer, breeding younger, breeding more often and producing more second clutches), and ii)
43 the breeding success per event through increased foraging performances (i.e. mass gained at
44 sea). While all three processes (stochasticity, individual quality and allocation trade-offs)
45 affected fitness, inter-individual variability in fitness was mainly driven by individual quality,
46 birds consistently breeding earlier in the season and displaying higher foraging efficiency
47 exhibiting higher fitness. Why some birds consistently can perform better at sea and breed
48 earlier remains a question to investigate to understand how selection applies to these traits.

49 **Key words:** *Fitness, individual heterogeneity, foraging, phenology, breeding ecology*

50

51 1. Introduction

52 Fitness is a measure of how an individual contributes to the population (De Jong, 1994),
53 which results from life-history traits such as survival and breeding success throughout an
54 animal's lifespan (Stearns 1992; McGraw & Caswell, 1996). Yet, due to competing paths
55 between survival and reproduction (Williams, 1966), parents are expected to make trade-offs
56 in relation to variations in benefits to their offspring and costs to themselves (Winkler, 1987).
57 An individual can thus maximise its fitness by producing as many healthy offspring (*i.e.*
58 offspring that would themselves exhibit high survival and breeding success) as possible in its
59 lifetime. In long-lived species, individuals are expected to maximise their breeding events
60 while ensuring the highest number of offspring produced per breeding event (Maccoll &
61 Hatchwell, 2004).

62 Such heterogeneity in individual fitness is thought to result from the differences that
63 individuals exhibit in their capacity to cope with environmental changes (Cam et al., 2002).

64 While some individuals efficiently cope with adverse conditions, others have difficulties
65 breeding and/or surviving (Grémillet & Boulinier, 2009; Reed et al., 2009). Thus, only a small
66 proportion of individuals contribute to the majority of offspring production (Aubry et al.,
67 2009), while others do not contribute at all.. This unequal contribution of individuals to the
68 population can be a major driver of population demography (Jenouvrier et al., 2015).

69 However, part of the variability observed across individuals may also be explained by the fact
70 that different individuals actually faced very different unpredictable conditions throughout
71 their lives, some individuals living mainly in very favorable years while other may face
72 unfavorable years all their lives (*i.e.* stochastic processes, Caswell, 2011; Steiner &
73 Tuljapurkar, 2012).

74 Individual heterogeneity also depends on different allocation trade-offs in their life-history
75 traits, which can be defined as different life-history "strategies" (Fay et al., 2022). In this case,
76 fitness is increased due to a change in one trait but decreased by a second trait (Roff &
77 Fairbairn, 2007). Although these processes are mainly visible at the species/population level,
78 it may also vary among individuals of the same population. Skipping breeding events is a
79 classic example of such strategy, as it will directly reduce individual fitness by removing a
80 breeding event, but it might also increase it on the long-term by improving longevity due to
81 lower breeding costs (Stearns 1989).

82 Apart from breeding success and longevity, fitness can depend on other life-history traits such
83 as early development (Lindström, 1999), phenology (Reed et al., 2009) or mating and
84 foraging behaviours (Grémillet et al., 2016; Patrick & Weimerskirch, 2014), although their
85 relative importance is rarely studied. The combination of the effects of such traits on fitness is
86 difficult to assess, due to the complex interactions amongst them that may indirectly affect
87 other traits, which may either compensate or amplify one another.

88 Here, we disentangled the different processes leading to individual heterogeneity in fitness
89 such as quality, strategies or environmental stochasticity by investigating simultaneously the
90 combined effects of 18 life-history traits on lifetime fitness and in the little penguin
91 (*Eudyptula minor*). The little penguin is a suitable model for this aim with regards to its
92 relatively short life compared to other seabirds (6.5 years in average, up to around 20 to 25
93 years; Dann et al., 2005), and because it exhibits inter-individual variability in survival and
94 breeding success, linked to many different breeding behaviours such as multiple clutches (1 or
95 2 clutches of two eggs) or skipped breeding events, high asynchrony in their breeding
96 phenology, high divorce rate (up to 50%) and a high variability in their foraging efficiency
97 and strategies at sea (A. F. Chiaradia & Kerry, 1999; Joly et al., 2022; Pelletier et al., 2014;
98 Reilly & Cullen, 1979, 1981; Ropert-Coudert et al., 2003; Saraux, Chiaradia, et al., 2011).

99 Variability in individual quality in breeding is mainly driven by differences in their capacity
100 to acquire and/or spare energy (Kahane Rapport et al. 2022). As reproduction is energetically
101 costly, we expected both the energy stored overwinter and foraging efficiency during breeding
102 to play essential roles in explaining interindividual variability in little penguin fitness. Further,
103 because foraging success while breeding is often related to the match of the breeding period
104 with prey abundance (Durant et al 2007), phenology was expected to affect foraging and
105 breeding performances strongly (Joly et al, 2022; LeBohec et al, 2007; Regular et al, 2014).
106 Reproducing earlier in the season might also give individuals access to better partners or
107 nesting sites.

108 Besides differences in intrinsic individual quality, we also expected interindividual
109 heterogeneity to result from differences in energy allocation trade-offs among individuals.
110 While breeding earlier in life or attempting two clutches per year could increase immediate
111 breeding success but decrease longevity through earlier senescence (Kim et al., 2011;
112 Zammuto, 1986), skipping breeding events should decrease short-term breeding success but
113 increase longevity (Le Bohec et al., 2007). Finally, the reproduction/maintenance trade-off
114 (Williams 1966) could also be translated at the breeding season scale by looking at parameters
115 such as the meal proportion given to chicks or the regularity of feeding (Weimerskirch, 1998).
116 To quantify the relative contribution of all these pathways to individual fitness, we built a
117 structural equation model including all the traits mentioned above and their interactions, using
118 a 19-year-long database of 162 individuals monitored throughout their entire life (including
119 87 for which we knew all 18 traits of interest). As individuals did not all live through the same
120 years and some may have benefited or suffered from the conditions of the years they lived in,
121 we ran a second model removing potential stochastic processes by expressing individual life-
122 history traits relative to the other individuals living simultaneously. We expected the effects

123 of most environment-dependent variables, such as foraging or phenology, to be downscaled in
124 amplitude.

125 **2. Methods**

126 **1. Little penguins monitoring**

127 The studied colony is located in the Summerland Peninsula on Phillip Island (38°15' S,
128 143°30' E), Victoria, Australia, consisting of 28,000 to 32,000 breeding adults (Sutherland &
129 Dann, 2012). This study spans 20 consecutive breeding years (from 2001 to 2020). As little
130 penguin breeding season occurs during the austral spring and summer (December to March), a
131 breeding year refers to austral spring, *e.g.* 2001 corresponds to the breeding season 2001-
132 2002.

133 Penguins were implanted as chicks with a 23 mm ISO HDX transponder (Allflex, Australia)
134 between the shoulder blades (Chiaradia & Kerry 1999) and nested in a site containing 100
135 artificial wooden nest boxes burrows, known to have no to slightly positive impact of
136 penguins' survival and breeding (Sutherland et al. 2014). Sex was assessed using bill
137 measurement (Arnould et al., 2004) and confirmed by reproductive behaviour. All nests were
138 checked for breeding status thrice a week during the breeding season.

139 Nest monitoring was coupled to an Automated Penguin Monitoring System (APMS) located
140 on the primary penguin entrance between the colony and the sea – see details in Chiaradia and
141 Kerry (1999). The APMS records individual penguins' ID and body mass going in or out of
142 the colony. Only body masses ranging from 700 to 1700g were considered valid (see Salton *et*
143 *al.* 2015 and Saraux & Chiaradia 2021). A second entry point with a transponder reading was
144 used to detect individual ID only (26% of the detections during the breeding period).

145 Only individuals monitored through their entire life (*i.e.* from birth to death) and which tried
146 breeding at least once (*i.e.* laid at least one egg) were included in the analysis (N = 162).

147 Individuals were considered dead when they were not observed in the colony nor on the
148 APMS for more than one year (*Supplementary material S1*).

149 **2. Little penguins fitness and life-history traits**

150 *2.1 Fitness*

151 Individual fitness was assessed using an adapted population projection matrix (Leslie, 1945)
152 as described by McGraw & Caswell (1996). Each individual's fitness was estimated as the
153 dominant eigenvalue of an age-structured projection matrix, where the matrix is the size of the
154 individual's lifespan, the first row is the number of chicks fledged per year divided by two (as
155 only half of the genome is given by a single parent) and below the diagonal is yearly survival
156 (1 until death). As such, individual fitness should represent the asymptotic growth of an
157 individual genotype through time.

158 *2.2 Breeding behaviour and survival*

159 Longevity was measured as the number of years between hatching and death. The number of
160 breeding events was the number of times eggs were laid. The mean proportion of chicks
161 fledged was estimated as the number of chicks fledged during life divided by the number of
162 eggs laid. Age at 1st breeding was the age at first recorded laying. As some little penguins can
163 lay a second clutch in the same season (Reilly & Cullen, 1981), we assessed the proportion of
164 2nd clutch as the number of breeding seasons during which an individual attempted two
165 clutches divided by the number of breeding seasons (*i.e* seasons with at least one laying
166 event). We calculated the proportion of skipped breeding events as the number of seasons an
167 adult penguin did not attempt breeding divided by the number of years between its first
168 breeding attempt and its death.

