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# Unpacking the lifelong secrets of little penguins: individual quality, energy allocation, and stochasticity in defining fitness

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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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6

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12

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14

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31

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 1<sup>st</sup> 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 2<sup>nd</sup> 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 (1<sup>st</sup> 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:

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

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 1<sup>st</sup> 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 ( $5.4 \pm 3.9$  SD years), resulting in a 0 fitness. However,  
293 135 individuals (83%) produced at least one chick during their life ( $9.3 \pm 4.3$  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 ( $1.27 \pm 0.11$  on average), i.e., they fledged more than two chicks ( $10.1 \pm 5.5$  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 ( $8.6 \pm 4.5$  years). Around 38% of individuals never  
303 attempted to lay a 2<sup>nd</sup> clutch, and 37% never skipped any breeding seasons during their lives.  
304 Conversely, 14% of individuals missed breeding seasons and 34% produced a 2<sup>nd</sup> clutch more  
305 than half of the time.

306 Age at 1<sup>st</sup> 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 ( $19.5 \pm 3.5$  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  $282 \pm 23$  (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 ( $3.1 \pm 3.9$ ) 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 2<sup>nd</sup> clutches (rel. est. = 0.27 [0.20; 0.34],  $p < 0.001$ ), while it was  
331 negatively affected by older age at 1<sup>st</sup> 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, 2<sup>nd</sup> clutches, 1<sup>st</sup> 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 2<sup>nd</sup> 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 2<sup>nd</sup> 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 2<sup>nd</sup> 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 2<sup>nd</sup> 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 2<sup>nd</sup> 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 2<sup>nd</sup> 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 2<sup>nd</sup> 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 1<sup>st</sup> 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 1<sup>st</sup> 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 1<sup>st</sup>  
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 2<sup>nd</sup> 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.

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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.

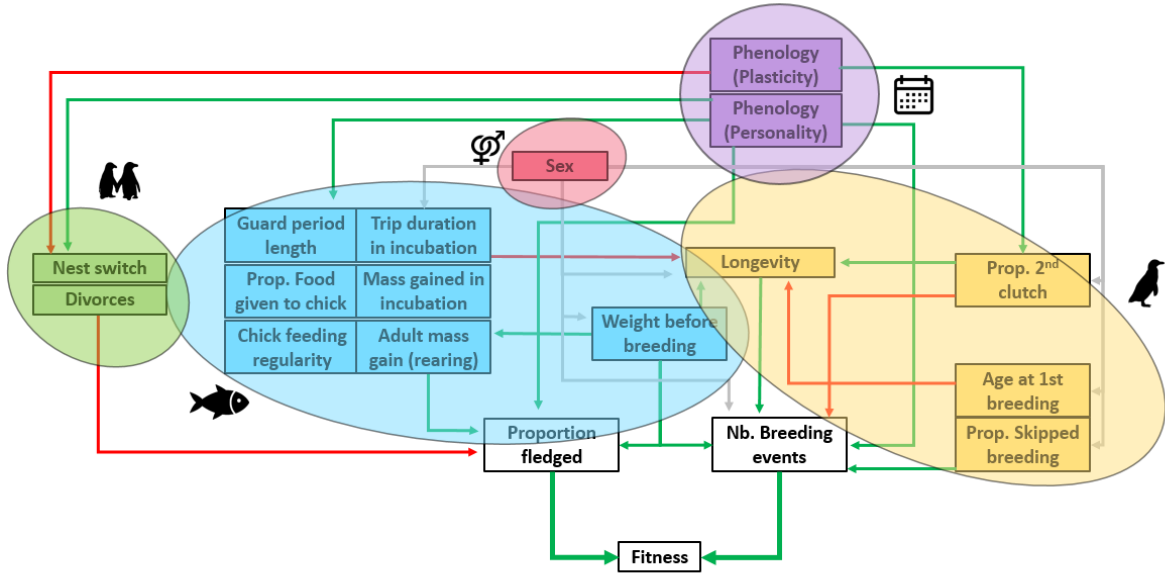
742 **Figure 2:** Individual fitness histogram for all 162 mature little penguins known for their entire  
743 life.

744 **Figure 3:** Histograms of life-history traits associated to survival, breeding and mating  
745 behaviour and phenology (skipped breeding, 2<sup>nd</sup> clutches, age at 1<sup>st</sup> 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.

