Evidence for high inter-generational individual quality in yellow-eyed penguins

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Longitudinal studies focusing on lifetime reproductive success (LRS) have been used to measure individual breeding performance and identify commonalities among successful breeders. By extending the focus to subsequent generations we identify a proportion of high-quality individuals that contribute disproportionately to the population over multiple generations. We used 23 years of yellow-eyed penguin (*Megadyptes antipodes*) breeding data from one breeding area to identify the proportion of individual birds that raised successful breeders, which in turn raised offspring. We explored which life-history components influenced lifetime reproductive success, as this knowledge would enable conservation resources to be focused on high-performing individuals in this endangered population. From 2147 birds marked as chicks, 370 (17.2%) survived to adulthood and recruited to their natal location, of which 219 (10.2%) fledged offspring: 124 (56.6%) of the 219 birds produced offspring that recruited as breeders. Only 102 birds (4.8% of 2147) fledged first-generation offspring that in turn fledged offspring (second-generation offspring, or grand-offspring). We found that c. 25% of the birds that survived to breed had above-average LRS as well as above-average numbers of grand-offspring, and were more likely to have produced first-generation chicks that recruited and also produced above-average numbers of second-generation chicks. Our findings suggest that there is a core of "super-breeders" that contribute disproportionately to the population over successive generations. Lifespan and age-at-first-breeding were correlated with LRS. We suggest that traits of birds relating to longevity, health (e.g. immunocompetence) and fitness could be examined to identify potential links with high LRS and inter-generational fecundity. "Super-breeders" appear to consistently achieve high LRS and long lifespans in a stochastic environment, demonstrating greater resilience in the face of extreme events.

1   **Evidence for high inter-generational individual quality in yellow-eyed**

2   **penguins**

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9   **ABSTRACT**

10   Longitudinal studies focusing on lifetime reproductive success (LRS) have been used to measure

11   individual breeding performance and identify commonalities among successful breeders. By

12   extending the focus to subsequent generations we identify a proportion of high-quality

13   individuals that contribute disproportionately to the population over multiple generations. We

14   used 23 years of yellow-eyed penguin (*Megadyptes antipodes*) breeding data from one breeding

15   area to identify the proportion of individual birds that raised successful breeders, which in turn

16   raised offspring. We explored which life-history components influenced lifetime reproductive

17   success, as this knowledge would enable conservation resources to be focused on high-

18   performing individuals in this endangered population. From 2147 birds marked as chicks, 370

19   (17.2%) survived to adulthood and recruited to their natal location, of which 219 (10.2%)

20   fledged offspring: 124 (56.6%) of the 219 birds produced offspring that recruited as breeders.

21   Only 102 birds (4.8% of 2147) fledged first-generation offspring that in turn fledged offspring

22   (second-generation offspring, or grand-offspring). We found that c. 25% of the birds that

23   survived to breed had above-average LRS as well as above-average numbers of grand-offspring,

24   and were more likely to have produced first-generation chicks that recruited and also produced

25   above-average numbers of second-generation chicks. Our findings suggest that there is a core of

26   "super-breeders" that contribute disproportionately to the population over successive

27   generations. Lifespan and age-at-first-breeding were correlated with LRS. We suggest that traits

28   of birds relating to longevity, health (e.g. immunocompetence) and fitness could be examined to

29   identify potential links with high LRS and inter-generational fecundity. "Super-breeders" appear

30   to consistently achieve high LRS and long lifespans in a stochastic environment, demonstrating

31   greater resilience in the face of extreme events.

34 **INTRODUCTION**

35 Unlike cross-sectional studies across one or two breeding seasons, longitudinal studies based on

36 lifetime reproductive success (LRS) average out occasional breeding failures, and increase the

37 accuracy of measurement of individual success (Krüger & Lindström, 2001). The collection of

38 long-term life-history data from a population of marked individuals makes it possible to identify

39 the proportion of animals that produce recruits, enabling conservation efforts to be efficiently

40 focused on individuals with successful traits (Moreno, 2003). Moreover, the overall contribution

41 of individuals with different lifespans or reproductive strategies to subsequent generations can be

42 compared (Clutton-Brock, 1988; Newton, 1989; Wooller, Bradley & Croxall, 1992; Brommer,

43 Pietiäinen & Kolunen 1998).

44   Studies of LRS have revealed commonalities across bird species: a significant proportion

45 of fledglings from a given population will die before sexual maturity (Bryant, 1979; Newton,

46 1989); not all individuals that attempt to breed will be successful; and successful individuals vary

47 in their productivity (Newton, 1989). The LRS distribution of a population is typically highly

48 skewed, with large numbers of individuals producing small numbers of young, and only a small

49 proportion of adults producing large numbers of young (Clutton-Brock, 1988, Newton, 1989).

50 Specific life-history and reproductive traits can be indicative of LRS. Lifespan is the strongest

51 correlate, with longer-lived individuals commonly achieving a higher LRS (Gustafsson, 1986;

52 Clutton-Brock, 1988; Newton, 1989). In seabirds, where individuals can start breeding at various

53 ages, variance in LRS is largely related to variation in breeding lifespan (Moreno, 2003), because

54 an increased number of breeding seasons allows individuals more opportunities to successfully

55 fledge offspring.

56   If only a small proportion of individuals maintain most of the population, the

57   identification of traits affecting lifetime reproductive success of an individual are relevant for

58   conservation efforts. Resources can be diverted towards protecting particularly productive

59   individuals at times when the population is assailed by environmental challenges such as adverse

60   climate conditions, reduced food availability, disease outbreaks, or catastrophic events (e.g. oil

61   spills, Gartrell et al., 2013). In the case of a pest species, culling efforts could be focused on

62   these highly productive individuals (Moreno, 2003).

63   Factors known to affect reproductive performance in seabirds and which can interact with

64   each other include age, experience, pair bond duration, health condition, sex, number of mates,

65   mate fidelity and site fidelity (Ryder ,1980; Clutton-Brock, 1988; Gavin & Bollinger, 1988;

66   Bradley et al., 1990; Wooller et al., 1990; Chastel, Weimerskirch & Jouventin, 1995). For

67   example, in long-lived seabird species, a period of poor reproductive success at a young age or at

68   a lower level of experience may be superseded by a period at which the individual performs at

69   their peak reproductive output (Forslund & Pärt, 1995). At an older age, senescence may begin to

70   reduce reproductive output, followed by terminal illness and death (Fowler, 1995; Nisbet &

71   Dann, 2009; Froy et al., 2013). With increasing age, maternal efficiency might allow for control

72   of the timing, size, volume, composition and pore density of eggs, and high levels of pair

73   synchrony through maintenance of long-term pair bonds may reduce incubation periods and

74   increase nesting success (Massaro et al., 2002; Massaro et al., 2004). Breeding skills may

75   therefore improve with both age and experience, as well as with improved synchrony between

76   mated pairs (Forslund & Pärt, 1995). The relative importance of each of these factors in

77   estimating LRS is difficult to assess, and can differ dramatically between species and geographic

78   locations.

79   Breeder quality might not necessarily be age related. Some birds might just be better than

80   others because they have better skills. State-based assessment of individual breeder quality often

81   requires the assumption or prediction that a component of the individual's health or skill within

82   that system is a driving factor determining its reproductive success (Wendeln & Becker, 1999;

83   Moreno, 2003), and that this superior skill is independent of age-related performance. These

84   state-based qualities and their relationship with breeding success and LRS can be highly variable

85   within a population of seabirds, but might have low variation for individual birds over time (e.g.