169 Finally, the breeding cycle was separated into 3 stages: 1) the incubation period lasting for
170 about 35 days, 2) the guard period (~2 weeks) when one parent stays with young chicks while

171 the other forages at sea and 3) the post-guard period (5 to 8 weeks), when chicks are left alone
172 during the day and parents return ashore at night to feed them (Chiaradia & Kerry 1999).

173 *2.3 Mating behaviour*

174 We assessed the partner and nest changing proportion as the proportion of the breeding season
175 during which an individual had a different partner/nest from the previous season. Only the
176 first breeding event of each season (1st clutch) was considered.

177 *2.4 Phenology*

178 Phenology was investigated through the combination of two factors: i) personality: the
179 average level of behaviour through life and ii) plasticity: the penguin response to
180 environmental variation as defined in (Dingemanse et al., 2010), Plasticity was calculated for
181 each individual as the slope of the linear model between its laying dates and the timing of the
182 annual decrease in chlorophyll concentration, which is known to affect little penguins
183 phenology (Ramírez et al., 2021, Joly et al. 2022). Chlorophyll concentration data were
184 extracted from MODIS/SeaWifs from the NASA (<https://earthdata.nasa.gov/>) dataset
185 following Joly et al. 2022 (see *Supplementary Material S2*). The end of the chlorophyll peak
186 was defined as the date at which 90% of the yearly cumulated daily chlorophyll was reached
187 (Brody et al., 2013). Individual plasticity was then extracted from the following model:

$$188 \textit{Laying date} \sim \textit{Chloro end} * \textit{Individual} + (1/\textit{year})$$

189 In this model, the date at which the chlorophyll peak ends (Chloro end) is the seasonal
190 environmental cue to which penguins should react to assess the best moment to breed
191 (Ramírez et al. 2016; Joly et al. 2022). While the penguin's laying date should be responsive
192 to this variable, each individual is expected to respond with strong or weak strength (*i.e.* be
193 more or less plastic). Here the model computes a slope per individual, *i.e.* the strength of the

194 laying date shift in response to environmental cue shift, while considering the different years
195 penguins lived in.

196 *2.5 Body mass before breeding*

197 Because body mass was not always recorded on the exact day of the laying date, body mass
198 before breeding is the closest mass in a [-5,+5] days interval for males and a [-5,0] days
199 interval for females (to avoid mass loss after egg-laying). Lifetime mass before breeding is as
200 the mean of every breeding season's value.

201 *2.6 Foraging performance during the breeding season*

202 Adult foraging performance was based on trip duration and associated mass gain estimated
203 through the APMS. Foraging trip duration was the number of days between "departure" and
204 "arrival" dates (Chiaradia & Kerry, 1999). As most foraging trips lasted one day during guard
205 (96% 1-d trips and 4% 2-d trips), trip duration was only investigated during incubation and
206 post-guard. Trips longer than 17 days were considered as missing detections from the APMS
207 and discarded (Saraux et al., 2016).

208 Adult body mass change was the mass change per foraging trip, calculated as the difference
209 between a penguin's body mass after and before a given foraging trip. Only body mass
210 changes ranging from [-75 to 500 g] during incubation and [0 to 600 g] during chick-rearing
211 were considered in this study (see Salton *et al.* 2015 and Saraux & Chiaradia 2021). For trip
212 duration and mass gain to be independent, mass gain was corrected for each breeding stage
213 separately using residual values from the linear model [mass gain ~ trip duration] (Joly *et al.*
214 2022). Body mass gain during guard and post-guard trips were then scaled (i.e. standardised
215 according to mean and standard deviation) by stage and grouped as mass gained during chick-
216 rearing.

217 Lifetime foraging variables were assessed separately for different breeding stages (incubation
218 and post-guard/chick-rearing) as the mean of each season's trip average to ensure that every
219 season had the same weight in the final value, correcting for different numbers of trips.

220 *2.7 Parental care*

221 We built three investment variables to distinguish between energy allocated to chick growth
222 and adults' survival. First, a chick-feeding irregularity was defined as the standard deviation
223 of seasonal trip durations (post guard only). Because this variable was highly correlated to
224 post-guard trip duration (*Supplementary Material S3*), we only kept chick feeding irregularity
225 in our model.

226 Second, the proportion of meal mass delivered to the chicks was estimated during post-guard.
227 Chick meal mass was calculated as the mass change difference between each "arrival" and the
228 following "departure", as recorded by the APMS (Saraux, Chiaradia, et al., 2011). Based on
229 previous data, only meal masses ranging from [0 to 500 g] were considered to avoid
230 unrealistic values (Chiaradia & Nisbet, 2006). The meal proportion given to chicks was then
231 calculated as the chick meal mass divided by the mass change of the adult over the previous
232 foraging trip. Note that the meal mass proportion given to chicks can be over 100%, if the
233 adult entailed its own reserve while foraging for the chicks. Still, to avoid potential bias due to
234 false negatives, proportions higher than the 95% interval around the mean proportion of food
235 given to chicks [48%;146%] were not considered.

236 As longer guard periods result in higher growth and fledging success due to longer intensive
237 chick care (Chiaradia and Nisbet, 2006), lifetime guard length in days (mean over all breeding
238 seasons) was also used as an index of reproductive effort. To avoid misinterpretation due to
239 failed breedings, only guard lengths within a 95% interval around the mean (11-35 days) were
240 kept.

241 3. Statistical analysis

242 We conducted two path models to examine the interindividual variability of fitness. Path
243 models are used to assess the relative strength of direct and indirect relations among variables
244 (Wold, 1980; Wright, 1934, more details in *Supplementary Material S4*). Structural equation
245 modelling was computed using the partial least square path modelling method from `plspm`
246 `0.4.9` `plspm` function (Sanchez 2017, more details in *Supplementary Material S4*). Fitting
247 model assumptions were checked following (Kline, 2015) and are detailed in *Supplementary*
248 *Material S5*. Overall, model validation was based on robust Satorra-Bentler corrected values
249 (Hu & Bentler, 1999) of $RMSEA < 0.08$, $CFI > 0.90$ and $SRMR < 0.08$, although small
250 deviations from these values (< 0.02) were accepted due to our small sample size for such
251 model (87 values). Direct relations between variables are presented with their 95% CI and
252 associated p-value, while total effects of variables on fitness (i.e. sum of all direct and indirect
253 effects of a given variable) are presented with their bootstrap estimated ($n = 10000$) 95%
254 confidence interval around the mean and were considered significant when the 95% CI did
255 not overlap 0. Lavaan grammar allows an input under the form of multiple linear relationships
256 that have been included in the model as available in *Supplementary Material S6*.

257 3.1 Raw path analysis

258 The direct relationships tested in the path were defined a priori based on current knowledge
259 and detailed in *Figure 1*. In general, foraging performances and investment in chicks were
260 expected to affect breeding success positively, but investment was also expected to negatively
261 affect longevity, while mating behaviour, phenology and the main life-history traits (age at
262 first breeding, skipping reproduction events, etc.) should play an essential role in fitness.

263 3.2 Path analysis without year effect

264 Because individuals did not all live at the same time in our study, differences in fitness
265 amongst individuals could translate to differences in individual quality or strategies, resulting
266 from differences in environmental conditions over years (*i.e.* stochastic processes). To
267 distinguish those individuals having winning strategy/high quality vs. the "lucky" ones
268 experiencing excellent conditions throughout their life, we conducted a second path analysis
269 including the same variables and relationships as the first path model, but for a correction
270 applied to all variables to remove the effect of the different years. This was done by centering
271 all values per year, *i.e.* subtracting each event's average annual population value from the
272 individual value for each variable. We distinguished three cases to accommodate different
273 types of variables,: i) parameters measured once a year (e.g. the number of clutches,
274 phenology personality, guard duration, proportion of chick fledged), for which we centred by
275 removing the annual mean of the population to the annual individual value, ii) parameters
276 estimated several times a year (*i.e.* foraging trips and meal proportion given to chicks) for
277 which we removed the annual mean of the population to all trip values before averaging the
278 relative variable to get an annual value and iii) parameters estimated once across an
279 individual's life (e.g. longevity, pair switch and nest infidelity), decomposed in a series of 0 or
280 1 each year to which the population mean was subtracted. Examples of cases ii and iii can be
281 found in *Supplementary Material S7*. All corrected annual values were then averaged over the
282 individual's life. Phenology plasticity was estimated as the slope of the same relationship as
283 before, albeit on yearly-centred laying dates instead of raw laying dates.

284 Only fitness, the number of breeding events (for which we wanted to understand how they
285 were affected by relative variables) as well as sex and age at 1st breeding were not corrected
286 for. The path analysis was then conducted as detailed in 3.1.

287 **3. Results**

288 **1. Fitness and life-history traits**

289 *1.1 Individual fitness*

290 Individual fitness was assessed for 162 breeding individuals that laid at least one egg and
291 were monitored from birth to death (*Figure 2*). Among them, 27 individuals (17%) failed to
292 fledge a single chick during their life (5.4 ± 3.9 SD years), resulting in a 0 fitness. However,
293 135 individuals (83%) produced at least one chick during their life (9.3 ± 4.3 years). Among
294 them, 14 individuals (9%) had a fitness of less than one, meaning they only produced one
295 chick during their life. A total of 24 individuals (15%) had a fitness of exactly one, meaning
296 they fledged two chicks in their life. Most individuals (97 penguins, i.e. 60%) had a fitness
297 above one (1.27 ± 0.11 on average), i.e., they fledged more than two chicks (10.1 ± 5.5 chicks
298 in average).

