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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 that bred successfully. 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. 26% 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 balance high LRS with long- life-span in a stochastic environment, demonstrating greater resilience in the face of extreme events.

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

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ABSTRACT

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 that bred successfully. 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. 26% 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 balance high LRS with long- life-span in a stochastic environment, demonstrating greater resilience in the face of extreme events.

Keywords: Yellow-eyed penguin, lifetime reproductive success, intergenerational fecundity, breeding, seabird

INTRODUCTION

Unlike cross-sectional studies across one or two breeding seasons, longitudinal studies based on lifetime reproductive success (LRS) average out occasional breeding failures, and increase the accuracy of measurement of individual success (Krüger & Lindström, 2001). By collecting long-term life-history data from a population of marked individuals, it becomes possible to identify the proportion of animals that produce recruits, enabling conservation efforts to be efficiently focused on individuals with successful traits (Moreno, 2003), and the overall contribution of individuals with different lifespans or reproductive strategies to subsequent generations can be compared (Clutton-Brock, 1988; Newton, 1989; Wooller, Bradley & Croxall, 1992; Brommer, Pietiäinen & Kolunen 1998).

Studies of LRS have revealed commonalities across bird species: a significant proportion of fledglings from a given population will die before sexual maturity (Bryant, 1979; Newton, 1989); not all individuals that attempt to breed will be successful; and successful individuals vary in their productivity (Newton, 1989). The LRS distribution of a population is typically highly skewed, with large numbers of individuals producing small numbers of young, and only a small proportion of adults producing large numbers of young (Clutton-Brock, 1988, Newton, 1989). Specific life-history and reproductive traits can be indicative of LRS. Lifespan is the strongest correlate, with longer-lived individuals commonly achieving a higher LRS (Gustafsson, 1986; Clutton-Brock, 1988; Newton, 1989). In seabirds, where individuals can start breeding at various ages, variance in LRS is largely related to variation in breeding lifespan (Moreno, 2003), because an increased number of breeding seasons allows individuals more opportunities to successfully fledge offspring.

If only a small proportion of individuals maintain most of the population, the identification of traits affecting lifetime fecundity of an individual are relevant for conservation efforts. Resources can be diverted towards protecting particularly productive individuals at times when the population is assailed by environmental challenges such as adverse climate conditions, reduced food availability, disease outbreaks, or catastrophic events (e.g. oil spills, Gartrell et al., 2013). In the case of a pest species, culling efforts could be focused on these highly productive individuals (Moreno, 2003).

Factors known to affect reproductive performance in seabirds and which can interact with each other include age, experience, pair bond duration, health condition, sex, number of mates, mate fidelity and site fidelity (Ryder ,1980; Clutton-Brock, 1988; Gavin & Bollinger, 1988; Bradley et al., 1990; Wooller et al., 1990; Chastel, Weimerskirch & Jouventin, 1995). For example, in long-lived seabird species, a period of poor reproductive success at a young age or at a lower level of experience may be superseded by a period at which the individual performs at their peak reproductive output (Forslund & Pärt, 1995). At an older age, senescence may begin to reduce reproductive output, followed by terminal illness and death (Fowler, 1995; Nisbet & Dann, 2009; Froy et al., 2013). With increasing age, maternal efficiency might allow for control of the timing, size, volume, composition and pore density of eggs, and high levels of pair synchrony through maintenance of long-term pair bonds may reduce incubation periods and increase nesting success (Massaro et al., 2002; Massaro et al., 2004). Gaining breeding experience has been postulated to be no different to the honing of other skills, such as foraging. Breeding skills may therefore improve with both age and experience, as well as with improved synchrony between mated pairs (Forslund & Pärt, 1995). The relative importance of each of

these factors in estimating LRS is difficult to assess, and can differ dramatically between species and geographic locations.

Breeder quality might not necessarily be age related; some birds might just be better than others because they have better skills. State-based assessment of individual breeder quality often requires the assumption or prediction that a component of the individual's health or skill within that system is a driving factor determining its reproductive success (Wendeln & Becker, 1999; Moreno, 2003), and that this superior skill is independent of age-related performance. Individual state explaining superior breeding abilities can be measured as mass, body condition or morphology at commencement of the breeding season (Wauters & Dhont, 1989; Wendeln & Becker, 1999; Jensen et al., 2004); foraging and predator evasion skills (Daunt et al., 2007; Lescroël, Ballard, Toniolo, Barton, et al., 2010); attractiveness or ornamental traits (Massaro, Davis & Darby, 2003; Brommer, Ahola & Karstinen, 2005; Kim et al., 2011; Potti, Canal & Serrano, 2013); health, hormonal stress response or immunocompetence (Wendeln & Becker, 1999; Moreno, 2003; Ellenberg et al., 2007; Costantini et al., 2014). These state-based qualities and their relationship with breeding success and LRS can be highly variable within a population of seabirds, but might have low variation for individual birds over time (e.g. common terns *Sterna hirundo*, Wendeln & Becker, 1999). Breeding seabirds have a range of responses to catastrophic climatic or weather events, e.g. El Niño Southern Oscillation (ENSO) (Boersma, 1978), and vary in the rate at which food is delivered to chicks (Ens et al., 1992). Territoriality also can be associated with individual quality in relation to nesting density (Stokes & Boersma, 2000), nest site characteristics (Stokes & Boersma, 1998) and rank dominance (Schubert et al., 2007).

LRS measures the number of offspring produced over a lifetime, however it does not consider the viability of those offspring. There may be variability in the quality of offspring produced by different individuals that further reduces the proportion of individuals contributing to subsequent generations. By using a 23-year dataset we were able to track reproductive success over more than one generation and identify the proportion of a penguin population that produces grand-offspring. Yellow-eyed penguins (hōiho, *Megadyptes antipodes*) are endemic to New Zealand and listed as 'endangered' on the IUCN Red List (Birdlife International, 2015). Some mainland populations are intensively managed to mitigate threats posed by introduced predators, disturbance and habitat destruction (McKinlay, 2001). Because yellow-eyed penguins are sedentary (Seddon, van Heezik & Ellenberg, 2013), long-lived, have high natal philopatry, high breeding site fidelity once breeding, and are monogamous (Richdale, 1957), they are an ideal species to study LRS. We investigated: (1) the proportion of birds that survive to adulthood; (2) the proportion of adults that breed; (3) the proportion of breeders that produce young that recruit to the breeding population (first-generation); and (4) the proportion of adults producing grand-offspring (second-generation). We also explored the characteristics of highly-fecund breeders, and the relationship of this trait between generations. We predicted that in line with other seabird species, only a small proportion of yellow-eyed penguins would survive to adulthood, breed, and produce young, and that differences in LRS between males and females exist due to the difference in age-at-first-breeding, with females known to begin breeding earlier than males (Richdale, 1957; Darby & Seddon, 1990). We predicted that lifespan would have the greatest influence on the number of offspring produced, and be positively correlated with LRS. Yellow-eyed penguins with earlier age-at-first-breeding and fewer overall mates were predicted to have greater LRS.