86   common terns *Sterna hirundo*, Wendeln & Becker, 1999). Breeding seabirds have a range of

87   responses to catastrophic climatic or weather events, e.g. El Niño Southern Oscillation (ENSO)

88   (Boersma, 1978), and vary in the rate at which food is delivered to chicks (Ens et al., 1992).

89   Territoriality also can be associated with: individual quality in relation to nesting density (Stokes

90   & Boersma, 2000); nest site characteristics (Stokes & Boersma, 1998); and rank dominance

91   (Schubert et al., 2007).

92   LRS measures the number of offspring produced over a lifetime, however it does not

93   consider the viability of those offspring. There may be variability in the quality of offspring

94   produced by different individuals that further reduces the proportion of individuals contributing

95   to subsequent generations. By using a 23-year dataset of individually-tracked yellow-eyed

96   penguins we were able to follow reproductive success over more than one generation and

97   identify the proportion of a penguin population that produces grand-offspring. Yellow-eyed

98   penguins (hōiho, *Megadyptes antipodes*) are endemic to New Zealand and listed as 'endangered'

99   on the IUCN Red List (Birdlife International, 2015). Some mainland populations are intensively

100   managed to mitigate threats posed by introduced predators, disturbance and habitat destruction

101   (McKinlay, 2001). Because yellow-eyed penguins are sedentary (Seddon, van Heezik &

102 Ellenberg, 2013), long-lived, have high natal philopatry, high breeding site fidelity once

103 breeding, and are monogamous (Richdale, 1957), they are an ideal species to study LRS. We

104 investigated: (1) the proportion of birds that survive to adulthood; (2) the proportion of adults

105 that breed; (3) the proportion of breeders that produce young that recruit to the breeding

106 population (first-generation); and (4) the proportion of adults producing grand-offspring (second-

107 generation). We also explored the characteristics of highly successful breeders, and the

108 relationship of this trait between generations. We predicted that in line with other seabird

109 species, only a small proportion of yellow-eyed penguins would survive to adulthood, breed, and

110 produce young, and that differences in LRS between males and females exist due to the

111 difference in age-at-first-breeding, with females known to begin breeding earlier than males

112 (Richdale, 1957; Darby & Seddon, 1990). We predicted that lifespan would have the greatest

113 influence on the number of offspring produced, and be positively correlated with LRS. Yellow-

114 eyed penguins with earlier age-at-first-breeding and fewer overall mates were predicted to have

115 greater LRS.

116 **METHODS**

117 Yellow-eyed penguins are solitary breeders, in contrast with most other penguin species and

118 seabirds that breed colonially (Richdale, 1957; Darby & Seddon, 1990). In September-October

119 clutches of up to two eggs are laid, and chicks fledge at c. 106 days from late January to late

120 February (Richdale, 1957; Seddon & Davis, 1989; Darby & Seddon, 1990).

121 **Yellow-eyed Penguin Database**

122 We obtained breeding data from the Yellow-eyed Penguin Database administered by the New

123 Zealand Department of Conservation (DOC) and accessed through a Memorandum of

124 Understanding between DOC, representing the contributors to the database, and the University of

125   Otago. We analysed only data from yellow-eyed penguins breeding at the Boulder Beach

126   complex on the Otago Peninsula, New Zealand, (45°500 S and 170°300 E; Fig. 1) because it

127   supports a relatively large population of yellow-eyed penguins, has an inter-decadal history of

128   intensive monitoring and it has been trapped for introduced predators over time. This site has the

129   longest history of chick marking, with the majority of chicks fledged at this site marked with a

130   stainless steel flipper band issued by the New Zealand National Bird Banding Scheme (NZBBS).

131   We acknowledge that the use of flipper bands might present bias (*sensu* Petersen et al., 2005),

132   however in contrast to the foraging ranges of penguin species for which negative impacts of

133   flipper bands have been identified, yellow-eyed penguins are inshore foragers and have much

134   shorter foraging trips (van Heezik & Seddon, 1990; Mattern et al., 2007). Consequently impacts

135   of flipper bands are likely to be minimal. While negative impacts have been documented for

136   some penguin species (e.g. king penguins, *Aptenodytes patagonicus*, Gauthier-Clerc et al.

137   (2004); Adélie penguins, *Pygoscelis adeliae*, Dugger et al. 2006; little penguins, *Eudyptula*

138   *mino*r, Hoskins et al. 2008), impacts have been negligible for others (e.g. African penguins,

139   *Spheniscus demersus*, Barham et al. 2008; Hampton et al. 2009; magellanic penguins, *S.*

140   *magellanicus*, Boersma and Rebstock 2009). A separate study analysing the impact of research

141   manipulations found that even a double banding study on yellow-eyed penguins in one season

142   had no effect on productivity or subsequent survival (Seddon, van Heezik & Ellenberg, 2013).

143   Before commencing this study, we completed a comprehensive error check, which involved

144   checking the original notebook records against electronic database records to ensure a high level

145   of accuracy and consistency.

146   **Data for survival to adulthood and breeding**

147   A total of 2147 birds were marked at Boulder Beach as chicks or juveniles between 1981 and

148   2003. We used this sample to calculate the proportion of birds that survived post-fledging, to

149   adulthood (defined as reaching two years of age, when sexually mature), the proportion that

150   recruited to Boulder Beach and attempted to breed, fledged offspring, fledged offspring that

151   survived to adulthood and recruited to the breeding population, and fledged offspring (first-

152   generation) that in turn successfully bred and produced offspring (second-generation, or grand-

153   chicks). Birds from cohorts 1981-2003 that were still alive or had been sighted after 2007 were

154   excluded from the sample as their breeding lifetime had not ended (n = 73 birds).

155   **Data for LRS analyses**

156   For the detailed analysis of life-history and lifetime reproductive success we used a subset of the

157   data which included information on 130 "founding generation" birds of known sex that survived

158   to breed at least once, from the 1981 to 2003 cohorts, as we considered sex to be an important

159   factor, but sexing information was not always available. We excluded birds whose parents were

160   included in the data subset to avoid pseudoreplication (n = 87 birds). We chose the year 2003 as

161   the cut-off cohort, since mean age at first breeding is between three and four years (Richdale,

162   1957): this allowed for birds to have complete lifespans by age 4 in 2007, breed, have offspring

163   that survived to breed (up to 2011) and grand offspring that survived up until the 2014/15

164   breeding season, when these data were last updated. We did not include birds beyond the 2003

165   cohort, or birds that were alive after 2007, so that we were sure that all of their surviving

166   offspring had recruited to breed by 2014.. The latest year a bird with a complete life history

167   could be recorded as breeding at least once, and be presumed dead was 2007 (i.e. birds from the

168   2003 cohort would have had a complete lifespan of 4 years to meet the study's parameters). We

169   excluded birds if they were marked before the 1981 cohort when intensive monitoring began.

170   We defined LRS as the number of offspring produced by an individual over their lifetime.

171   Only data recorded from birds marked as chicks or as juveniles (one-year olds) could be used to

172   ensure complete life-histories, as they were of known age due to plumage differences (duller

173   colouration and lack of the distinctive yellow eye and crown of the adults). Yellow-eyed

174   penguins are typically marked at *c.* 80 - 90 days, before fledging at *c.* 106 days (Seddon et al.,

175   2013). If a bird was marked as a juvenile, we estimated the cohort year by subtracting one year.