299 *1.2 Life-history traits*

300 The distribution of life-history traits highlights inter-individual variability (*Figure 3*).
301 Individuals that reached maturity most commonly died at the age of 5, while the average
302 longevity remained much higher (8.6 ± 4.5 years). Around 38% of individuals never
303 attempted to lay a 2nd clutch, and 37% never skipped any breeding seasons during their lives.
304 Conversely, 14% of individuals missed breeding seasons and 34% produced a 2nd clutch more
305 than half of the time.

306 Age at 1st breeding attempt (laying) was 3 years old most of the time (60%), but was also
307 regularly 2 or 4 years old, and rarely at 1 (n=5) or above 4 years old (n=6). The mating
308 behaviours (partner or nest changes from one season to the next) varied from individual to
309 individual, from no change during their life to every season changes.

310 Guard period length was variable, from 11 to 34 days, but it was, on average, around 20 days
311 long (19.5 ± 3.5 days). Phenology was highly unsynchronised, the time from the earliest and

312 latest breeders of a given season being almost half a year (177 days, from day 194 to day
313 349), although the average laying date was day 282 ± 23 (mid-October).

314 The plasticity in phenology in response to the peak of chlorophyll concentration was again
315 very variable among individuals. Still, most individuals (90%) advanced breeding when the
316 end of the chlorophyll peak occurred earlier and only a few displayed the opposite
317 relationship of delaying breeding. On average, individuals bred 3 days earlier (3.1 ± 3.9) for
318 each day the end of the chlorophyll peak ended earlier, although some displayed a much
319 stronger response, advancing reproduction by 10 days per day of shift in the bloom end.

320 **2. Direct relationships between traits**

321 The first path analysis (chi-square < 0.001 , CFI = 0.91, RMSEA = 0.082, SRMR = 0.078),
322 has been conducted on 87 individuals (breeding at least twice) for which the 18 variables
323 included in the model were available. Outcomes are presented in *Figure 4*, details are in
324 *Supplementary material S8*.

325 The proportion of chicks fledged and the number of breeding events both had a strong effect
326 of similar strength on individual fitness (0.63 and 0.51 respectively, $p < 0.001$, $R^2 = 0.659$)
327 although being poorly correlated with each other (Pearson's $R^2 = 0.18$, *Supplementary*
328 *Material S9*). Number of breeding events strongly depended on individual longevity (relative
329 estimate of 0.83, CI95% [0.76; 0.90], $p < 0.001$). Breeding events also benefited from a
330 higher proportion of 2nd clutches (rel. est. = 0.27 [0.20; 0.34], $p < 0.001$), while it was
331 negatively affected by older age at 1st breeding (rel. est. = -0.21 [-0.27; -0.15], $p < 0.001$) and
332 skipped breeding seasons (rel. est. = -0.27 [-0.37; -0.19], $p < 0.001$). These four variables
333 (longevity, 2nd clutches, 1st breeding, skipped breeding) explained 96% of the variability in
334 the number of breeding events (plspm $R^2 = 0.964$).

335 Foraging and investment in the chicks affected breeding success through mass gained at sea
336 and chick feeding, although the results were not statistically significant. Individuals gaining
337 more mass at sea during chick-rearing tended to fledge more chicks per breeding event (rel.
338 est. = 0.22 [-0.04; 0.48], $p = 0.089$). Conversely, individuals that managed to provide a higher
339 proportion of the meal mass to their chicks exhibited a lower proportion of chicks fledged
340 (rel. est. = -0.25 [-0.56; 0.00], $p = 0.057$).

341 Average phenology (personality) had broad effects on several parameters. Earlier breeding
342 was linked with a higher proportion of 2nd clutches (rel. est. = 0.71 [0.59; 0.81], $p < 0.001$)
343 and higher mass gained at sea during chick-rearing (rel. est. = 0.46 [0.26; 0.64], $p < 0.001$)
344 and tended to result in shorter foraging trips during incubation ($p = 0.011$), longer guard
345 periods ($p = 0.005$) and lower partner switch ($p = 0.003$) and nest switch ($p = 0.017$).

346 Conversely, plasticity in phenology only affected the proportion of 2nd clutches (rel. est. = -
347 0.24 [-0.38; -0.06], $p = 0.003$). Phenology (and sex) explained respectively 53% and 24% of
348 the variability in proportion of 2nd clutches and mass gain during chick-rearing (plspm $R^2 =$
349 0.526 and 0.238).

350 Mating behaviour (partner and nest switches) had small to no effects on breeding success.
351 And while other variables such as sex significantly affected some life-history traits (mainly
352 linked to foraging), these effects did not impact breeding success and fitness. Females were
353 for instance, lighter before breeding and gave less food to the chicks in proportion compared
354 to males (full stats $p < 0.001$), without any consequences on the number of breeding events or
355 the proportion of chicks fledged.

356 The second path analysis (chi-square < 0.001 , CFI = 0.88, RMSEA = 0.092, SRMR = 0.078)
357 presented the same model as in *Figure 4*, but data were corrected by year to only account for
358 interindividual differences rather than differences due to individuals living in different years.

359 In most cases, relationships were similar to what was found with raw data and presented
360 above, albeit some changes in effect strength and a few rare occasions, where the
361 relationships changed (*see Supplementary Material S10 & S11*).

362

363 **3. Overall effect on fitness**

364 Variables' total effects on fitness are the combination of their direct and indirect effects
365 through other variables (*Table 1*). First, penguins' fitness was directly affected by the
366 proportion of chicks fledged, and number of breeding events (total effects = direct effects
367 presented above). Longevity also significantly affected fitness (0.42 CI95% [0.32; 0.56])
368 through an increased number of breeding events. While looking at indirect variables, the
369 penguin fitness increased by skipping fewer breeding seasons (rel. est. = -0.13 [-0.25; -0.05])
370 and conducting more 2nd clutches (rel. est. = 0.22 [0.11; 0.37]). In terms of foraging,
371 individuals gaining more mass at sea during chick-rearing also exhibited higher fitness (rel.
372 est. = 0.23 [0.03; 0.41]). Finally, early breeding had the strongest and most beneficial total
373 effect on fitness, with a strength almost as important as breeding success and longevity (rel.
374 est. = -0.35 [-0.48; -0.22]). No other studied variables affected fitness, despite a significant
375 direct effect on chick-fledging or the number of breeding events for some of them (such as the
376 proportion of mass gained given to chicks or plasticity in phenology, *Figure 4*) as other
377 indirect effects partly compensated it.

378 Once stochastic processes and year effects were removed from our variables (*Table 1*), the
379 results of the new path analyses were highly consistent with those of the first model on raw
380 data. Indeed, the variables that significantly affected fitness were strictly the same in both
381 analyses. Further, the effect sizes of the proportion of chicks fledged, the number of breeding
382 events, longevity and mass gained during chick-rearing remained similar between both
383 analyses (although slightly decreased for longevity, rel. est = 0.36 [0.26; 0.50]). Nevertheless,

384 some interesting differences also appeared. The effects of 2nd clutches and earlier breeding,
385 while still significantly positive, were notably decreased in amplitude once the year effects
386 were removed. More surprisingly, one relationship changed. While missing breeding seasons
387 had an adverse impact on fitness before, here (*i.e.* after removing the year effect), it showed
388 positive effects (rel. est. = 0.22 [0.11; 0.38]). Finally, switching partners had an overall
389 positive (although non-significant) effect on fitness (rel. est. = 0.15 [-0.01; 0.34]).

390 **4. Discussion**

391 Fitness as an evolutionary concept refers to the overall genetic contribution of an individual to
392 its population (De Jong, 1994). The fact that some individuals disproportionately contribute to
393 the population implies that others display a much less critical contribution (Aubry, Koons, et
394 al., 2009). This variability in individual contribution to their population is vital to
395 understanding population demography, especially in climate change (Grémillet & Boulinier,
396 2009; Jenouvrier et al., 2015). In this study, little penguins reached maturity at very different
397 fitness profiles, either not contributing to the population (16%), making one chick (9%),
398 contributing just enough to propagate their genes into the next generation (exactly 2 chicks,
399 15%) or over-contributing (> 2 chicks, 60%). While several factors have been proposed and
400 tested to explain such differences in individual fitness in other species (Naves et al., 2006;
401 Patrick & Weimerskirch, 2014; Reed et al., 2009), the relative contribution of each one of
402 them has rarely, if ever been assessed.

403 We showed that although stochastic processes explained part of the variability, fitness was
404 mainly due to different individual capacities to multiply the number of their breeding
405 attempts. In general, increased breeding attempts were achieved by living longer, laying more
406 second clutches, skipping fewer breeding events, while fledging proportion was mainly driven
407 by foraging efficiency. Besides those variables, the average phenology of an individual

408 appeared to be one of the main contributors to its fitness due to very indirect but ubiquitous
409 effects on many different life-history traits.