METHODS

Yellow-eyed penguins are solitary breeders, in contrast with most other penguin species and seabirds that breed colonially (Richdale, 1957; Darby & Seddon, 1990). In September-October clutches of up to two eggs are laid, and chicks fledge at c. 106 days from late January to late February (Richdale, 1957; Seddon & Davis, 1989; Darby & Seddon, 1990).

Yellow-eyed Penguin Database

We obtained breeding data from the Yellow-eyed Penguin Database administered by the New Zealand Department of Conservation (DOC). We analysed only data from yellow-eyed penguins breeding at the Boulder Beach complex on the Otago Peninsula, New Zealand, (45°500 S and 170°300 E; Fig. 1) because it supports a relatively large population of yellow-eyed penguins, has an inter-decadal history of intensive monitoring and it has been trapped for introduced predators over time. This site has the longest history of chick marking; the majority of chicks fledged at this site have been marked with a stainless steel flipper band issued by the New Zealand Bird Banding Scheme (NZBBS). We acknowledge that the use of flipper bands might present bias (*sensu* Petersen et al., 2005), however yellow-eyed penguins are inshore foragers (van Heezik & Seddon, 1990; Mattern et al., 2007) and this bias is likely to be minimal. A separate study analysing the impact of research manipulations found that even a double banding study in one season had no effect on productivity or subsequent survival (Seddon, van Heezik & Ellenberg, 2013). Before commencing this study, we completed a comprehensive error check, which involved checking the original notebook records against electronic database records to ensure a high level of accuracy and consistency.

Data for survival to adulthood and breeding, and LRS analyses

148 A total of 2147 birds were marked at Boulder Beach as chicks between 1981 and 2003. We used
149 this sample to calculate the proportion of birds that survived to adulthood (defined as reaching
150 two years of age), attempted to breed, fledged offspring, fledged offspring that survived to
151 adulthood and returned to the breeding population but did not necessarily breed (recruited), and
152 fledged offspring (first-generation) that in turn successfully bred and produced offspring
153 (second-generation, or grand-chicks). We chose the year 2003 as the cut-off for including any
154 new breeders in the sample, since mean age at first breeding is between three and four years
155 (Richdale, 1957): this allowed for birds to be re-sighted by age 4, breed, have offspring that
156 survived to breed and grand offspring that survived up until the 2014/15 breeding season, when
157 these data were last updated. Inclusion of birds from the cohort beyond 2003 might have been re-
158 sighted only once or not at all, and could have skewed the results. Birds that were still alive or
159 had been sighted after 2007 were excluded from the sample as their breeding lifetime might not
160 have ended (n = 73 birds).

161 We defined LRS as the number of offspring produced by an individual over their lifetime.
162 Only data recorded from birds marked as chicks or as juveniles (one-year olds) could be used to
163 ensure complete life-histories, as they were of known age due to plumage differences (duller
164 colouration and lack of the distinctive yellow eye and crown of the adults). Yellow-eyed
165 penguins are typically marked at *c.* 80 - 90 days, before fledging at *c.* 106 days (Seddon et al.,
166 2013). If a bird was marked as a juvenile, we estimated the cohort year by subtracting one year.
167 Only birds that survived to adulthood (two or more years of age) could be used for life-history
168 analysis, as these were potential breeders and by default, had sufficient data recorded for
169 measuring LRS. The majority of birds that were never recorded to have attempted breeding
170 typically lacked recorded data of any kind. A bird was considered to have attempted to breed if it

171 or its mate laid an egg.

172 Analysis of LRS requires complete detectability of the focal population: this would be
173 compromised if individuals bred elsewhere, or skipped breeding years and were consequently
174 recorded as having died. We are confident that we have full records of birds due to the intensive
175 monitoring at the study site and annual monitoring at adjacent sites along the coast, and the high
176 level of natal (*c.* 81%) and breeding philopatry (*c.* 98%), and monogamy exhibited by this
177 species (Richdale, 1957; Ratz et al., 2004). Birds that skip breeding remain largely undetectable
178 during the breeding season, with only *c.* 8% of skipped birds in our sample being resighted as a
179 non-breeder, however detection of breeders is close to 100% (Hegg et al., 2012). In our sample,
180 72 yellow-eyed penguins that survived to breed skipped at least one breeding season once they
181 had established breeding, which is not uncommon, particularly in the year following a poor
182 season, death of a mate or a divorce (Moore, 1994; Ratz et al., 2004; Setiawan et al., 2005). Due
183 to the small, discrete size of nesting areas, the intensity of monitoring at this and in surrounding
184 sites, and the high degree of breeding site fidelity, we assumed that if a bird or breeding pair
185 were not seen during multiple visits to the breeding area and to other surrounding areas from
186 early incubation to the end of the guard period they were undertaking a breeding skip. None of
187 the birds we assumed to be undertaking a breeding skip were re-sighted at adjacent monitored
188 breeding areas during their skipped year.

189 We excluded birds if they were found dead two or more years after marking at a location
190 other than Boulder Beach, or were found dead on Boulder Beach more than five years after
191 marking with no other resightings or nesting records in between. The latest year a bird could be
192 recorded as observed and be presumed dead was 2007. We excluded birds if they were marked
193 before the 1981 cohort when intensive monitoring began.

Sample parameters

The sample parameters for modelling included sex, total number of breeding attempts, recruitment of first-generation offspring, recruitment of successful first-generation offspring, age-at-first-breeding, breeding lifespan, total number of mates and lifespan.