176   A bird was considered to have attempted to breed if it or its mate laid an egg.

177   Analysis of LRS requires complete detectability of the focal population: this would be

178   compromised if individuals bred elsewhere, or skipped breeding years and were consequently

179   recorded as having died. We are confident that we have full records of birds due to the intensive

180   monitoring at the study site and annual monitoring at adjacent sites along the coast, and the high

181   level of natal (*c.* 81%) and breeding philopatry (*c.* 98%), and monogamy exhibited by this

182   species (Richdale, 1957; Ratz et al., 2004). Birds that skip breeding remain largely undetectable

183   during the breeding season, with only *c.* 8% of skipped birds in our sample being resighted as a

184   non-breeder, however detection of breeders is close to 100% (Hegg et al., 2012). In our sample,

185   53 yellow-eyed penguins that survived to breed skipped at least one breeding season once they

186   had established breeding, which is not uncommon, particularly in the year following a poor

187   season, death of a mate or a divorce (Moore, 1994; Ratz et al., 2004; Setiawan et al., 2005). Due

188   to the small, discrete size of nesting areas, the intensity of monitoring at this and in surrounding

189   sites, and the high degree of breeding site fidelity, we assumed that if a bird or breeding pair

190   were not seen during multiple visits to the breeding area and to other surrounding areas from

191   early incubation to the end of the guard period they were undertaking a breeding skip. None of

192   the birds we assumed to be undertaking a breeding skip were re-sighted at adjacent monitored

193   breeding areas during their skipped year.

194   **Sample parameters**

195   The sample parameters for modelling life-history included sex, total number of breeding

196   attempts, recruitment of first-generation offspring, recruitment of successful first-generation

197   offspring, age-at-first-breeding, breeding lifespan, total number of mates and lifespan. We did

198   not include 'Cohort' as a factor because the longer-lived birds in later cohorts had not completed

199   their breeding lifetimes, unlike shorter-lived birds. Therefore including cohort would give a false

200   impression that the super breeder phenomenon ceased at 1994. To ensure that cohort was not an

201   important variable we ran a modified model on a subset of the total data set - the birds from

202   cohorts 1981 – 1994, which included both short-lived and long-lived birds for which we had full

203   LRS (n = 161), and found no strong effects (Suppl. Material S2, T2).

204   Birds were sexed by adult head and foot measurements according to Setiawan, Darby &

205   Lambert (2004). In instances where birds had never been measured or when fledgling

206   measurements were analysed, we inferred the sex from mates where possible, on the assumption

207   that pairings were between males and females only and that the mate had been correctly

208   identified. If there were no measurements or sex recorded for mates, we removed these birds

209   from any lifetime data analysis. We limited our sample for the analysis of life-history traits

210   affecting LRS to birds that survived to breed from the original sample of 2147 birds, that we

211   were able to sex, and we excluded their offspring ("founding generation", females n =62, and

212   males n = 68), so as not to pseudoreplicate breeding pairs, or parents and their offspring.

213   We measured lifespan in whole years at the time of marking as chicks (*c.* 3 months old),

214   to the time of either being found dead or 'missing' after three consecutive years. Age-at-first-

215   breeding was recorded as the age of the bird during its first recorded breeding attempt. We

216   calculated the number of mates as the minimum possible number of mates, due to 60 of 130 birds

217   in the sample having unidentified mates in some years. We assumed that if a bird's mate was not

218   recorded but it was breeding with a particular bird in the previous and subsequent years that it

219   was the same mate in all three seasons.

220   **Statistical analysis**

221   We carried out all statistical analyses using R (Version 3.3.1, R Core Team 2016). We used two-

222   sample Wilcoxon rank-sum tests to test for statistical significance between males and females,

223   for parameters including LRS, age-at-first-breeding, recruitment of first-generation offspring,

224   recruitment of successful first-generation offspring, lifespan, total number of mates, total number

225   of breeding attempts and breeding lifespan (see Supplementary Material S1).

226   The relationships between recruitment of first-generation breeders, successful first-generation

227   breeders, sex, and the effect of life-history traits (age-at-first-breeding, lifespan, total number of

228   mates, total number of breeding attempts, breeding lifespan) on LRS were analysed using a

229   generalised linear mixed models (GLMM) with a Poisson distribution and a random factor, mate

230   code, to account for pseudoreplication associated with mated pairs being included in the analysis,

231   using the *lme4* package (Bates et al., 2015). Fit of the maximal model was assessed using

232   R^2GLMM from the AICcmodavg package (Mazerolle 2016). We included only uncorrelated

233   variables within the same model ($r < 0.6$; Hosmer & Lemeshow 2005) to avoid multi-

234   collinearity. We used an information-theoretic approach to model selection, by constructing a

235   maximal model containing all probable input variables (based on *a priori* reasoning), and then

236   ranking this model against all of its derivatives using QAICc. To account for model selection

237   uncertainty, model-averaging was conducted for the best models (2ΔQAICc, see Supplementary

238   Material S3), using the *MuMIn* and *AICcmodavg* packages in R (Bartoń, 2016; Mazerolle, 2016).

239   In order to compare specifically the life-history characteristics (age-at-first-breeding,

240   lifespan, total number of mates, total number of breeding attempts, breeding lifespan) between

241   birds which proved over the two generations to be highly successful breeders ("high quality"),

242   and the remainder of the birds ("ordinary"), we defined the highly successful individuals as

243   follows: those birds with above-average LRS relative to their sex (females ≥ 7, males ≥ 6) and

244   those that had an above-average number of grand-offspring (second-generation chicks; females $\geq$

245   10, males ≥ 6). Using the same GLMM approach, we analysed the effect of life-history

246   parameters on the LRS of these two groups of birds to determine differences in breeder quality.

247

248   **RESULTS**

249   Of the total sample of 2147 birds marked as chicks or juveniles from 1981 to 2003, 1546

250   (72.0%) were thought to have died before reaching adulthood, whereas 441 birds survived to be

251   seen at least once as an adult: 71 of these birds were sighted away from Boulder Beach at other

252   monitoring locations where they subsequently bred. Of the 370 birds that were re-sighted at

253   Boulder Beach as an adult at least once (17.2%), 264 attempted to breed at least once (12.3%),

254   and 219 bred successfully at least once (10.2%). Only 124 birds produced at least one first-

255   generation chick that recruited to the breeding population and attempted to breed at least once

256   (5.8%), and 102 had first-generation offspring that not only recruited but bred successfully at

257   least once (4.8%). Overall figures are presented in Table 1.

258   **LRS of male and female yellow-eyed penguins**

259   There was high individual variance in LRS calculated for both males and females (n = 130), with

260   this variance being higher for females (Table 2; Figure 2). The maximum number of total

261   offspring a female yellow-eyed penguin produced was 24, compared to 23 for males. The only

262   significant differences between males and females were for recruitment of breeders (W = 2554,

263   p-value = 0.03212) and recruitment of successful breeders (W = 2615, p-value = 0.01198). There

264   was no difference between males and females for LRS (W = 2452, p-value = 0.1077), age-at-

265   first-breeding (W = 1750.5, p-value = 0.0791), lifespan (W = 2169.5, p-value = 0.7755), total

266   number of mates, (W = 2187.5, p-value = 0.6948), total number of breeding attempts (W = 2370,

267   p-value = 0.2197), and breeding lifespan (W = 2359.5, p-value = 0.2392).

268   **Relationships between fledging and recruitment**

269   There was a strong positive relationship between number of chicks fledged per parent (LRS) and

270   number that recruited for females ($\lambda(\text{Female}_i) = \exp(-0.27) * \exp(0.12*\text{LRS}_i)$) and males

271   ($\lambda(\text{Male}_i) = \exp(-0.60) * \exp(0.13*\text{LRS})$). There was also a significant positive relationship

272   between the number of chicks fledged (LRS) and number of successful recruits (i.e. recruits that

273   in turn successfully fledged offspring during at least one breeding attempt) for females

274   ($\lambda(\text{Female}_i) = \exp(-0.65) * \exp(0.12*\text{LRS}_i)$) and males ($\lambda(\text{Male}_i) = \exp(-1.26) *$

275    $\exp(0.14*\text{LRS})$).