410 Lifetime fitness depends on the individual's capacity to maximise its survival, as longer life
411 may lead to multiple breeding events (Stearns, 1976) and on its capacity to efficiently fledge
412 chicks at each breeding event (Brommer et al., 1998; Maccoll & Hatchwell, 2004). In long-
413 lived species such as seabirds, individuals are expected to favour survival over breeding
414 success when trading-off energy allocation, as the number of future breeding prospects is
415 important (Goodman, 1974; Stearns, 1992), so longevity is often expected to be the main
416 component of individual fitness. Here, the number of breeding events and the proportion of
417 fledged chicks had a similarly important effect on the variability in individual fitness. These
418 results imply that both long-lived and short-lived strategies are somewhat equivalent at the
419 individual lifetime scale for this species. Yet, this is not unexpected as little penguins are one
420 of the shortest-lived seabirds, placing them at an intermediate position on the short-lived /
421 long-lived species gradient, implying that the costs of a failed breeding event tends to have a
422 more important impact on fitness than for species with much longer lifespan. Indeed,
423 longevity is known to drive fitness through factors such as gained experience in long-lived
424 species (e.g. albatrosses, Aubry et al. 2011). However, such interests of surviving might be
425 less important in shorter-lived species where decreased performances tend to happen after
426 only a few breeding events (Saraux et al. 2022).

427 Here, the number of breeding events still depended on longevity, but was also affected by the
428 number of skipped breeding seasons, the proportion of 2nd clutches and the age at first
429 breeding. The variability in these three parameters is a well-known trade-off between survival
430 and breeding (*i.e* balance of allocation to breeding or self-maintenance, Le Bohec et al. 2007,
431 Dobson and Jouventin 2010). While skipping a breeding event (season or 2nd clutch)
432 decreases the immediate offspring production, it simultaneously reduces the costs of

433 reproduction and increases the number of potential future breeding events (Desprez et al.,
434 2018). The same trade-off applies for later age at 1st breeding (Aubry, Koons, et al., 2009), as
435 starting to breed at an older age tends to decrease an individual overall number of breeding
436 events but also allows individuals to delay the energetic costs of reproduction to optimum
437 ages in their foraging and chick provisioning performance (Aubry, Cam, et al., 2009; Krüger,
438 2005; Limmer & Becker, 2009; Saraux & Chiaradia, 2021). However, in this study we
439 showed that no significant increase in longevity was associated with an increased number of
440 skipped breeding events, leading to a significant detrimental effect of missed breeding events
441 on individual fitness. Thus, if skipping breeding events to maximise longevity may be a good
442 strategy in very long-lived species (Jenouvrier et al., 2005), this may not be true in relatively
443 shorter-lived species such as the little penguin.

444 Regarding age at 1st breeding, there was no significant effect on fitness, although it led to
445 slightly fewer breeding events. This may be explained by the lack of variability in age at 1st
446 breeding in little penguins (*i.e* between 2 and 4 years old in almost all cases) and that the
447 breeding success of young individuals is lower than older ones (Saraux & Chiaradia 2021).
448 Thus, adding one failed breeding event might not affect lifelong fitness.

449 Finally, the balance between maintenance and reproduction can also be perceived at finer
450 scales within breeding seasons. Higher parental investment should increase breeding success
451 but decrease a parent's body condition and future success (Storey et al., 2017). This was
452 investigated through 3 parameters in our study: the duration parents could maintain the
453 intensive care guard period, the regularity of chick feeding and the proportion of the captured
454 food allocated to the chicks. Yet, none of this affected fitness and their effects on either side
455 of the energy balance were not significant either. This may be because individuals rarely
456 overreach while favouring their own body reserves (Saraux, Robinson-Laverick, et al., 2011)
457 to avoid decreased longevity. On the other hand, a decreased parental investment may be

458 partly compensated by the partner, as little penguins exhibit unequal parental investment
459 (Saraux, Chiaradia, et al., 2011). Interestingly, we found no sex-specific strategies that
460 directly affected fitness, while it is known to affect survival in many birds taxa (Liker &
461 Székely, 2005). Zhang et al (2015) also showed that although common terns exhibit sex-
462 specific recruitment and survival, these effects did not translate to reproductive value.

463 Beyond energy allocation trade-offs, fitness should depend on an individual's quality
464 (Blomqvist et al., 1997; Bolton, 1991; Coulson & Porter, 1985). Individual quality defines the
465 capacity of an individual to maximise its life-history traits simultaneously and is often
466 perceived through positive correlations between traits (Wilson and Nussey 2010, Vedder and
467 Bouwhuis 2018), e.g. individuals reproducing better also surviving better.

468 Mass gained at sea during chick-rearing positively affected both longevity and breeding
469 success (in lines with previous studies: Berlincourt & Arnould, 2015; Chiaradia & Kerry,
470 1999; Saraux et al., 2016), which indicates that an individual capacity to acquire energy (i.e.
471 foraging efficiency) might be a major driver of individual quality (Lescroël et al., 2009,
472 2010).

473 Certain traits may not directly affect breeding success, but instead affect other life-history
474 traits, thus reaching fitness through their capacity to influence various other traits rather than
475 by the strength of a single effect. We established the strong positive impact of early
476 phenology on fitness due to the cumulative sum of small effects on different parameters. We
477 showed that earlier breeding was associated with varying behaviours of breeding, mainly
478 significantly increasing 2nd clutch events, consistent with Reed et al. (2013). Earlier breeding
479 was also important in affecting foraging and chick provisioning through increased mass gain
480 at sea, decreased trip duration, or increased length of chick guard. If early phenology is so
481 important for little penguins as seem to be the case for most seabirds (Keogan et al., 2018),
482 one can wonder why individuals do not all breed early and why this is species so

483 asynchronous. Evidence shows that individual breeding may start when reaching an energetic
484 threshold (*i.e.* carry-over effect of wintering; Robinson et al., 2005; Salton et al., 2015). Thus,
485 some individuals may delay their breeding until they reach this threshold (the required
486 duration could then depend again on individuals' capacity to acquire energy or in their
487 reproductive investment in the previous season for instance). While the shift in seabird
488 breeding timing is often described as the result of individuals exhibiting plastic phenology to
489 match with environment cycles (Frederiksen et al., 2004; Keogan et al., 2018; Reed et al.,
490 2009), few significant effects of plasticity in phenology were found in this study. Likely, the
491 overall population switch in phenology to cope with environmental shifts is so strong that it
492 hides the inter-individual compound of this variability.

493 The role of stochastic processes in inter-individual variability is subject to much debate
494 (Caswell, 2011; Davison et al., 2019; Steiner & Tuljapurkar, 2012). Individuals may perform
495 better because of their quality or because they live in favourable conditions. We compared our
496 results with those of a second model minimising stochastic processes by looking at individual
497 performances relative to the population living in the same year. Based on our results, we
498 argue that if stochastic processes tend to exacerbate individual variability; life-history traits
499 were never entirely driven by unpredictable events while presenting no individual variation in
500 the capacity to face the event. Some individuals lived in better years of earlier breeding and
501 higher foraging performances, increasing their fitness. However, these processes did not
502 explain the significant part of interindividual variability. This is not surprising as relatively
503 long-lived species using a partly capital breeding strategy should have a higher capacity to
504 buffer environmental changes (Morris et al., 2008; Stephens et al., 2009). However, it implies
505 that even when processes are strongly driven by overall population shifts and inherent
506 variability (*i.e.* independently from the environment), such as phenology (Keogan et al., 2018;
507 Youngflesh et al., 2018), some individuals still perform better than others in the trait (*i.e.*

508 breeding earlier in the case of phenology). Whether this might have a genetic basis
509 (heritability, (Dobson et al., 2017) or derive from early-life conditions (environmental and
510 maternal effects, (Hamel et al., 2009) or other processes will need to be further investigated.

511 Conclusion

512 Using a 20-year dataset from 162 little penguins, we constructed a detailed map showing the
513 different paths these iconic penguins take to lifelong fitness. Individual variability in life-
514 history traits seemed to depend primarily on individual quality and secondarily on different
515 trade-off strategies. Although energy allocation trade-offs are expected to mediate the effect
516 of individual quality, our study demonstrates that they may not compensate for high intrinsic
517 differences among individuals (Kim et al., 2011). We also showed that penguins' individual
518 quality mainly relied on efficient foraging and early phenology, which are highly dependent
519 on the environment (Joly et al., 2022), raising major questions about population demography
520 in the context of rapid environmental changes.