Birds were sexed by adult head and foot measurements according to Setiawan, Darby & Lambert (2004). In instances where birds had never been measured or when fledgling measurements were analysed, we inferred the sex from mates where possible, on the assumption that pairings were between males and females only and that the mate had been correctly identified. If there were no measurements or sex recorded for mates, we removed these birds from any lifetime data analysis. A total of 264 (12.3%) birds survived to breed out of the original sample of 2147 birds marked as chicks or juveniles, however data for sexing were available for 217 birds from the sample (females n =112, and males n = 105). We used this sample of sexed birds for the analysis of life-history traits affecting LRS. It was critical to limit this study to birds that had been sexed so as not to pseudo-replicate breeding pairs.

We measured lifespan in whole years at the time of marking as chicks (*c.* 3 months old), to the time of either being found dead or 'missing' after three consecutive years. Age-at-first-breeding was recorded as the age of the bird during its first recorded breeding attempt. We calculated the number of mates as the minimum possible number of mates, due to 38 of 217 birds in the sample having unidentified mates in some years. We assumed that if a bird's mate was not recorded but it was breeding with a particular bird in the previous and subsequent years that it was the same mate in all three seasons.

Statistical analysis

We carried out all statistical analyses using R (Version 3.3.0, R Core Team 2016). We used two-sample Wilcoxon rank-sum tests to test for statistical significance between males and females, for parameters including LRS, age-at-first-breeding, recruitment of first-generation offspring, recruitment of successful first-generation offspring, lifespan, total number of mates, total number of breeding attempts and breeding lifespan.

The relationships between recruitment of first-generation breeders, successful first-generation breeders, sex, and the effect of life-history traits on LRS were analysed using generalised linear models (GLM) with a quasi-Poisson error distribution to account for overdispersion and log-link function, using the *lme4* package (Bates et al., 2015). There was the potential for bias, as the response and predictor variables were non-independent. We used an information-theoretic approach to model selection, by constructing a maximal model containing all probable input variables (based on *a priori* reasoning), and then ranking this model against all of its derivatives using QAICc. To account for model selection uncertainty, model-averaging was conducted for the best models (2ΔQAICc), using the *MuMIn* and *AICcmodavg* packages in R (Bartoń, 2016; Mazerolle, 2016).

In order to compare specifically the life-history characteristics between birds which proved over the three generations to be highly fecund ("high quality"), and the remainder of the birds ("ordinary"), we defined the highly fecund individuals as follows: those birds with above-average LRS relative to their sex (females ≥ 6, males ≥ 5) and those that had an above-average number of grand-offspring (second-generation chicks; females ≥ 7, males ≥ 4). Using the same GLM approach, we analysed the effect of life-history parameters on the LRS of these two groups of birds to determine differences in breeder quality.

RESULTS

Of the total sample of 2147 birds marked as chicks or juveniles from 1981 to 2003, 1546 (72.0%) were thought to have died before reaching adulthood, whereas 441 birds survived to be seen at least once as an adult: 71 of these birds were sighted away from Boulder Beach at other monitoring locations where they subsequently bred. Of the 370 birds that were re-sighted at Boulder Beach as an adult at least once (17.2%), 264 attempted to breed at least once (12.3%), and 219 bred successfully at least once (10.2%). Only 124 birds produced at least one first-generation chick that recruited to the breeding population and attempted to breed at least once (5.8%), and 102 had first-generation offspring that not only recruited but bred successfully at least once (4.8%). Overall figures are presented in Table 1.

LRS of male and female yellow-eyed penguins

There was high individual variance in LRS calculated for both males and females (n = 217), with this variance being higher for females (Table 2; Figure 2). The maximum number of total offspring a female yellow-eyed penguin produced was 24, compared to 23 for males. The only significant differences between males and females was age-at-first-breeding (Wilcoxon rank-sum test, W = 4373, P = 0.0004; Fig. 2), and recruitment of successful breeders (W = 6803, P = 0.026); There was no difference between males and females for LRS (W = 6563.5, P = 0.14); recruitment (W = 6594, P = 0.10); lifespan (W = 5538, P = 0.46); total number of mates, (W = 5879.5, P = 1.00); total number of breeding attempts (W = 6292, P = 0.37), and breeding lifespan (W = 6142.5, P = 0.57).

Relationships between fledging and recruitment

There was a strong positive relationship between number of chicks fledged per parent (LRS) and number that recruited for females ($\lambda(Female_i)$ = exp (-0.659) * exp(0.14*LRS_i) and males ($\lambda(Male_i)$ = exp (-0.864) * exp(0.149*LRS). There was also a significant positive relationship between the number of chicks fledged (LRS) and number of successful recruits (i.e. recruits that in turn successfully fledged offspring during at least one breeding attempt) for females ($\lambda(Female_i)$ = exp (-1.06) * exp(0.14*LRS_i)) and males ($\lambda(Male_i)$ = exp (-1.51) * exp(0.158*LRS).

Life-history traits

Lifespan was the strongest positive correlate of LRS, followed by a negative correlation with age-at-first-breeding (Pseudo R-squared = 59.6%; Table 3). There was a trend associated with sex, with males having slightly lower LRS compared to females (Fig. 3). There was no association with the number of mates and LRS; or interactions between sex, age-at-first-breeding and lifespan (Table 3).

Determining the traits of highly fecund "high quality" breeders

"High-quality" birds (i.e., those with above-average LRS and fecundity; females = 32, males = 24) produced 604 fledged chicks, of which 204 first-generation offspring recruited, and 146 were successful, producing 1002 grand-offspring (second-generation chicks) (Fig. 4). These higher-quality breeding birds produced 76 first-generation offspring with an above-average LRS ≥ 6. In contrast, the remaining "ordinary" birds (females = 80, males = 81) produced 503 chicks, of which 92 first-generation offspring recruited, and 42 were successful in producing 154 grand-offspring (second-generation chicks) (Fig. 4). The ordinary breeding birds (n = 161) produced 8 above-average first-generation offspring.

An interaction effect between breeder type and lifespan was detected, but there was no interaction between age-at-first breeding and breeder type (Table 4), despite the ordinary birds beginning breeding at least one year younger than the high-quality birds (Table 5). The ordinary birds had shorter lifespans and therefore lower LRS, with high-quality birds having on average double the longevity of their short-lived conspecifics (Table 5).