276   **Life-history traits**

277   Lifespan was the strongest positive correlate of LRS (0.61 ± 0.03), followed by a negative

278   correlation with age-at-first-breeding (-0.14 ± 0.04; GLMM R^2m =0.56 , R^2c = 0.79; Table 3).

279   There was a trend associated with sex, with males having slightly lower LRS compared to

280   females (Fig. 3). There was no association with the number of mates and LRS; or interactions

281   between sex, age-at-first-breeding or lifespan (Table 3).

282 **Determining the traits of "high quality" breeders**

283 "High-quality" birds (i.e., those with above-average LRS and higher than average numbers of

284 successful breeding offspring; females = 16, males = 16) produced 389 fledged chicks, of which

285 133 first-generation offspring recruited, and 94 were successful, producing 713 grand-offspring

286 (second-generation chicks) (Fig. 4). These higher-quality breeding birds produced 26 first-

287 generation offspring with an above-average LRS $\geq$ 6. In contrast, the remaining "ordinary" birds

288 (females = 46, males = 52) produced 379 chicks, of which 100 first-generation offspring

289 recruited, and 55 were successful in producing 252 grand-offspring (second-generation chicks)

290 (Fig. 4). The ordinary breeding birds (n = 98) produced 10 above-average first-generation

291 offspring.

292   An interaction effect between breeder type and lifespan was detected, but there was no

293 interaction between age-at-first breeding and breeder type (Table 4), despite the ordinary female

294 birds beginning breeding at least one year younger than the high-quality female birds (Table 5).

295 The ordinary birds had shorter lifespans and therefore lower LRS, with high-quality birds having

296 on average double the longevity of their short-lived conspecifics (Table 5).

297

298 **DISCUSSION**

299 By tracking reproductive success in yellow-eyed penguins over more than one generation we

300 show that only a small proportion of fledglings survive, recruit, and attempt to breed, however

301 lifetime reproductive success and survival appears to be an inter-generational trait, with above-

302 average breeders more likely to produce chicks that will be highly successful breeders. Fewer

303 than 1.5% (32 of 2147) of these breeding birds are what we call "super-breeders". These "super-

304   breeders" appear to be successful in producing offspring that will themselves survive and go on

305   to contribute disproportionately to the next generation.

306   Only 10.2% of the sample population of 2147 fledgling yellow-eyed penguins eventually

307   recruited and produced offspring at all, meaning that 89.8% of young fledged did not contribute

308   to the next generation at Boulder Beach. Low juvenile survival is likely to be the principal reason

309   for the low number of penguins recruiting to breeding populations. Only 20.5% of yellow-eyed

310   penguin fledglings survived to sexual maturity (two years of age, including birds that did not

311   recruit), a similar proportion to the 20.8% yellow-eyed penguins resighted as sexually-mature

312   adults at the Boulder Beach complex between 1981 to 1990 (Efford, Darby & Spencer, 1996),

313   although our reported result includes 3.3% of birds that were resighted away from Boulder

314   Beach. Our survival to adulthood rate was higher than the 10.4% of Adélie penguins (*Pygoscelis*

315   *adeliae)* that survived to age two (Ainley & DeMaster, 1980), but low compared to the range of

316   values for survivorship from fledging to sexual maturity for 19 species of passerines and seabirds

317   (42 - 86%; Newton, 1989). Survivorship to two years was significantly lower than reported in

318   several other studies of seabirds, including 57.6% for common guillemots (*Uria aalge*; Crespin

319   et al., 2006), 41 to 54% for sooty shearwaters (*Puffinus griseus*; Fletcher et al., 2013), and *c.*

320   77% for king penguins after one year (*Aptenodytes patagonicus*; Saraux et al., 2011). It was even

321   lower than the *c.* 32% of yellow-eyed penguins that survived to age two between 1936 and 1952

322   (Richdale, 1957).

323   The probability that birds survive the period between parental care and adulthood has a

324   large influence on population dynamics, but is highly variable (Maness & Anderson, 2013). The

325   most common hypothesis for high rates of mortality in young birds is their lack of experience,

326   poor foraging skills and physical immaturity (Lack, 1954; Ashmole, 1963; Orians, 1969; Dunn,

327   1972). Positive correlations are predicted between body mass and juvenile survival, based on the

328   assumption that heavier juveniles have fat reserves that buffer the food limitation associated with

329   inexperience (Lack, 1966; McClung et al., 2004; Maness & Anderson 2013). Yellow-eyed

330   penguins are sedentary foragers that lack a long-distance migratory phase in their life history,

331   however juveniles undergo a pelagic phase lasting for up to two years, during which time they

332   are sighted only erratically along the coast. No information exists on where juveniles disperse to

333   (Darby & Seddon, 1990), and most mortality occurs during this post-fledging pelagic phase. It is

334   unclear whether the low survival of juvenile penguins in this study is normal or depressed by

335   changing environmental conditions.

336   This study indicates that of the chicks seen again at Boulder Beach after fledging (24.7%

337   of the original sample), 69.8% were seen at two years of age (i.e. up to the onset of sexual

338   maturity, 69.8%, Table 1), but only 49.8% survived to breed at least once. These figures suggest

339   that juvenile mortality occurs in two or more stages: as high post-fledging mortality due to

340   inexperience, immaturity and lack of skill, and possibly due to seasonal fluctuations in prey

341   availability later in the breeding season when juveniles must prepare for their first annual moult.

342   The difference in juvenile survival between Richdale's (1957) study and ours may be indicative

343   of an adverse change in foraging conditions (Browne et al., 2011; Mattern et al., 2014),

344   entanglement in recreational or commercial fishing gear (Darby & Dawson, 2000), increasing

345   frequency of poor seasons (van Heezik 1990), and competition with or predation by recovering

346   otariid populations (Bradshaw, Lalas & Thompson, 2000; Lalas et al., 2007), all of which are

347   documented to affect adult yellow-eyed penguins. Marine pollution that results in disease

348   outbreaks and mass mortality events, have also been hypothesised (e.g. 1990 mass mortality

349   event, Gill & Darby 1993; e.g. diphtheritic stomatitis, Alley et al., 2004, 2017; Trathan et al.,

350   2015).

351   From the sample of 2147 fledglings, the proportions that survived and attempted breeding

352   (12.3%), fledged offspring (10.2%) and fledged offspring that recruited (5.8%) seem low.

353   However, the proportion of birds that attempted breeding and were successful is relatively high

354   (219 of 264, 82.9%). In other words, if a bird was successful in surviving to make a breeding

355   attempt, there was an 83% probability that it would be successful in fledging at least one chick in

356   its lifetime, a 47% (124/264) probability it would fledge at least one chick that would recruit to

357   the breeding population, and a 39% (102/264) probability that the bird would fledge chicks that

358   would recruit and subsequently fledge offspring. The proportion of yellow-eyed penguins

359   surviving to attempt to breed at least once was comparatively lower than in red-billed gulls

360   (*Larus novaehollandiae*, 18 - 22%), little penguins (*Eudyptula minor*, 28 -35%), kittiwakes

361   (*Rissa tridactyla*, 34 - 42%) and short-tailed shearwaters (*P. tenuirostris*, 69 - 73%). However

362   the proportion of breeding yellow-eyed penguins that produced recruits (47%) is one of the

363   highest, with only kittiwakes having similar recruitment rates (*c.* 41 - 50%) (Coulson, 1988;

364   Wooler et al., 1988; Mills, 1989; Dann & Cullen, 1990; Moreno, 2003). In yellow-eyed

365   penguins, recruitment into the breeding population appears to be driven in part by the higher

366   survival rate of the offspring of a subset of breeders, with high-quality birds, labelled here as

367   "super-breeders", producing more recruits (133 first-generation recruits from 32 birds, 57.1%)

368   than the ordinary breeders (100 first-generation recruits from 98 birds, 42.9%).