521 References

- 522 Arnould, J. P. Y., Dann, P., & Cullen, J. M. (2004). Determining the sex of Little Penguins (*Eudyptula*
523 *minor*) in northern Bass Strait using morphometric measurements. *Emu - Austral Ornithology*,
524 *104*(3), 261–265. <https://doi.org/10.1071/MU04035>
- 525 Aubry, L. M., Cam, E., & Monnat, J.-Y. (2009). Habitat Selection, Age-Specific Recruitment and
526 Reproductive Success in a Long-Lived Seabird. In D. L. Thomson, E. G. Cooch, & M. J. Conroy (Eds.),
527 *Modeling Demographic Processes In Marked Populations* (pp. 365–392). Springer US.
528 https://doi.org/10.1007/978-0-387-78151-8_16
- 529 Aubry, L. M., Koons, D. N., Monnat, J.-Y., & Cam, E. (2009). Consequences of recruitment decisions
530 and heterogeneity on age-specific breeding success in a long-lived seabird. *Ecology*, *90*(9), 2491–
531 2502. <https://doi.org/10.1890/08-1475.1>
- 532 Blomqvist, D., Johansson, O. C., & Götmark, F. (1997). Parental quality and egg size affect chick
533 survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia*, *110*(1), 18–24.
534 <https://doi.org/10.1007/s004420050128>
- 535 Bohec, C. L., Gauthier-Clerc, M., Grémillet, D., Pradel, R., Béchet, A., Gendner, J.-P., & Maho, Y. L.
536 (2007a). Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and
537 breeding probability in unbanded king penguins. *Journal of Animal Ecology*, *76*(6), 1149–1160.
538 <https://doi.org/10.1111/j.1365-2656.2007.01268.x>

539 Bohec, C. L., Gauthier-Clerc, M., Grémillet, D., Pradel, R., Béchet, A., Gendner, J.-P., & Maho, Y. L.
540 (2007b). Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and
541 breeding probability in unbanded king penguins. *Journal of Animal Ecology*, 76(6), 1149–1160.
542 <https://doi.org/10.1111/j.1365-2656.2007.01268.x>

543 Bolton, M. (1991). Determinants of Chick Survival in the Lesser Black-Backed Gull: Relative
544 Contributions of Egg Size and Parental Quality. *Journal of Animal Ecology*, 60(3), 949–960.
545 <https://doi.org/10.2307/5424>

546 Brody, S. R., Lozier, M. S., & Dunne, J. P. (2013). A comparison of methods to determine
547 phytoplankton bloom initiation. *Journal of Geophysical Research: Oceans*, 118(5), 2345–2357.
548 <https://doi.org/10.1002/jgrc.20167>

549 Brommer, J. E., Pietiäinen, H., & Kolunen, H. (1998). The effect of age at first breeding on Ural owl
550 lifetime reproductive success and fitness under cyclic food conditions. *Journal of Animal Ecology*,
551 67(3), 359–369. <https://doi.org/10.1046/j.1365-2656.1998.00201.x>

552 C. Naves, L., Yves Monnat, J., & Cam, E. (2006). Breeding performance, mate fidelity, and nest site
553 fidelity in a long-lived seabird: Behaving against the current? *Oikos*, 115(2), 263–276.
554 <https://doi.org/10.1111/j.2006.0030-1299.14883.x>

555 Cam, E., Link, W. A., Cooch, E. G., Monnat, J., & Danchin, E. (2002). Individual Covariation in
556 Life-History Traits: Seeing the Trees Despite the Forest. *The American Naturalist*, 159(1), 96–105.
557 <https://doi.org/10.1086/324126>

558 Caswell, H. (2011). Beyond R0: Demographic Models for Variability of Lifetime Reproductive Output.
559 *PLOS ONE*, 6(6), e20809. <https://doi.org/10.1371/journal.pone.0020809>

560 Chiaradia, A. F., & Kerry, K. R. (1999). DAILY NEST ATTENDANCE AND BREEDING PERFORMANCE IN
561 THE LITTLE PENGUIN EUDYPTULA MINOR AT PHILLIP ISLAND, AUSTRALIA. *Marine Ornithology*, 27,
562 13–20.

563 Chiaradia, A., & Nisbet, I. C. T. (2006). *Plasticity in parental provisioning and chick growth in Little*
564 *Penguins Eudyptula minor in years of high and low breeding success*. 15.

565 Coulson, J. C., & Porter, J. M. (1985). Reproductive success of the Kittiwake Rissa tridactyla: The roles
566 of clutch size, chick growth rates and parental quality. *Ibis*, 127(4), 450–466.
567 <https://doi.org/10.1111/j.1474-919X.1985.tb04841.x>

568 Davison, R., Stadman, M., & Jongejans, E. (2019). Stochastic effects contribute to population fitness
569 differences. *Ecological Modelling*, 408, 108760. <https://doi.org/10.1016/j.ecolmodel.2019.108760>

570 De Jong, G. (1994). The Fitness of Fitness Concepts and the Description of Natural Selection. *The*
571 *Quarterly Review of Biology*, 69(1), 3–29. <https://doi.org/10.1086/418431>

572 Desprez, M., Gimenez, O., McMahon, C. R., Hindell, M. A., & Harcourt, R. G. (2018). Optimizing
573 lifetime reproductive output: Intermittent breeding as a tactic for females in a long-lived,
574 multiparous mammal. *Journal of Animal Ecology*, 87(1), 199–211. <https://doi.org/10.1111/1365-2656.12775>

576 Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal
577 personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81–89.
578 <https://doi.org/10.1016/j.tree.2009.07.013>

579 Dobson, F. S., Becker, P. H., Arnaud, C. M., Bouwhuis, S., & Charmantier, A. (2017). Plasticity results in
580 delayed breeding in a long-distant migrant seabird. *Ecology and Evolution*, 7(9), 3100–3109.
581 <https://doi.org/10.1002/ece3.2777>

582 Dobson, F. S., & Jouventin, P. (2010). The trade-off of reproduction and survival in slow-breeding
583 seabirds. *Canadian Journal of Zoology*, 88(9), 889–899. <https://doi.org/10.1139/Z10-054>

584 Fay, R., Authier, M., Hamel, S., Jenouvrier, S., van de Pol, M., Cam, E., Gaillard, J.-M., Yoccoz, N. G.,
585 Acker, P., Allen, A., Aubry, L. M., Bonenfant, C., Caswell, H., Coste, C. F. D., Larue, B., Le Coeur, C.,
586 Gamelon, M., Macdonald, K. R., Moiron, M., ... Sæther, B.-E. (2022). Quantifying fixed individual
587 heterogeneity in demographic parameters: Performance of correlated random effects for Bernoulli
588 variables. *Methods in Ecology and Evolution*, 13(1), 91–104. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.13728)
589 [210X.13728](https://doi.org/10.1111/2041-210X.13728)

590 Frederiksen, M., Harris, M. P., Daunt, F., Rothery, P., & Wanless, S. (2004). Scale-dependent climate
591 signals drive breeding phenology of three seabird species. *Global Change Biology*, 10(7), 1214–1221.
592 <https://doi.org/10.1111/j.1529-8817.2003.00794.x>

593 Goodman, D. (1974). Natural Selection and a Cost Ceiling on Reproductive Effort. *The American*
594 *Naturalist*, 108(961), 247–268. <https://doi.org/10.1086/282906>

595 Grémillet, D., & Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing global
596 climate change: A review. *Marine Ecology Progress Series*, 391, 121–137.
597 <https://doi.org/10.3354/meps08212>

598 Grémillet, D., Péron, C., Kato, A., Amélineau, F., Ropert-Coudert, Y., Ryan, P. G., & Pichegru, L. (2016).
599 Starving seabirds: Unprofitable foraging and its fitness consequences in Cape gannets competing
600 with fisheries in the Benguela upwelling ecosystem. *Marine Biology*, 163(2), 35.
601 <https://doi.org/10.1007/s00227-015-2798-2>

602 Hamel, S., Gaillard, J.-M., Festa-Bianchet, M., & Côté, S. D. (2009). Individual quality, early-life
603 conditions, and reproductive success in contrasted populations of large herbivores. *Ecology*, 90(7),
604 1981–1995. <https://doi.org/10.1890/08-0596.1>

605 Hu, L., & Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure analysis:
606 Conventional criteria versus new alternatives. *Structural Equation Modeling: A Multidisciplinary*
607 *Journal*, 6(1), 1–55. <https://doi.org/10.1080/10705519909540118>

608 Jenouvrier, S., Barbraud, C., & Weimerskirch, H. (2005). Long-Term Contrasted Responses to Climate
609 of Two Antarctic Seabird Species. *Ecology*, 86(11), 2889–2903. <https://doi.org/10.1890/05-0514>

610 Jenouvrier, S., Péron, C., & Weimerskirch, H. (2015). Extreme climate events and individual
611 heterogeneity shape life-history traits and population dynamics. *Ecological Monographs*, 85(4), 605–
612 624. <https://doi.org/10.1890/14-1834.1>

613 Joly, N. B., Chiaradia, A., Georges, J.-Y., & Saraux, C. (2022). Environmental effects on foraging
614 performance in little penguins: A matter of phenology and short-term variability. *Marine Ecology*
615 *Progress Series*, 692, 151–168. <https://doi.org/10.3354/meps14058>

616 Keogan, K., Daunt, F., Wanless, S., Phillips, R. A., Walling, C. A., Agnew, P., Ainley, D. G., Anker-
617 Nilssen, T., Ballard, G., Barrett, R. T., Barton, K. J., Bech, C., Becker, P., Berglund, P.-A., Bollache, L.,
618 Bond, A. L., Bouwhuis, S., Bradley, R. W., Burr, Z. M., ... Lewis, S. (2018). Global phenological

619 insensitivity to shifting ocean temperatures among seabirds. *Nature Climate Change*, 8(4), 4.
620 <https://doi.org/10.1038/s41558-018-0115-z>

621 Kim, S.-Y., Velando, A., Torres, R., & Drummond, H. (2011). Effects of recruiting age on senescence,
622 lifespan and lifetime reproductive success in a long-lived seabird. *Oecologia*, 166(3), 615–626.
623 <https://doi.org/10.1007/s00442-011-1914-3>

624 Kline, R. B. (2015). *Principles and Practice of Structural Equation Modeling, Fourth Edition*. Guilford
625 Publications.