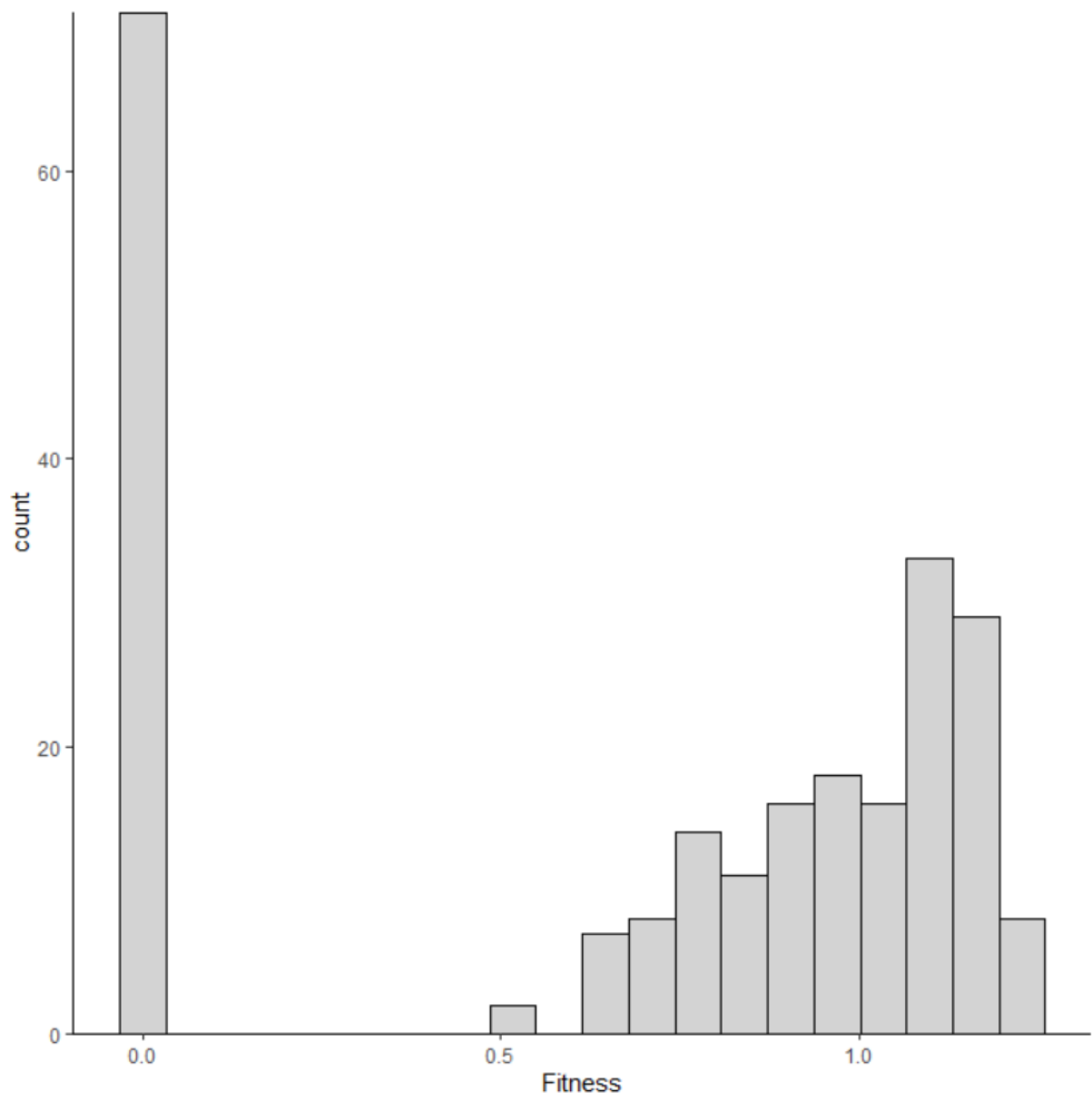
750 **Figure 4:** Path modelling of the relation between fitness and 18 different life-history traits  
751 (light grey nodes). Numbers correspond to relative estimates of partial least square path  
752 model. Arrows and numbers colours indicate the positive/negative (blue/orange) sign of the  
753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