369   Both male and female penguins that survived to breed varied considerably in the total

370   number of offspring they fledged. For a long-lived species, the average number of fledged young

371   seems relatively small (female mean = 6.82, male mean = 5.07), but falls within the range of

372   values reported from the few studies that have estimated mean LRS in seabirds, passerines and

373   birds of prey, demonstrating that LRS for many species of birds remain similar as a result of life-

374   history trade-offs (Table 6). Females had slightly longer lifespans and longer breeding lifespans

375   than males, because females started breeding earlier than males. Females may have more

376   opportunities to breed than males, due to an apparent sex-skew, with males outnumbering

377   females (Richdale, 1957). The maximum number of fledged offspring for both male (23) and

378   female yellow-eyed penguins (24) was much higher than mean values, reflecting the highly

379   negatively skewed distribution of LRS (Fig.2). This is consistent with the observation that most

380   individuals produce small numbers of young, and only a few produce many (Newton 1989).

381   Nevertheless, there was a wide range in the number of young fledged by individual birds

382   regardless of sex, despite the greater cost of reproduction incurred by breeding females. Newton

383   (1989) concluded that LRS is generally similar for males and females in species that lack high

384   levels of sexual dimorphism, which is the case for yellow-eyed penguins (Seddon et al., 2013).

385   **LRS predictors**

386   Lifespan was the strongest correlate of LRS, with the number of offspring produced increasing

387   significantly with increased lifespan. This trend is very common for seabirds (Clutton-Brock,

388   1988; Newton, 1989; Newton, 1995), and is attributed to a number of factors: increased breeding

389   opportunities, and increasing parental experience with lifespan, as has been demonstrated in

390   other seabird species (Limmer & Becker, 2009; Saraux et al., 2012), and the general fitness

391   required for a long lifespan. Long-lived birds are the primary contributors to the gene pool in

392   many species, meaning there is likely to be selection for viability (Moreno, 2003; Mauck,

393   Huntington & Grubb, 2004). We found that high-quality breeders had lifespans that were on

394   average double that of ordinary breeders, but they produced three to four times more offspring in

395   their lifetimes than ordinary birds (Table 5). In other species lifespan explains less of the

396   variance when the number of recruits is examined, as opposed to number of offspring produced

397   (Newton, 1989). In contrast, we found a highly significant relationship between LRS and the

398   number of recruits and successful recruits produced for yellow-eyed penguins, meaning that the

399   characteristics of birds with longer lifespans are likely to be reliable predictors of parental quality

400   for this species.

401   Age-at-first-breeding was the second strongest predictor of LRS in yellow-eyed

402   penguins, with birds that began breeding later having lower lifetime totals of offspring, due to a

403   decrease in total breeding opportunities (Newton, 1989). The theory of antagonistic pleiotropy

404   suggests that high early-life reproductive output is at the expense of later-life productivity, and

405   can be selected for if selection is stronger at early stages of life, so that early benefits outweigh

406   later costs (Williams, 1957). While there was a difference between the LRS of males and

407   females in this study, no interaction effect could be detected, despite earlier reproduction in

408   females, which may potentially result in accelerated reproductive senescence (Partridge, 1992,

409   Reed et al., 2008). This trend has been observed in several long-lived bird species, which all

410   showed a positive correlation between age-at-first-breeding and survival in females, suggesting a

411   trade-off between early recruitment and lifespan (Ollason & Dunnet,1978; Ainley & DeMaster,

412   1980; Pyle et al., 1997; Tavecchia et al., 2001). Individual variation in LRS for yellow-eyed

413   penguins therefore appears to be due to variation in lifespan (1-24 years) and age-at-first-

414   breeding (2-12 years), together determining the length of the breeding lifespan (1-18 years).

415   It is common for many species of seabirds to show reduced breeding success after

416   changing mates, most likely due to a trade-off in time and energy expenditure for finding a new

417   mate and foraging, and also due to lack of familiarity with the new mate (Ollason & Dunnet,

418   1978; Coulson & Thomas, 1985; Newton, 1989). In short-tailed shearwaters a mate change

419   results in a temporary decrease in breeding success, but this effect is smaller in individuals that

420   are more experienced breeders (Wooller et al., 1989). Breeding success of male common

421   guillemots decreased with an increasing number of mates (Lewis et al. 2006). Yellow-eyed

422   penguins that change mates are more likely to experience breeding failure the subsequent year

423   (Setiawan et al., 2005). We did not detect a significant negative effect of number of mates on

424   lifetime number of offspring produced, possibly due to the tendency for longer-lived birds to

425   outlive their mates, resulting in higher overall numbers of mates.

426   **Conservation implications**

427   Chronic and acute stress as a result of climate change, marine pollution, disturbance at terrestrial

428   breeding sites and extreme nutritional stress may decrease LRS, as the cumulative effects of

429   increasing types of stressors force individuals to reduce their investment in productivity, increase

430   breeding skip behaviours (e.g. red-footed boobies *Sula sula*, Cubayanes et al., 2011) or result in

431   breeder mortality (Kitaysky et al., 2010). In black-legged kittiwakes, breeding behaviour is

432   mediated by increased corticosterone production during periods of poor food supply (Kitaysky et

433   al., 2010; Schultner et al. 2013). Clarifying the factors that separate the success of the few that

434   produce many offspring from the many that do not may therefore need to take into account the

435   role of chronic or acute stress on the parameters that may be used to measure their fitness.

436   Likewise, birds that contribute disproportionately to successive generations may have higher

437   thresholds for anthropogenic and environmental stressors than average birds. The impact of

438   extreme events on different phenotypes of conspecifics may differ as a consequence of the

439   "super-breeder" phenomenon, since these birds tend to consistently achieve high LRS and long-

440   lifespans in a stochastic environment.

441   It appears that the Boulder Beach population of yellow-eyed penguins is sustained by a

442   small proportion of high-quality, long-lived birds, the "super-breeders". High levels of philopatry

443   may drive high-quality and ordinary breeding recruits to return to their natal area, and once they

444   begin breeding they are likely to remain at these breeding sites for life. This behaviour may be

445   hazardous for population stability should either one of their marine or terrestrial habitats become

446   threatened. If circumstances require it necessary to protect specific individuals in a population

447   from catastrophe, or to differentially allocate resources due to budget constraints, it would be

448   important to distinguish between potentially very successful breeders and the evolutionary

449   "living dead" (Moreno, 2003). Oiling is the greatest anthropogenic threat to penguins (Trathan et

450   al., 2015), requiring triage of breeders for temporary captive management. The unexplained mass

451   mortalities of adult and juvenile yellow-eyed penguins on the Otago Peninsula in 1990, 1996 and

452   2013 due to exposure to an unknown toxic agent have presented conservation managers with

453   opportunities to safeguard specific individuals from harm (Gill & Darby, 1993; DOC,

454   unpublished data). While effort should be placed on safeguarding all individuals in a threatened

455   population during a period of catastrophe, only a small proportion of individuals will contribute

456   to the recovery of the population following such an event.