DISCUSSION

By tracking reproductive success in yellow-eyed penguins over more than one generation we show that only a small proportion of fledglings survive, recruit, and attempt to breed, however fecundity and survival appears to be an inter-generational trait, with above-average breeders more likely to produce chicks that will be highly successful breeders. Fewer than 2.6% (56 of 2147) of these breeding birds are what we call "super-breeders", that appear to be successful in producing offspring that will themselves survive and go on to contribute disproportionately to the next generation.

Only 10.2% of the sample population of 2147 fledgling yellow-eyed penguins eventually recruited and produced offspring at all, meaning that 89.8% of young fledged did not contribute to the next generation at Boulder Beach. Low juvenile survival is likely to be the principal reason for the low number of penguins recruiting to breeding populations. Only 20.5% of yellow-eyed penguin fledglings survived to adulthood (two years of age), a similar proportion to the 20.8% yellow-eyed penguins resighted as adults at the Boulder Beach complex between 1981 to 1990 (Efford, Darby & Spencer, 1996), however our reported result includes 3.3% of birds that were resighted away from Boulder Beach. Our results (370 of 441 birds surviving to two years and sighted at Boulder Beach, 83.9%) suggest a similar rate of philopatry to Richdale's (1957) study

(c. 81%). Our survival to adulthood rate was higher than the 10.4% of Adélie penguins (*Pygoscelis adeliae)* that survived to age two (Ainley & DeMaster, 1980), but low compared to the range of values for survivorship from fledging to sexual maturity for 19 species of passerines and seabirds (42 - 86%; Newton, 1989). Survivorship to two years was significantly lower than reported in several other studies of seabirds, including 57.6% for common guillemots (*Uria aalge*; Crespin et al., 2006), 41 to 54% for sooty shearwaters (*Puffinus griseus*; Fletcher et al., 2013), and *c.* 77% for king penguins after one year (*Aptenodytes patagonicus*; Saraux et al., 2011): it was even lower than the *c.* 32% of yellow-eyed penguins that survived to age two between 1936 and 1952 (Richdale, 1957).

The probability that birds survive the period between parental care and adulthood has a large influence on population dynamics, but is highly variable (Maness & Anderson, 2013). The most common hypothesis for high rates of mortality in young birds is their lack of experience, poor foraging skills and physical immaturity (Lack, 1954; Ashmole, 1963; Orians, 1969; Dunn, 1972), with positive correlations predicted between body mass and juvenile survival, based on the assumption that heavier juveniles have fat reserves that buffer the food limitation associated with inexperience (Lack, 1966; McClung et al., 2004; Maness & Anderson 2013). Yellow-eyed penguins are sedentary foragers that lack a long-distance migratory phase in their life history, however juveniles undergo a pelagic phase lasting for up to two years, during which time they are sighted only erratically along the coast. No information exists on where juveniles disperse to (Darby & Seddon, 1990), and most mortality occurs during this post-fledging pelagic phase. It is unclear whether the low survival of juvenile penguins in this study is normal or depressed by changing environmental conditions.

This study indicates that while 530 marked chicks (24.7% of the original sample) were seen at Boulder Beach after fledging, 370 were seen at Boulder Beach by age 2 (69.8%), but only 264 survived to breed at least once (49.8%). These figures suggest that juvenile mortality occurs in two or more stages: as high post-fledging mortality due to inexperience, immaturity and lack of skill, and possibly due to seasonal fluctuations in prey availability later in the breeding season when juveniles must prepare for their first annual moult. The difference in juvenile survival between Richdale's (1957) study and ours may be indicative of an adverse change in foraging conditions (Browne et al., 2011; Mattern et al., 2014), entanglement in recreational or commercial fishing gear (Darby & Dawson, 2000), increasing frequency of poor seasons (van Heezik 1990), and competition with or predation by recovering otariid populations (Bradshaw, Lalas & Thompson, 2000; Lalas et al., 2007). Marine pollution that results in disease outbreaks and mass mortality events, have also been hypothesised (e.g. 1990 mass mortality event, Gill & Darby 1993; e.g. diphtheritic stomatitis, Alley et al., 2004; Trathan et al., 2015).

From the sample of 2147 fledglings, the proportions that survived and attempted breeding (12.3%), fledged offspring (10.2%) and fledged offspring that recruited (5.8%) seem low, however, the proportion of birds that attempted breeding and were successful is relatively high (219 of 264, 82.9%). In other words, if a bird was successful in surviving to make a breeding attempt, there was an 83% probability that it would be successful in fledging at least one chick in its lifetime, a 47% (124/264) probability it would fledge at least one chick that would recruit to the breeding population, and a 39% (102/264) probability that the bird would fledge chicks that would recruit and subsequently fledge offspring. The proportion of yellow-eyed penguins surviving to attempt to breed at least once was comparatively lower than in red-billed gulls (*Larus novaehollandiae*, 18 - 22%), little penguins (*Eudyptula minor*, 28 -35%), kittiwakes

(*Rissa tridactyla*, 34 - 42%) and short-tailed shearwaters (*P. tenuirostris*, 69 - 73%); however the proportion of breeding yellow-eyed penguins that produced recruits (47%) is one of the highest, with only kittiwakes having similar recruitment rates (*c.* 41 - 50%) (Coulson, 1988; Wooller et al., 1988; Mills, 1989; Dann & Cullen, 1990; Moreno, 2003). In yellow-eyed penguins, recruitment into the breeding population appears to be driven in part by the higher survival rate of the offspring of a subset of breeders, with high-quality birds, labelled here as "super-breeders", producing more recruits (204 first-generation recruits from 56 birds, 68.9%) than the ordinary breeders (92 first-generation recruits from 181 birds, 31.1%).