626 Krüger, O. (2005). Age at first breeding and fitness in goshawk *Accipiter gentilis*. *Journal of Animal*
627 *Ecology*, 74(2), 266–273. <https://doi.org/10.1111/j.1365-2656.2005.00920.x>

628 Lescroël, A., Ballard, G., Toniolo, V., Barton, K. J., Wilson, P. R., Lyver, P. O., & Ainley, D. G. (2010).
629 Working less to gain more: When breeding quality relates to foraging efficiency. *Ecology*, 91(7),
630 2044–2055. <https://doi.org/10.1890/09-0766.1>

631 Lescroël, A., Dugger, K. M., Ballard, G., & Ainley, D. G. (2009). Effects of individual quality,
632 reproductive success and environmental variability on survival of a long-lived seabird. *Journal of*
633 *Animal Ecology*, 78(4), 798–806. <https://doi.org/10.1111/j.1365-2656.2009.01542.x>

634 Leslie, P. H. (1945). On the Use of Matrices in Certain Population Mathematics. *Biometrika*, 33(3),
635 183–212. <https://doi.org/10.2307/2332297>

636 Liker, A., & Székely, T. (2005). MORTALITY COSTS OF SEXUAL SELECTION AND PARENTAL CARE IN
637 NATURAL POPULATIONS OF BIRDS. *Evolution*, 59(4), 890–897. <https://doi.org/10.1111/j.0014-3820.2005.tb01762.x>

639 Limmer, B., & Becker, P. H. (2009). Improvement in chick provisioning with parental experience in a
640 seabird. *Animal Behaviour*, 77(5), 1095–1101. <https://doi.org/10.1016/j.anbehav.2009.01.015>

641 Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology &*
642 *Evolution*, 14(9), 343–348. [https://doi.org/10.1016/S0169-5347\(99\)01639-0](https://doi.org/10.1016/S0169-5347(99)01639-0)

643 Maccoll, A. D. C., & Hatchwell, B. J. (2004). Determinants of lifetime fitness in a cooperative breeder,
644 the long-tailed tit *Aegithalos caudatus*. *Journal of Animal Ecology*, 73(6), 1137–1148.
645 <https://doi.org/10.1111/j.0021-8790.2004.00887.x>

646 McGraw, J. B., & Caswell, H. (1996). Estimation of Individual Fitness from Life-History Data. *The*
647 *American Naturalist*, 147(1), 47–64. <https://doi.org/10.1086/285839>

648 Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., Bruna, E. M.,
649 Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J.-M., Horvitz, C. C., Kalisz, S., Kendall, B.
650 E., Knight, T. M., Lee, C. T., & Menges, E. S. (2008). Longevity Can Buffer Plant and Animal Populations
651 Against Changing Climatic Variability. *Ecology*, 89(1), 19–25. <https://doi.org/10.1890/07-0774.1>

652 Patrick, S. C., & Weimerskirch, H. (2014). Personality, Foraging and Fitness Consequences in a Long
653 Lived Seabird. *PLoS ONE*, 9(2). <https://doi.org/10.1371/journal.pone.0087269>

654 Pelletier, L., Chiaradia, A., Kato, A., & Ropert-Coudert, Y. (2014). Fine-scale spatial age segregation in
655 the limited foraging area of an inshore seabird species, the little penguin. *Oecologia*, 176(2), 399–
656 408. <https://doi.org/10.1007/s00442-014-3018-3>

657 Ramírez, F., Chiaradia, A., O'Leary, D. A., & Reina, R. D. (2021). Making the most of the old age:
658 Autumn breeding as an extra reproductive investment in older seabirds. *Ecology and Evolution*,
659 *11*(10), 5393–5401. <https://doi.org/10.1002/ece3.7431>

660 Reed, T. E., Jenouvrier, S., & Visser, M. E. (2013). Phenological mismatch strongly affects individual
661 fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, *82*(1),
662 131–144. <https://doi.org/10.1111/j.1365-2656.2012.02020.x>

663 Reed, T. E., Warzybok, P., Wilson, A. J., Bradley, R. W., Wanless, S., & Sydeman, W. J. (2009a). Timing
664 is everything: Flexible phenology and shifting selection in a colonial seabird. *Journal of Animal*
665 *Ecology*, *78*(2), 376–387. <https://doi.org/10.1111/j.1365-2656.2008.01503.x>

666 Reed, T. E., Warzybok, P., Wilson, A. J., Bradley, R. W., Wanless, S., & Sydeman, W. J. (2009b). Timing
667 is everything: Flexible phenology and shifting selection in a colonial seabird. *Journal of Animal*
668 *Ecology*, *78*(2), 376–387. <https://doi.org/10.1111/j.1365-2656.2008.01503.x>

669 Reilly, P. N., & Cullen, J. M. (1979). The little penguin *Eudyptula minor* in Victoria. I: Mortality of
670 adults. *Emu*, *79*(3), 97–102. <https://doi.org/10.1071/mu9790097>

671 Reilly, P. N., & Cullen, J. M. (1981). The Little Penguin *Eudyptula minor* in Victoria, II: Breeding. *Emu*,
672 *81*(1), 1–19. <https://doi.org/10.1071/mu9810001>

673 Robinson, S., Chiaradia, A., & Hindell, M. A. (2005). The effect of body condition on the timing and
674 success of breeding in Little Penguins *Eudyptula minor*. *Ibis*, *147*(3), 483–489.
675 <https://doi.org/10.1111/j.1474-919x.2005.00431.x>

676 Roff, D. A., & Fairbairn, D. J. (2007). The evolution of trade-offs: Where are we? *Journal of*
677 *Evolutionary Biology*, *20*(2), 433–447. <https://doi.org/10.1111/j.1420-9101.2006.01255.x>

678 Ropert-Coudert, Y., Kato, A., Naito, Y., & Cannell, B. L. (2003). Individual Diving Strategies in the Little
679 Penguin. *Waterbirds*, *26*(4), 403. [https://doi.org/10.1675/1524-4695\(2003\)026\[0403:IDSITL\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2003)026[0403:IDSITL]2.0.CO;2)

680 Salton, M., Saraux, C., Dann, P., & Chiaradia, A. (2015). Carry-over body mass effect from winter to
681 breeding in a resident seabird, the little penguin. *Royal Society Open Science*, *2*(1), 140390.
682 <https://doi.org/10.1098/rsos.140390>

683 Saraux, C., & Chiaradia, A. (2021). Age-related breeding success in little penguins: A result of
684 selection and ontogenetic changes in foraging and phenology. *Ecological Monographs*.
685 <https://hal.archives-ouvertes.fr/hal-03322572>

686 Saraux, C., Chiaradia, A., Le Maho, Y., & Ropert-Coudert, Y. (2011). Everybody needs somebody:
687 Unequal parental effort in little penguins. *Behavioral Ecology*, *22*(4), 837–845.
688 <https://doi.org/10.1093/beheco/arr049>

689 Saraux, C., Chiaradia, A., Salton, M., Dann, P., & Viblanc, V. A. (2016). Negative effects of wind speed
690 on individual foraging performance and breeding success in little penguins. *Ecological Monographs*,
691 *86*(1), 61–77. <https://doi.org/10.1890/14-2124.1>

692 Saraux, C., Robinson-Laverick, S. M., Maho, Y. L., Ropert-Coudert, Y., & Chiaradia, A. (2011). Plasticity
693 in foraging strategies of inshore birds: How Little Penguins maintain body reserves while feeding
694 offspring. *Ecology*, *92*(10), 1909–1916. <https://doi.org/10.1890/11-0407.1>

695 Stearns, S. C. (1976). Life-History Tactics: A Review of the Ideas. *The Quarterly Review of Biology*,
696 *51*(1), 3–47. <https://doi.org/10.1086/409052>

697 Stearns, S. C. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology*, 3(3), 259.
698 <https://doi.org/10.2307/2389364>

699 Steiner, U. K., & Tuljapurkar, S. (2012). Neutral theory for life histories and individual variability in
700 fitness components. *Proceedings of the National Academy of Sciences*, 109(12), 4684–4689.
701 <https://doi.org/10.1073/pnas.1018096109>

702 Stephens, P. A., Boyd, I. L., McNamara, J. M., & Houston, A. I. (2009). Capital breeding and income
703 breeding: Their meaning, measurement, and worth. *Ecology*, 90(8), 2057–2067.
704 <https://doi.org/10.1890/08-1369.1>

705 Storey, A. E., Ryan, M. G., Fitzsimmons, M. G., Kouwenberg, A.-L., Takahashi, L. S., Robertson, G. J.,
706 Wilhelm, S. I., McKay, D. W., Herzberg, G. R., Mowbray, F. K., MacMillan, L., & Walsh, C. J. (2017).
707 Balancing personal maintenance with parental investment in a chick-rearing seabird: Physiological
708 indicators change with foraging conditions. *Conservation Physiology*, 5(1), cox055.
709 <https://doi.org/10.1093/conphys/cox055>

710 Sutherland, D. R., & Dann, P. (2012). Improving the accuracy of population size estimates for burrow-
711 nesting seabirds. *Ibis*, 154(3), 488–498. <https://doi.org/10.1111/j.1474-919X.2012.01234.x>

712 Vedder, O., & Bouwhuis, S. (2018). Heterogeneity in individual quality in birds: Overall patterns and
713 insights from a study on common terns. *Oikos*, 127(5), 719–727. <https://doi.org/10.1111/oik.04273>

714 Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's
715 Principle. *The American Naturalist*, 100(916), 687–690. JSTOR.