457   Although it seems sensible to focus conservation resources on "super-breeders", the

458   challenge lies in identifying them. The positive relationship between LRS and the number of

459   successful recruits indicates that birds demonstrating relatively high LRS are also those that

460   produce high-quality offspring. Lifespan is the main predictor of LRS, but unfortunately it

461   cannot be calculated until the death of an individual. Age-at-first-breeding can be identified

462   before death, although its association with potential LRS is much weaker, however high-quality

463   female birds tended to recruit a year later than ordinary birds. Fledging weight of the individual

464   could indicate that the individual comes from a high quality lineage and will be more likely to

465   survive (McClung et al. 2004) and go on to breed and produce high quality offspring that also

466   fledge at a higher than average weight. We could not explore this relationship with our dataset as

467   fledging weights were not reliably recorded for historical records. The value of other potential

468   indicators of living super-breeders include oxidative stress, white blood cell counts, hue and size

469   of the coloured eye and eye stripe; these are being explored in ongoing research.

470   It may be possible to single out birds on the basis of life-history traits that relate to state-

471   based quality. The importance of state-based assessments for yellow-eyed penguins has yet to be

472   fully explored, especially with regard to analysing the immunocompetence of individuals.

473   Disease prevalence has increased in recent years (Alley et al., 2004, 2017; Hill et al., 2010;

474   Argilla et al., 2013). Moreno et al. (1998) measured variables related to health state and cell-

475   mediated immunity between early and late breeders for chinstrap penguins (*P. antarctica*),

476   finding that early breeders experienced better health than later breeders. Female chinstrap

477   penguins with leukocytosis laid smaller eggs, had slower chick growth rates, and were more

478   prone to failure (Moreno et al., 1998). Information about foraging ecology, particularly in young

479   birds is also necessary. Foraging strategies in high quality Adélie penguins have been linked to

480   better provisioning of chicks, suggesting that some birds may be physiologically more capable

481   by virtue of genetic superiority (Lescroël et al., 2010).

482   Around half of all seabird species globally are thought to be in decline, many of which

483   have restricted numbers and ranges, and demographic characteristics that severely limit their rate

484   of recovery (Croxall et al. 2012). As long-lived species, and with demographic characteristics

485   similar to those of yellow-eyed penguins, it is likely that population persistence in other species

486   is also dependent to some extent on a subset of successful breeders. Understanding what causes

487   some birds to display enhanced resilience and identifying and protecting these individuals may

488   be vital in the face of growing threats.

489

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496

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758

759   **Table 1**. Breeding and recruitment overview of numbers and percentages of individual yellow-

760   eyed penguins marked between 1981 and 2003 at Boulder Beach, Otago Peninsula, New Zealand

761   (n = 2147).

	Number	Percent
Marked as chick or juvenile at Boulder Beach	2147	
Marked chicks that were never resighted	1546	72.0
Marked chicks that were resighted under 2 years	601	28.0
Survived to adulthood (2 years)	441	20.5
Sighted at Boulder Beach	*370*	*17.2*
Sighted elsewhere	*71*	*3.3*
Attempted breeding at Boulder Beach	264	12.3
Fledged offspring at Boulder Beach	219	10.2
Fledged first-generation offspring that recruited	124	5.8
Fledged successful first-generation offspring	102	4.8

762

764   **Table 2.** Mean LRS, number of recruits, number of recruits that bred successfully, lifespan, age-

765   at-first-breeding, breeding lifespan, number of breeding attempts and number of mates of

766   founding generation female (n = 62) and male (n = 68) yellow-eyed penguins breeding at

767   Boulder Beach, New Zealand. (Var = variance; se = standard error; min = minimum; med =

768   median; max = maximum).

Variable	mean	var	se	min	med	max
			FEMALES			
LRS	6.82	33.8	0.74	0	6	24
Recruits	2.24	5.01	0.28	0	2	9
Successful recruits	1.52	2.71	0.21	0	1	7
Lifespan (years)	9.44	32.77	0.73	2	7.5	24
Age at first breeding	3.60	3.16	0.23	2	3	12
Breeding lifespan (years)	5.84	26.69	0.66	0	4	17
Breeding attempts	5.79	17.74	0.53	1	4.5	16
Total mates	2.03	1.57	0.16	1	2	7
			MALES			
LRS	5.07	22.07	0.57	0	4	23
Recruits	1.38	2.81	0.20	0	1	6
Successful recruits	0.81	1.29	0.14	0	0	5
Lifespan (years)	8.87	25.3	0.61	2	8	21
Age at first breeding	4.09	3.48	0.23	2	3	11
Breeding lifespan (years)	4.78	21.7	0.56	0	3	18
Breeding attempts	4.78	11.60	0.41	1	4	14
Total mates	1.93	1.32	0.14	1	2	6

770 **Table 3**. Model-averaged generalised linear mixed effects model of lifetime reproductive success

771 (LRS) and life-history parameters of 130 founding generation yellow-eyed penguins (n = 809

772 breeding attempts) that were marked at Boulder Beach, New Zealand between 1981 and 2003

773 (All non-binary data are standardised to have mean = 0 and SD = 1).

774

Coefficients	Estimate	SE	95% Confidence Interval	Relative Importance
(Intercept)*	2.02	0.04	(1.94, 2.09)	-
Sex (Male) [‡]	-0.16	0.04	(-0.25, -0.08)	1.00
z (Age at first breeding) [‡]	-0.14	0.04	(-0.21, -0.07)	1.00
z (Lifespan) [‡]	0.61	0.03	(0.55, 0.68)	1.00
Sex (Male): z (Lifespan)	0.01	0.03	(-0.07, 0.13)	0.24
z Total Mates	-0.004	0.02	(-0.08, 0.04)	0.23

775 *Sex (Female) is the reference category

776 [‡] Significant results

777
778 Model statement: glmer(LRS ~ zLifespan + zAgeatfirstbreeding + zTotalmates + factor(Sex) +
779 factor(Sex):zAgeatfirstbreeding + factor(Sex):zLifespan + (1|Matecode)
780
781

782 **Table 4.** Model-averaged generalised linear mixed-effects model of lifetime reproductive
783 success in yellow-eyed penguins marked at Boulder Beach between 1981 and 2003, including
784 breeder quality as well as (All non-binary data are standardised to have mean = 0 and SD = 1).

785

Coefficients	Estimate	SE	95% Confidence Interval	Relative Importance
(Intercept)*	1.84	0.04	(1.77, 1.91)	-
Breeder quality (higher-quality) [ǂ]	0.40	0.06	(0.29, 0.51)	1.00
z(Age at first breeding) [ǂ]	-0.10	0.03	(-0.15, -0.05)	1.00
z(Lifespan) [ǂ]	0.60	0.04	(0.52, 0.67)	1.00
Breeder quality (higher-quality):z(Lifespan) [ǂ]	-0.21	0.05	(-0.31, -0.11)	1.00
z(Total mates)	0.01	0.02	(-0.03, 0.08)	0.34

786 *Breeder quality (lower-quality) is the reference category

787 [ǂ] Significant results

788

789 Model statement: glmer(LRS ~ z(Lifespan) + z(Ageatfirstbreeding) + z(Totalmates) +
790 factor(BreederType) + factor(BreederType):z(Ageatfirstbreeding) +
791 factor(BreederType):z(Lifespan) + (1|Matecode)

792

793 **Table 5.** Mean LRS, number of first-generation offspring, number of first-generation offspring that bred
794 successfully, lifespan, age-at-first-breeding, breeding lifespan, number of breeding attempts and number
795 of mates of ordinary and high-quality yellow-eyed penguins breeding at Boulder Beach, New Zealand.
796 (Var = variance; se = standard error; min = minimum; med = median; max = maximum). Continued
797 overleaf.