755

756 **Figure 1**

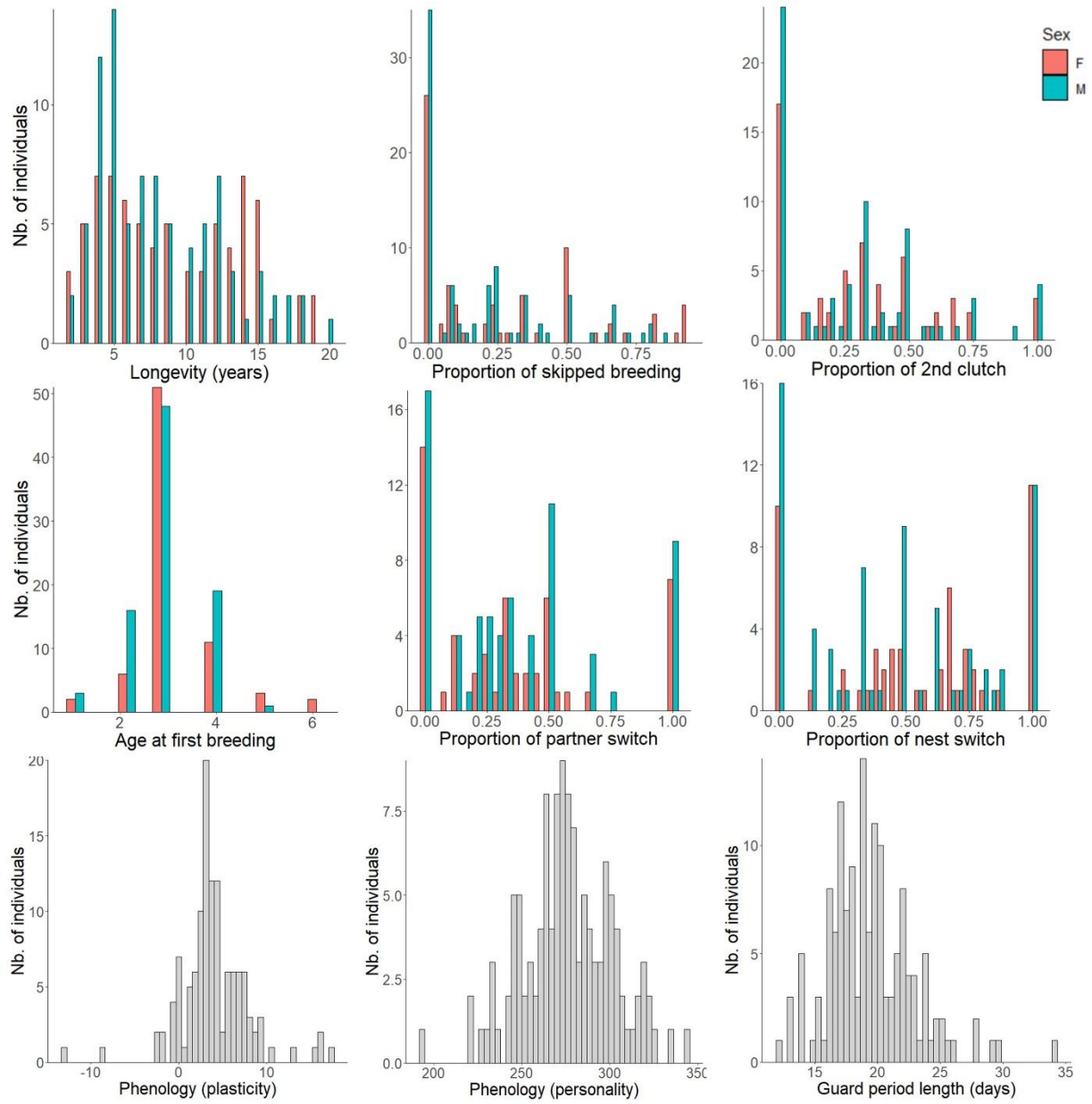


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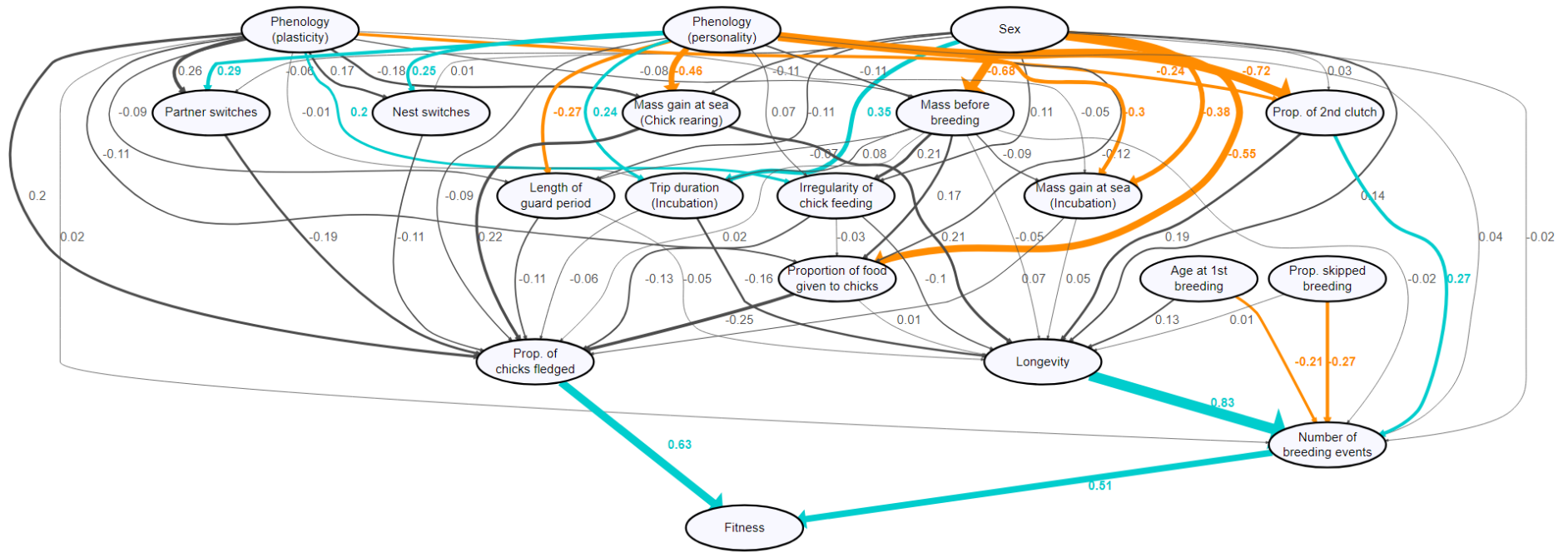
758  
759 **Figure 2**





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761 **Figure 3**



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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.

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<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 *

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