716 Wilson, A. J., & Nussey, D. H. (2010). What is individual quality? An evolutionary perspective. *Trends*
717 *in Ecology & Evolution*, 25(4), 207–214. <https://doi.org/10.1016/j.tree.2009.10.002>

718 Winkler, D. W. (1987). A General Model for Parental Care. *The American Naturalist*, 130(4), 526–543.
719 <https://doi.org/10.1086/284729>

720 Wold, H. (1980). Model Construction and Evaluation When Theoretical Knowledge Is Scarce: Theory
721 and Application of Partial Least Squares. In J. Kmenta & J. B. Ramsey (Eds.), *Evaluation of Econometric*
722 *Models* (pp. 47–74). Academic Press. <https://doi.org/10.1016/B978-0-12-416550-2.50007-8>

723 Wright, S. (1934). The Method of Path Coefficients. *The Annals of Mathematical Statistics*, 5(3), 161–
724 215.

725 Youngflesh, C., Jenouvrier, S., Hinke, J. T., DuBois, L., St. Leger, J., Trivelpiece, W. Z., Trivelpiece, S. G.,
726 & Lynch, H. J. (2018). Rethinking “normal”: The role of stochasticity in the phenology of a
727 synchronously breeding seabird. *Journal of Animal Ecology*, 87(3), 682–690.
728 <https://doi.org/10.1111/1365-2656.12790>

729 Zammuto, R. M. (1986). Life histories of birds: Clutch size, longevity, and body mass among North
730 American game birds. *Canadian Journal of Zoology*, 64(12), 2739–2749. <https://doi.org/10.1139/z86-398>

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732

733 **FIGURE CAPTIONS:**

734

735 **Figure 1:** Theoretical path modelling including main expected relations among foraging
736 (blue), chick investment (grey), breeding behaviour and longevity (yellow), phenology
737 (purple), mating behaviour (green) and sex (red) as well as their effect on breeding success
738 and fitness. Relationships expected to be negative are presented with red arrows while
739 positive ones are presented with green arrows. For clarity purposes, instead of displaying all
740 arrows, arrows pointing from/to a block composed of several variables were pooled into a
741 single one representing the whole block.

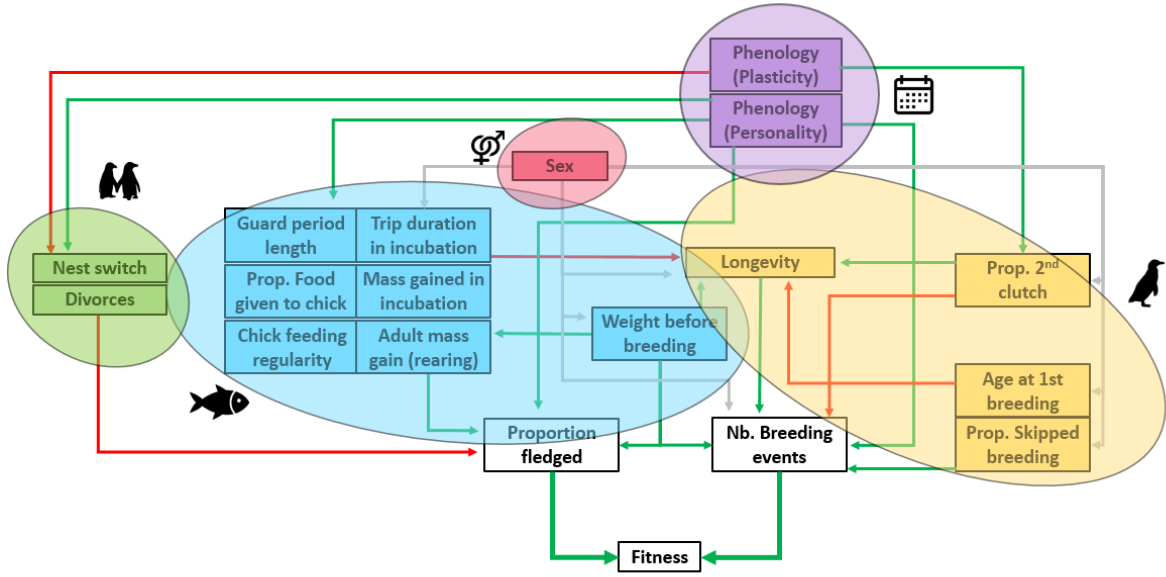
742 **Figure 2:** Individual fitness histogram for all 162 mature little penguins known for their entire
743 life.

744 **Figure 3:** Histograms of life-history traits associated to survival, breeding and mating
745 behaviour and phenology (skipped breeding, 2nd clutches, age at 1st breeding, partner/nest
746 switch and personality and plasticity in phenology) and longevity of 162 mature little
747 penguins known for their entire life depending on their sex when applicable (males are
748 represented by blue bars and females by red ones). Because all traits could not always been
749 estimated, the sample size varies for each histogram.

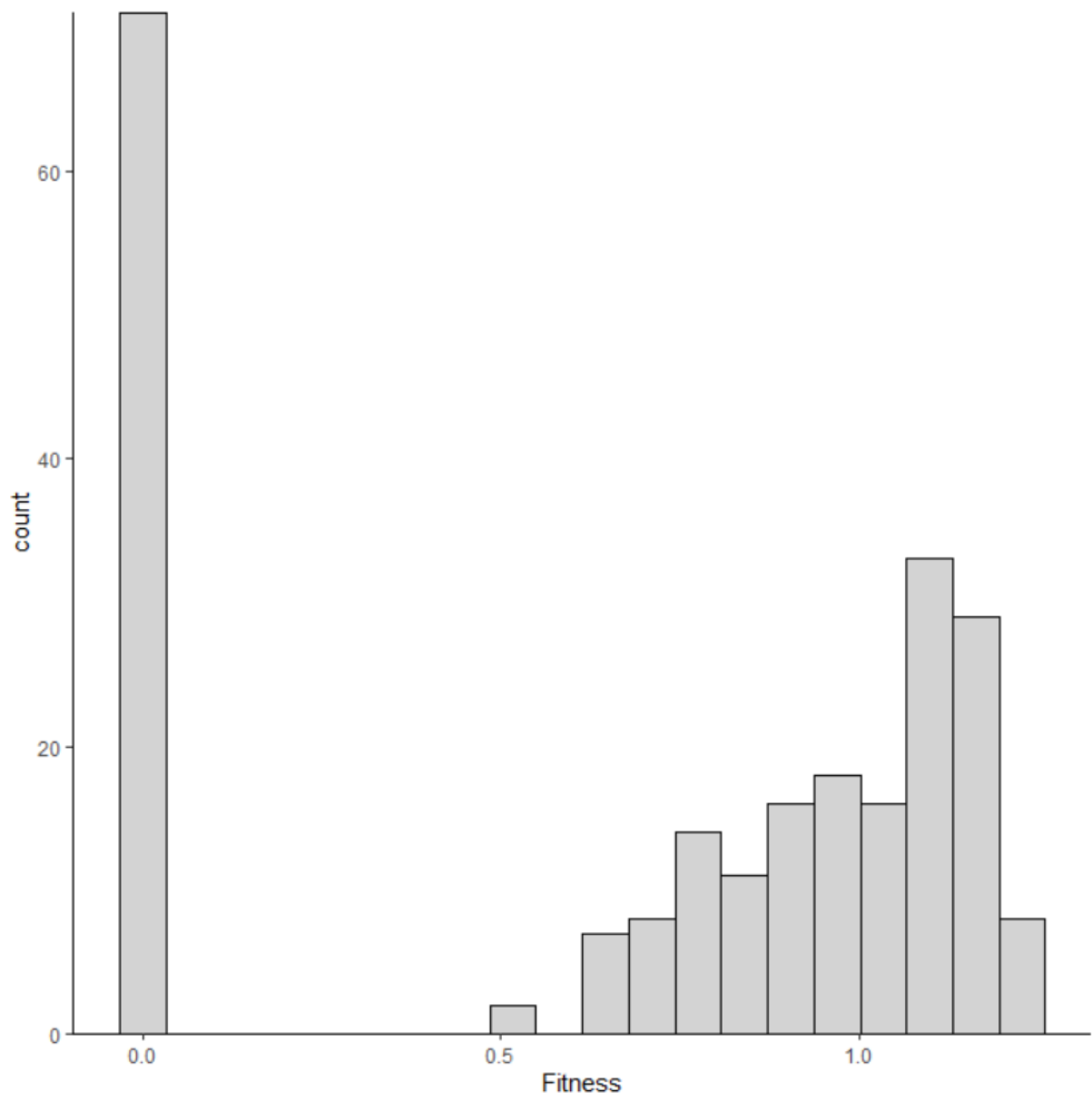
750 **Figure 4:** Path modelling of the relation between fitness and 18 different life-history traits
751 (light grey nodes). Numbers correspond to relative estimates of partial least square path
752 model. Arrows and numbers colours indicate the positive/negative (blue/orange) sign of the
753 relation when it was considered significant (bootstrap IC95% (n = 10000) does not include 0).
754 Grey arrows and numbers correspond to non-significant relations.