Variable	mean	var	se	min	med	max
Females (ordinary breeders, n = 46)						
LRS	4.37	14.06	0.55	0	4	17
Recruits	1.33	2.27	0.22	0	1	5
Successful recruits	0.83	1.12	0.16	0	0	4
Lifespan (years)	7.48	23.63	0.72	2	6	22
Age at first breeding	3.30	2.57	0.24	2	3	12
Breeding lifespan (years)	4.17	20.46	0.67	0	3	17
Breeding attempts	4.15	9.51	0.45	1	3.5	13
Total mates	1.80	1.36	0.17	1	1	7
Females (high-quality breeders, n = 16)						
LRS	13.88	23.85	1.22	7	12	24
Recruits	4.88	3.58	0.47	2	4.5	9
Successful recruits	3.5	2	0.35	1	3	7
Lifespan (years)	15.06	16.86	1.03	7	16	24
Age at first breeding	4.44	4.13	0.51	3	4	10
Breeding lifespan (years)	10.63	14.25	0.94	4	9.5	17
Breeding attempts	10.5	11.73	0.86	5	9	16
Total mates	2.69	1.70	0.33	1	3	5
Males (ordinary breeders, n = 52)						
LRS	3.42	9.82	0.43	0	2	14
Recruits	0.75	1.09	0.14	0	0	4
Successful recruits	0.33	0.30	0.08	0	0	2
Lifespan (years)	7.58	19.31	0.61	2	6	19
Age at first breeding	4.04	3.45	0.26	2	3	11
Breeding lifespan (years)	3.54	15.43	0.54	0	2.5	14
Breeding attempts	3.87	9.06	0.42	1	3	12
Total mates	1.83	1.52	0.17	1	1	6
Males (high-quality breeders, n = 16)						
LRS	10.44	25.06	1.25	5	8.5	23

Recruits	3.44	2.93	0.43	1	3	6
Successful recruits	2.38	1.32	0.29	1	2	5
Lifespan (years)	13.06	22.6	1.19	8	12	21
Age at first breeding	4.25	3.8	0.49	2	3.5	9
Breeding lifespan (years)	8.81	21.63	1.16	3	6.5	18
Breeding attempts	7.75	8.73	0.74	4	7	14
Total mates	2.25	0.6	0.19	1	2	4

798

799 **Table 6**. Comparison of LRS and maximum number of young fledged by individuals of five

800 different bird species for males and females (where data were available from Coulson 1988;

801 Mills 1989; Dann and Cullen 1990; Korpimäki 1992; Krüger and Lindström 2001; Garamszegi

802 *et al.* 2004).

803

Species	LRS (Female)	LRS (Male)	Max. fledged (Female)	Max. fledged (Male)
Yellow-eyed penguin (*Megadyptes antipodes*)	6.82	5.07	24	23
Black-legged kittiwake (*Rissa tridactyla*)	6.93	7.41	-	-
Red-billed gull (*Larus novaehollandiae*)	3.4	3	26	28
Little penguin (*Eudyptula minor*)	2.28	2.13	35	44
Tengmalm's owl (*Aegolius funereus*)	-	5.2	-	26
Common buzzard (*Buteo buteo*)	3.48	2.72	20	20
Collared flycatcher (*Ficedula albicollis*)	5.18	-	-	-

804

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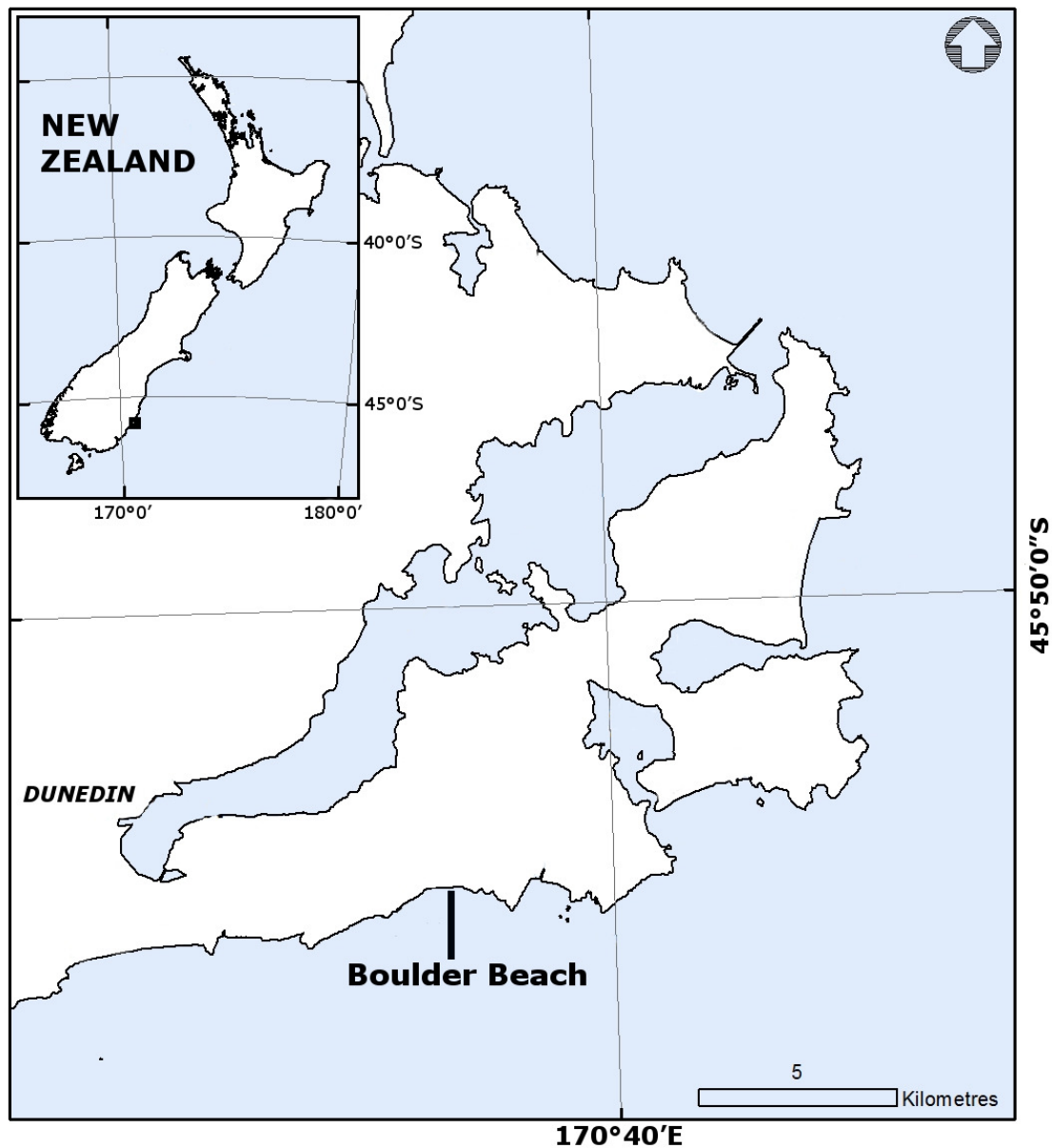
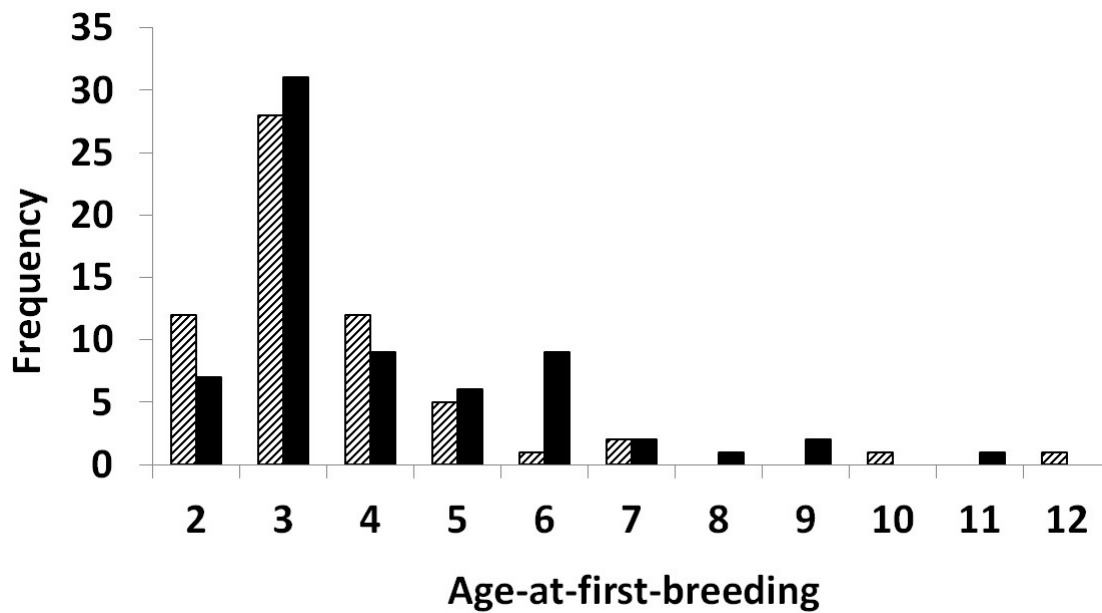