There was considerable variation between both male and female penguins that survived to breed in the total number of offspring they fledged. For a long-lived species, the average number of fledged young seems relatively small (female mean = 5.61, male mean = 4.56), however it is within the range of values reported from the few studies that have estimated mean LRS in seabirds, passerines and birds of prey, demonstrating that LRS for many species of birds remain similar as a result of life-history trade-offs (Table 6). Females had shorter lifespans but longer breeding lifespans than males, because females started breeding earlier than males. Females may have more opportunities to breed than males, due to an apparent sex-skew, with males outnumbering females (Richdale, 1957). Inexperience, and a high energetic cost from the first breeding attempt may compromise the survival of young females, whereas males may have more time to hone foraging and predator avoidance skills before being recruited, and because there is a surplus of males each season, sporadic breeding may allow them to have longer lifespans but similar LRS to females, because they do not have to bear the cost of breeding every year. The maximum number of fledged offspring for both male (23) and female yellow-eyed penguins (24) was much higher than mean values, reflecting the highly negatively skewed distribution of LRS

(Fig.2), and consistent with the observation that most individuals produce small numbers of young, and only a few produce many (Newton 1989). However, there was a wide range in the number of young fledged by individual birds regardless of sex, despite the greater cost of reproduction incurred by breeding females. Newton (1989) concluded that LRS is generally similar for males and females in species that lack high levels of sexual dimorphism, which is the case for yellow-eyed penguins (Seddon et al., 2013).

LRS predictors

Lifespan was the strongest correlate of LRS, with the number of offspring produced increasing significantly with increased lifespan. This trend is very common for seabirds (Clutton-Brock, 1988; Newton, 1989; Newton, 1995), and is attributed to a number of factors: increased opportunities for these long-lived birds to breed, the association between success and experience observed in many seabird species (Limmer & Becker, 2009; Saraux et al., 2012), and the general fitness required for a long lifespan. Long-lived birds are the primary contributors to the gene pool in many species, meaning there is likely to be selection for viability (Moreno, 2003; Mauck, Huntington & Grubb, 2004). We found that high-quality breeders had lifespans that were on average double that of ordinary breeders, but they produced 3 to 4 times more offspring in their lifetimes than ordinary birds (Table 5). In other species lifespan explains less of the variance when the number of recruits is examined, as opposed to number of offspring produced (Newton, 1989). In contrast, we found a highly significant relationship between LRS and the number of recruits and successful recruits produced for yellow-eyed penguins, meaning that the characteristics of birds with longer lifespans are likely to be reliable predictors of parental quality for this species.

Age-at-first-breeding was the second strongest predictor of LRS in yellow-eyed penguins, with birds that began breeding later having lower lifetime totals of offspring, due to a decrease in total breeding opportunities (Newton, 1989). The theory of antagonistic pleiotropy suggests that increased early-life fecundity is at the expense of later-life fitness, and can be selected for if selection is stronger at early stages of life, so that early benefits outweigh later costs (Williams, 1957). While there was a difference between the LRS of males and females in this study, no interaction effect could be detected, despite earlier reproduction in females, which may potentially result in accelerated reproductive senescence (Partridge, 1992, Reed et al., 2008). This trend has been observed in several long-lived bird species, which all showed a positive correlation between age-at-first-breeding and survival in females, suggesting a trade-off between early recruitment and lifespan (Ollason & Dunnet ,1978; Ainley & DeMaster, 1980; Pyle et al., 1997; Tavecchia et al., 2001). Individual variation in LRS for yellow-eyed penguins therefore appears to be due to variation in lifespan (1-24 years) and age-at-first-breeding (2-12 years), together determining the length of the breeding lifespan (1-18 years).

It is common for many species of seabirds to show reduced breeding success after changing mates, most likely due to a trade-off in time and energy expenditure for finding a new mate and foraging, and also due to lack of familiarity with the new mate (Ollason & Dunnet, 1978; Coulson & Thomas, 1985; Newton, 1989). In short-tailed shearwaters a mate change results in a temporary decrease in breeding success, but this effect lessens with each new pairing of an individual as breeding experience increases (Wooller et al., 1989), while breeding success of male common guillemots decreased with an increasing number of mates (Lewis et al. 2006). Yellow-eyed penguins that change mates are more likely to experience breeding failure the subsequent year (Setiawan et al., 2005). We did not detect a significant negative effect of number

418 of mates on lifetime number of offspring produced, possibly due to the tendency for longer-lived
419 birds to outlive their mates, resulting in higher overall numbers of mates.

420 **Conservation implications**

421 Chronic and acute stress as a result of climate change, marine pollution, disturbance at terrestrial
422 breeding sites and extreme nutritional stress may decrease LRS, as the cumulative effects of
423 increasing types of stressors force individuals to reduce their investment in productivity, increase
424 breeding skip behaviours (e.g. red-footed boobies *Sula sula*, Cubayanes et al., 2011) or result in
425 breeder mortality (Kitaysky et al., 2010). In black-legged kittiwakes, breeding behaviour is
426 mediated by increased corticosterone production during periods of poor food supply (Kitaysky et
427 al., 2010; Schultner et al. 2013), with luteinising hormone levels decreasing with increased
428 mercury contamination, resulting in increased breeding skips (Tartu et al., 2013). Clarifying the
429 factors that separate the success of the few that produce many offspring from the many that do
430 not may therefore need to take into account the role of chronic or acute stress on the parameters
431 that may be used to measure their fitness. Likewise, birds that contribute disproportionately to
432 successive generations may have higher thresholds for anthropogenic and environmental
433 stressors than average birds. The impact of extreme events on different phenotypes of
434 conspecifics may differ as a consequence of the "super-breeder" phenomenon, since these birds
435 tend to consistently balance high LRS with long-lifespans in a stochastic environment.

436 It appears that the Boulder Beach population of yellow-eyed penguins is sustained by a
437 small proportion of high-quality, long-lived birds, the “super-breeders”. High levels of philopatry
438 may drive high- quality and ordinary breeding recruits to return to their natal area, and once they
439 begin breeding they are likely to remain at these breeding sites for life, which may be hazardous
440 for population stability should either one of their marine or terrestrial habitats become

441 threatened. If circumstances require that it is deemed necessary to protect specific individuals in
442 a population from catastrophe, or to differentially allocate resources due to budget constraints, it
443 would be important to distinguish between potentially very successful breeders and the
444 evolutionary "living dead" (Moreno, 2003). Oiling is the greatest anthropogenic threat to
445 penguins (Trathan et al., 2015), requiring triage of breeders for temporary captive management.
446 The unexplained mass mortalities of adult and juvenile yellow-eyed penguins on the Otago
447 Peninsula in 1990, 1996 and 2013 due to exposure to an unknown toxic agent have presented
448 opportunities to safeguard specific individuals from harm (Gill & Darby, 1993; DOC,
449 unpublished data). While effort should be placed on safeguarding all individuals in a threatened
450 population during a period of catastrophe, only a small proportion of individuals will contribute
451 to the recovery of the population following such an event.