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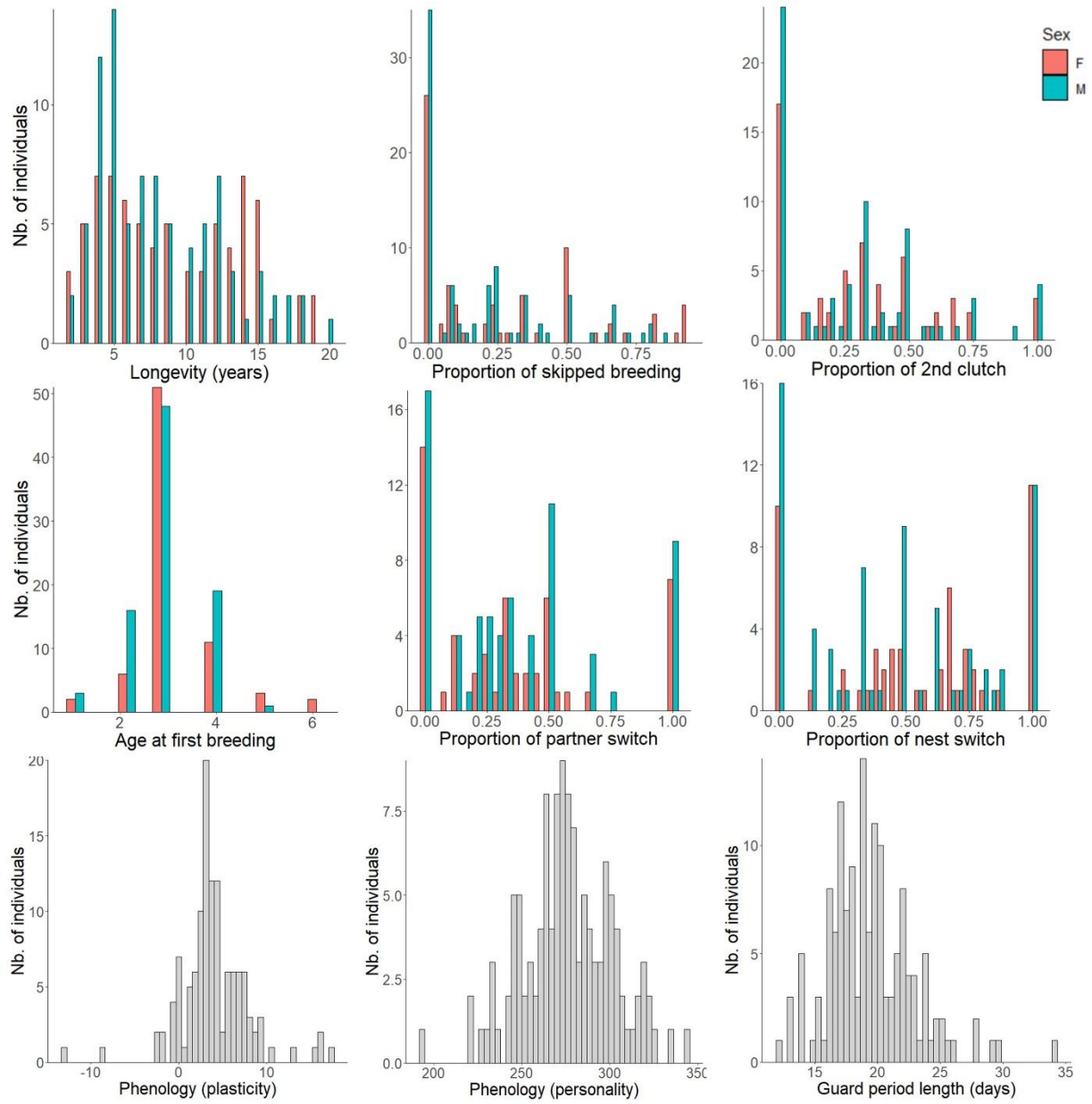
756 **Figure 1**



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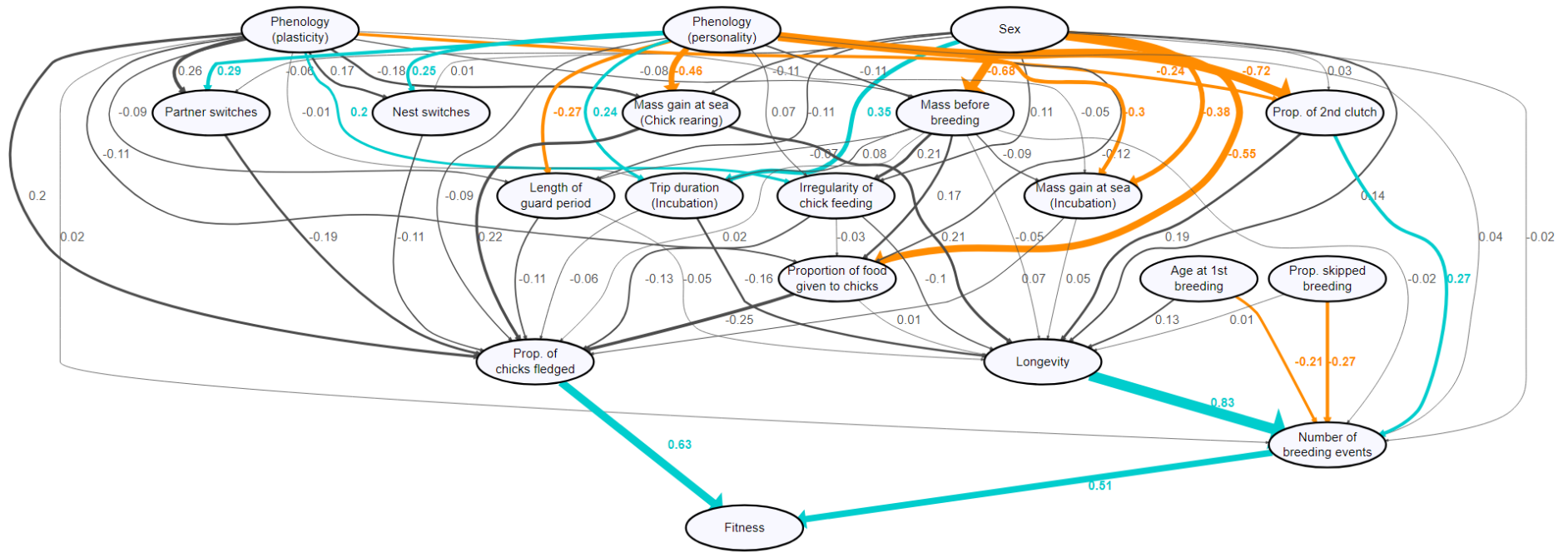


758
759 **Figure 2**



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761 **Figure 3**



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763

764 **Figure 4**

765 **TABLES:**

766 **Table 1:** Total effect (sum of direct and indirect) of 18 different life-history traits on fitness either using raw data or transformed data to remove
 767 stochastic year effect. "Tot. rel." stands for the total relative estimates of partial least square path model. 95% Confidence Interval bootstrap (n =
 768 10,000) are given. Significant relationships (i.e. CI95% not intersecting 0) are indicated by stars.

<i>Affects fitness</i>	<i>Raw data</i>			<i>Data without year effect</i>		
	<i>Tot. Rel</i>	<i>CI95%</i>		<i>Tot. Rel</i>	<i>CI95%</i>	
<i>Sex</i>	0.10	-0.05	0.24	0.08	-0.08	0.23
<i>Age at 1st breeding</i>	-0.05	-0.16	0.04	0.06	-0.04	0.17
<i>Prop. Skipped breeding</i>	-0.13	-0.25	-0.05 *	0.22	0.11	0.38 *
<i>Phenology (plasticity)</i>	0.01	-0.14	0.15	0.05	-0.11	0.21
<i>Phenology (personality)</i>	-0.35	-0.48	-0.22 *	-0.19	-0.36	-0.04 *
<i>Mass before breeding</i>	-0.08	-0.31	0.17	-0.16	-0.35	0.05
<i>Guard period length</i>	-0.09	-0.27	0.09	-0.08	-0.23	0.08
<i>Prop. Partner switch</i>	-0.12	-0.31	0.05	0.15	-0.01	0.34 .
<i>Prop. Nest switch</i>	-0.07	-0.21	0.07	0.02	-0.12	0.16
<i>Irregularity of chick feeding</i>	-0.12	-0.31	0.11	-0.16	-0.36	0.06
<i>Prop. Food given to chicks</i>	-0.15	-0.44	0.08	0.00	-0.28	0.20
<i>Mass gained in incubation</i>	0.07	-0.12	0.30	-0.04	-0.21	0.16
<i>Trip duration in incubation</i>	-0.11	-0.26	0.06	-0.06	-0.21	0.11
<i>Mass gained chick rearing</i>	0.23	0.03	0.41 *	0.23	0.06	0.40 *
<i>Prop. 2nd clutch</i>	0.22	0.11	0.37 *	0.15	0.05	0.29 *
<i>Longevity</i>	0.42	0.32	0.56 *	0.36	0.26	0.50 *
<i>Prop. Chicks fledged</i>	0.63	0.50	0.72 *	0.62	0.50	0.72 *
<i>Nb. Breeding events</i>	0.51	0.37	0.70 *	0.47	0.33	0.66 *