808

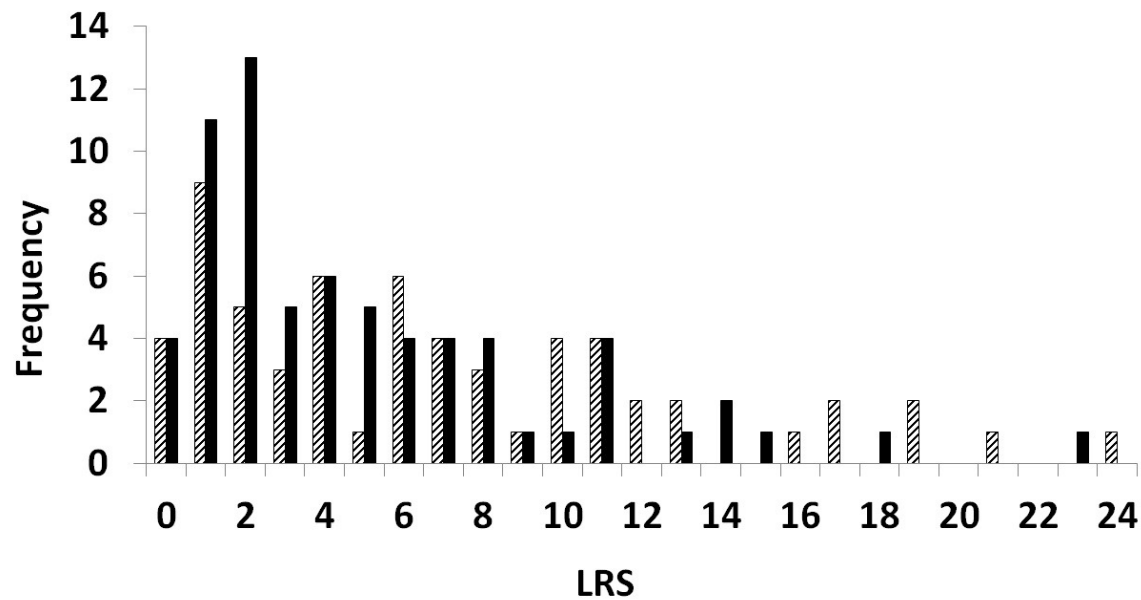
809   **Figure 1.** Map showing the location of Boulder Beach on the Otago Peninsula, Dunedin, New

810   Zealand.

811

812   **Figure 2.** Age-at-first-breeding of female (striped, n = 62) and male (black, n = 68) yellow-eyed

813   penguins with complete life histories that bred at Boulder Beach, Dunedin, New Zealand.

815

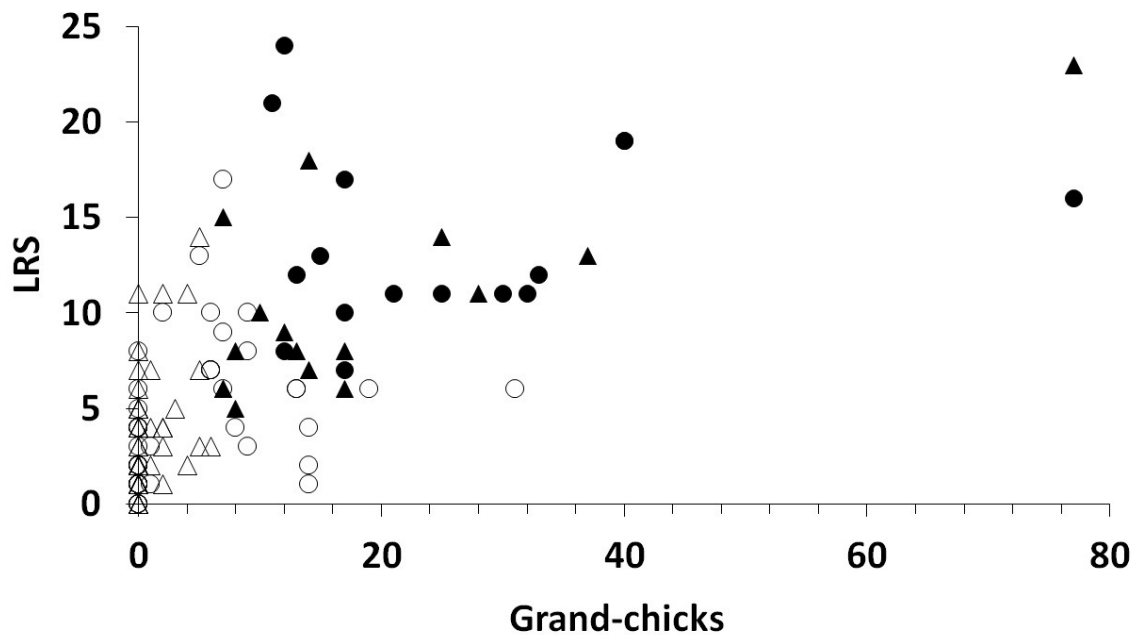



Figure

816   **3.** Frequencies of the total number of chicks fledged (lifetime reproductive success, LRS) by

817   female (striped, n = 62) and male (black, n = 68) yellow-eyed penguins with complete life

818   histories that bred at Boulder Beach, New Zealand.

819

820

821

822   **Figure 4.** The relationship between lifetime reproductive success (LRS) and the production of

823   second-generation offspring (grand-offspring) for female (filled dots = "high-quality breeder",

824   empty dots = "low-quality breeder") and male (filled triangles = "high-quality breeder", open

825   triangles = "low-quality breeder") yellow-eyed penguins with complete life histories that bred at

826   Boulder Beach, New Zealand.