452 Although it seems sensible to focus conservation resources on "super-breeders", the
453 challenge lies in identifying them. The positive relationship between LRS and the number of
454 successful recruits indicates that birds demonstrating relatively high LRS are also those that
455 produce high-quality offspring. Lifespan is the main predictor of LRS, but unfortunately it
456 cannot be calculated until the death of an individual. Age-at-first-breeding can be identified
457 before death, although its association with potential LRS is much weaker, however high-quality
458 birds tended to recruit a year later than ordinary birds.

459 It may be possible to single out birds on the basis of life-history traits that relate to state-
460 based quality. The importance of state-based assessments for yellow-eyed penguins has yet to be
461 fully explored, especially with regard to analysing the immunocompetence of individuals.
462 Disease prevalence has increased in recent years (Alley et al., 2004; Hill et al., 2010; Argilla et
463 al., 2013). Moreno et al. (1998) measured variables related to health state and cell-mediated

immunity between early and late breeders for chinstrap penguins (*P. antarctica*), finding that early breeders experienced better health than later breeders. Female chinstrap penguins with leukocytosis laid smaller eggs, had slower chick growth rates, and were more prone to failure (Moreno et al., 1998). Future studies could investigate state-based aspects that may coincide with age-specific breeding success, in order to gain an understanding of what makes some of these birds resilient and consistently successful breeders. Information about foraging ecology, particularly in young birds is also necessary. Foraging strategies in high quality Adélie penguins have been linked to better provisioning of chicks, suggesting that some birds may be physiologically more capable by virtue of genetic superiority (Lescroël et al., 2010). Given the ongoing decline in the population of yellow-eyed penguins at Boulder beach, management would benefit from further research into how super-breeders and their offspring may contribute to population viability and effective population size.

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740

741 **Table 1**. Breeding and recruitment overview of numbers and percentages of individual yellow-
742 eyed penguins marked between 1981 and 2003 at Boulder Beach, Otago Peninsula, New Zealand
743 (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	264	12.3
Fledged offspring	219	10.2
Fledged first-generation offspring that recruited	124	5.8
Fledged successful first-generation offspring	102	4.8

744

746 **Table 2.** Mean LRS, number of recruits, number of recruits that bred successfully, lifespan, age-
747 at-first-breeding, breeding lifespan, number of breeding attempts and number of mates of female
748 (n = 112) and male (n = 105) yellow-eyed penguins breeding at Boulder Beach, New Zealand.
749 (Var = variance; se = standard deviation; min = minimum; med = median; max = maximum).

Variable	mean	var	se	min	med	max
			FEMALES			
LRS	5.61	26.17	0.48	0	4	24
Recruits	1.60	3.88	0.19	0	1	9
Successful recruits	1.08	2.11	0.14	0	0	7
Lifespan (years)	8.00	25.96	0.48	2	6.5	24
Age at first breeding	3.28	2.02	0.13	2	3	12
Breeding lifespan (years)	4.72	21.25	0.44	0	3	17
Breeding attempts	4.95	14.23	0.36	1	4	16
Total mates	1.97	1.49	0.12	1	2	7
			MALES			
LRS	4.56	19.21	0.43	0	4	23
Recruits	1.11	2.31	0.15	0	1	6
Successful recruits	0.64	1.10	0.10	0	0	5
Lifespan (years)	8.17	20.98	0.45	2	8	21
Age at first breeding	3.87	2.58	0.16	2	3	11
Breeding lifespan (years)	4.30	18.02	0.41	0	3	18
Breeding attempts	4.39	10.36	0.31	1	4	14
Total mates	1.97	1.41	0.12	1	2	6

751 **Table 3**. Model-averaged generalised linear model of lifetime reproductive success (LRS) and
752 life-history parameters of yellow-eyed penguins that were marked at Boulder Beach, New
753 Zealand between 1981 and 2003 (All non-binary data are standardised to have mean = 0 and SD
754 = 1).

755

Coefficients	Estimate	SE	95% Confidence Interval	Relative Importance
(Intercept)*	1.50	0.06	(1.38, 1.61)	-
Sex (Male)	-0.20	0.09	(-0.38, -0.03)	0.88
z (Lifespan)ǂ	0.62	0.05	(0.53, 0.72)	1.00
z (Age at first breeding) ǂ	-0.12	0.05	(-0.22, -0.02)	1.00
z (Total mates)	-0.03	0.04	(-0.10, 0.05)	0.20
Sex (Male): z (Age at first breeding)	0.05	0.07	(-0.09, 0.19)	0.25
Sex (Male): z (Lifespan)	0.07	0.07	(-0.07, 0.20)	0.38

756 *Sex (Female) is the reference category
757 ǂ Significant results
758
759 Model statement: glm (LRS ~ zLIFESPAN + zAGEATFIRSTBREEDING + zTOTALMATES
760 + factor(SEX) + factor(SEX): zAGEATFIRSTBREEDING + factor(SEX): zLIFESPAN
761
762

763 **Table 4.** Model-averaged generalised linear model of lifetime reproductive success (LRS), life-
764 history parameters and breeder quality of yellow-eyed penguins that were marked at Boulder
765 Beach, New Zealand between 1981 and 2003 (All non-binary data are standardised to have mean
766 = 0 and SD = 1).

767

Coefficients	Estimate	SE	95% Confidence Interval	Relative Importance
(Intercept)*	1.19	0.05	(1.09, 1.20)	-
Breeder quality (higher-quality)	0.82	0.09	(0.65, 1.00)	1.00
z (Age at first breeding) ǂ	-0.13	0.06	(-0.26, -0.01)	1.00
z (Lifespan) ǂ	0.63	0.05	(0.53, 0.72)	1.00
Breeder quality (higher-quality): z (Age at first breeding) ǂ	-0.26	0.07	(-0.40, -0.13)	1.00
Breeder quality (higher-quality): z (Lifespan)	0.04	0.07	(-0.06, 0.25)	0.43

768 *Breeder quality (lower-quality) is the reference category
769 ǂ Significant results
770

771 Model statement: glm (LRS ~ zLIFESPAN + zAGEATFIRSTBREEDING + zTOTALMATES
772 + factor(BREEDERQUALITY) + factor(BREEDERQUALITY): zAGEATFIRSTBREEDING +
773 factor(BREEDERQUALITY): zLIFESPAN

775 **Table 5.** Mean LRS, number of first-generation offspring, number of first-generation offspring that bred
776 successfully, lifespan, age-at-first-breeding, breeding lifespan, number of breeding attempts and number
777 of mates of female (n = 112) and male (n = 105) yellow-eyed penguins breeding at Boulder Beach, New
778 Zealand. (Var = variance; se = standard deviation; min = minimum; med = median; max = maximum).
779 Continued overleaf.

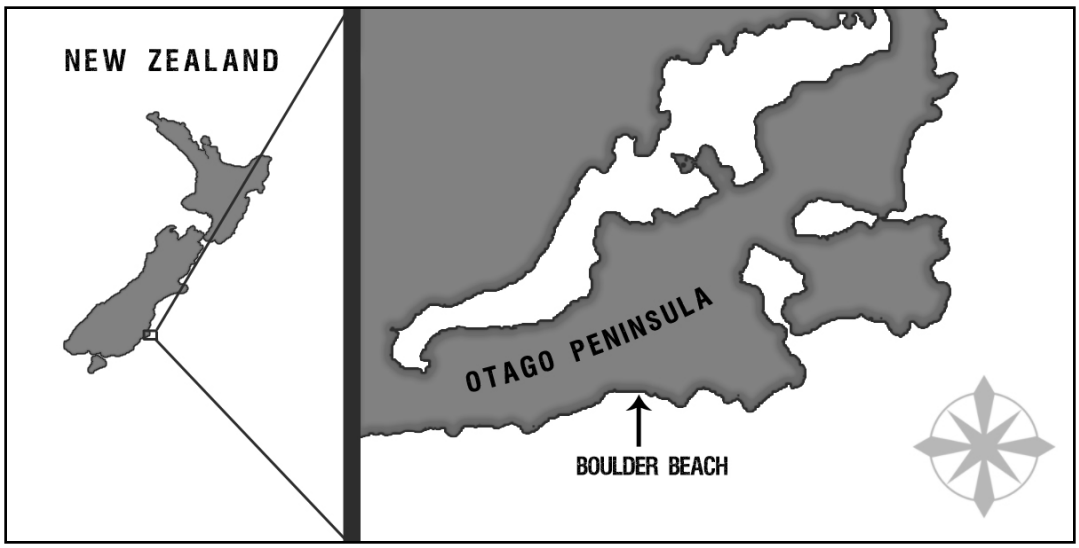
Variable	mean	var	se	min	med	max
	Females (ordinary breeders, n = 80)					
LRS	3.31	8.67	0.33	0	2	13
Recruits	0.63	0.87	0.10	0	0	4
Successful recruits	0.34	0.33	0.06	0	0	2
Lifespan (years)	6.10	14.8	0.43	2	5	22
Age at first breeding	2.96	0.62	0.09	2	3	5
Breeding lifespan (years)	3.14	13.49	0.41	0	2	17
Breeding attempts	3.46	6.94	0.29	1	3	13
Total mates	1.79	1.46	0.14	1	1	7
	Females (high-quality breeders, n = 32)					
LRS	11.34	24.04	0.87	6	10.5	24
Recruits	4.03	3.13	0.31	1	4	9
Successful recruits	2.94	1.74	0.23	1	3	7
Lifespan (years)	12.75	22.65	0.84	5	12	24
Age at first breeding	4.06	4.77	0.39	2	3	12
Breeding lifespan (years)	8.69	18.99	0.77	2	8	17
Breeding attempts	8.66	13.39	0.65	3	8	16
Total mates	2.44	1.29	0.20	1	2	5
	Males (ordinary breeders, n = 81)					
LRS	2.94	7.68	0.31	0	2	13
Recruits	0.52	0.70	0.09	0	0	4
Successful recruits	0.19	0.15	0.04	0	0	1
Lifespan (years)	6.88	13.43	0.41	2	6	17
Age at first breeding	3.73	1.83	0.15	2	3	9
Breeding lifespan (years)	3.15	12.28	0.39	0	2	14
Breeding attempts	3.44	7.30	0.30	1	3	10
Total mates	1.84	1.41	0.13	1	1	6

	Males (high-quality breeders, n = 24)					
LRS	10.04	19.52	0.90	5	9	23
Recruits	3.13	2.55	0.33	1	3	6
Successful recruits	2.17	1.28	0.23	1	2	5
Lifespan (years)	12.54	22.34	0.96	6	10.5	21
Age at first breeding	4.33	5.01	0.46	2	4	11
Breeding lifespan (years)	8.20	18.71	0.87	3	6.5	18
Breeding attempts	7.58	7.64	0.56	4	7	14
Total mates	2.41	1.21	0.22	1	2	6

780

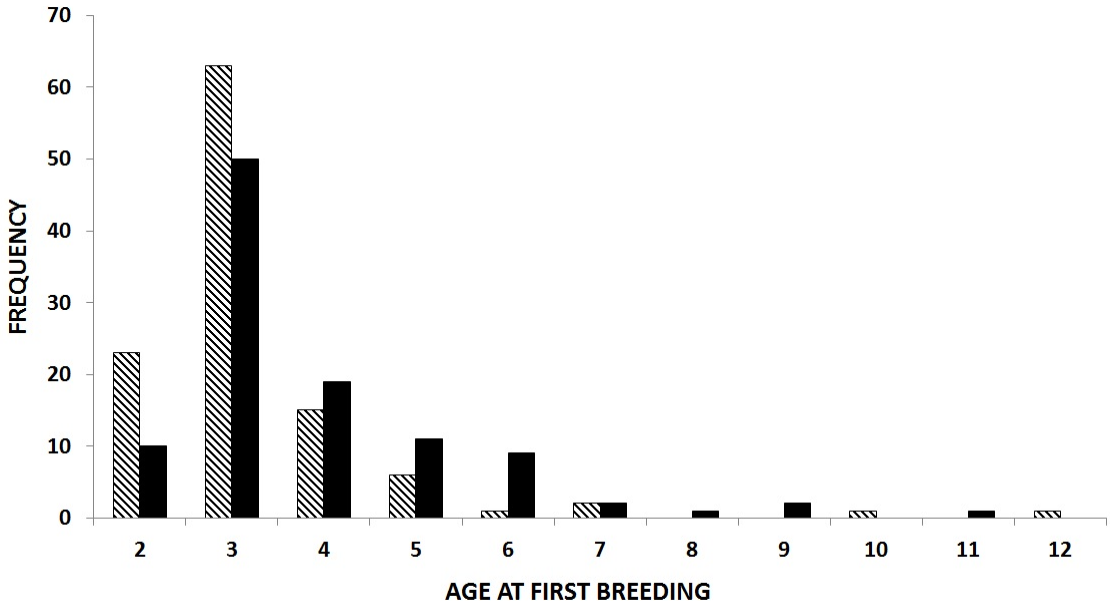
Table 6. Comparison of LRS and maximum number of young fledged by individuals of five different bird species for males and females (where data were available from Coulson 1988; Mills 1989; Dann and Cullen 1990; Korpimäki 1992; Krüger and Lindström 2001; Garamszegi *et al*. 2004).

Species	LRS (Female)	LRS (Male)	Max. fledged (Female)	Max. fledged (Male)
Yellow-eyed penguin (*Megadyptes antipodes*)	5.61	4.56	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	-	-	-



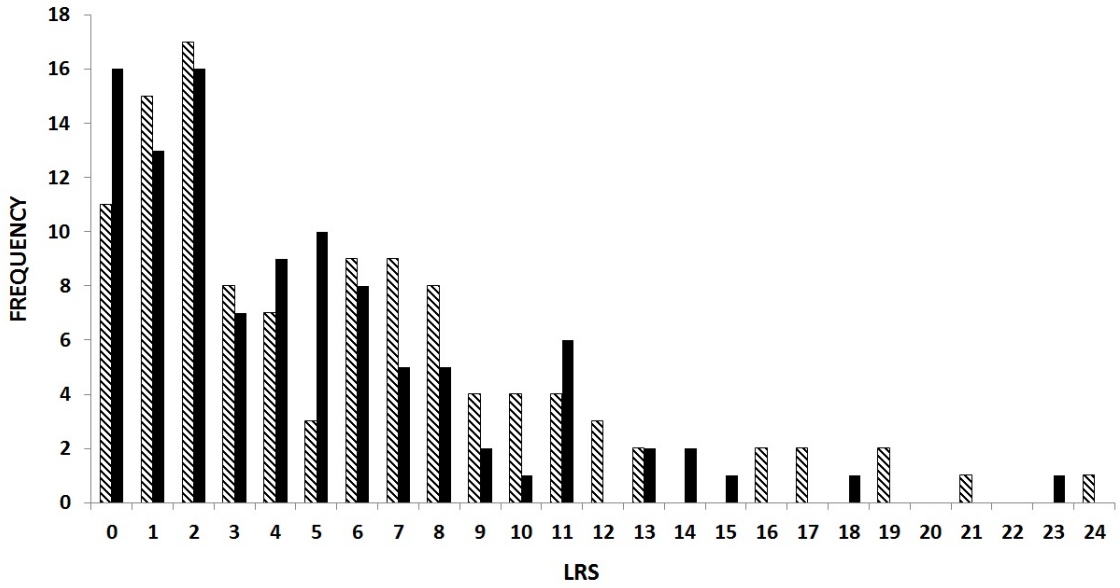
790

791 **Figure 1.** Map showing the location of Boulder Beach on the Otago Peninsula, Dunedin, New
792 Zealand (adapted from McClung *et al*. 2004).



793

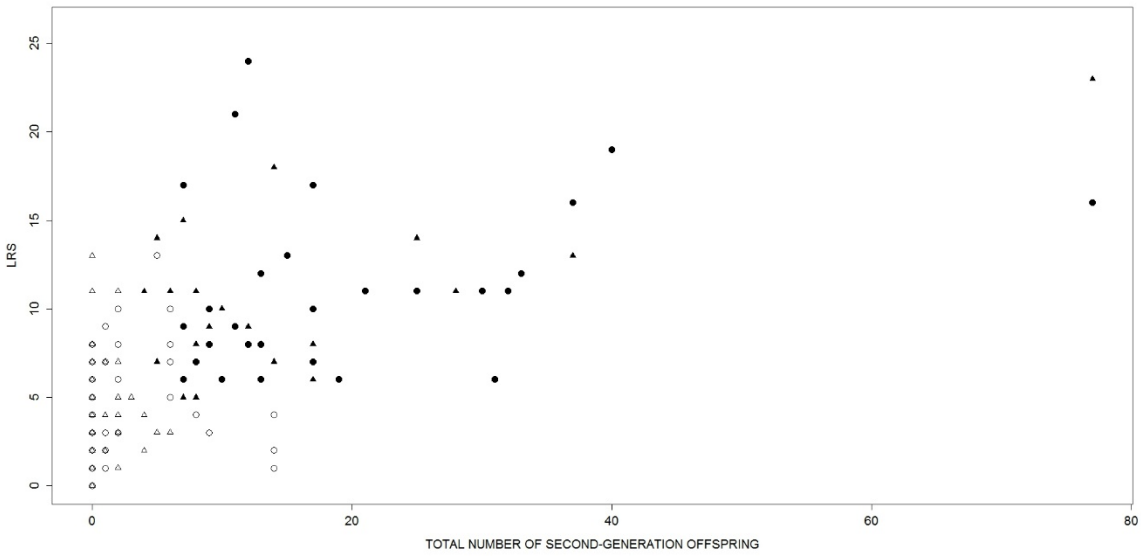
794 **Figure 2.** Age-of-first-breeding of female (striped, n = 112) and male (black, n = 105) yellow-
795 eyed penguins with complete life histories that bred at Boulder Beach, New Zealand.



797

798 **Figure 3.** Frequencies of the total number of chicks fledged (lifetime reproductive success, LRS)
799 by female (striped, n = 112) and male (black, n = 105) yellow-eyed penguins with complete life
800 histories that bred at Boulder Beach, New Zealand.

801



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803

804 **Figure 4.** The relationship between lifetime reproductive success (LRS) and the production of
805 second-generation offspring (grand-offspring) for female (ꗃ = "high-quality breeder", ꗂ =
806 "low-quality breeder", n = 112) and male (□ = "high-quality breeder", ❒ = "low-quality
807 breeder", n = 105) yellow-eyed penguins with complete life histories that bred at Boulder Beach,
808 New Zealand.