Sex-specific costs of reproduction on survival in a long-lived seabird

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22 Costs of reproduction on survival have captured the attention of researchers since Life History

23 Theory (LHT) was formulated. Adults of long-lived species may increase survival by reducing their

24 breeding effort or even skipping reproduction. In this study, we aimed to evaluate the costs of

25 current reproduction on survival and whether skipping reproduction increases adult survival in

26 a long-lived seabird. We used capture-mark-recapture data (1,450 encounters) from two

27 populations of Bulwer's petrel (*Bulweria bulwerii*), breeding in the Azores and Canary Islands,

28 North Atlantic Ocean. Using a multievent model with two different breeding statuses (breeders

29 vs. non-breeders), we calculated probabilities of survival and of transitions between breeding

30 statuses, evaluating potential differences between sexes. Females had lower survival

31 probabilities than males, independent of their breeding status. When considering breeding

32 status, breeding females had lower survival probabilities than non-breeding females, suggesting

33 costs of reproduction on survival. Breeding males had higher survival probabilities than non-

34 breeding males, suggesting that males do not incur costs of reproduction on survival and that

35 only the highest quality males have access to breeding. The highest and the lowest probabilities

36 of skipping reproduction were found in breeding males from the Azores and in breeding

37 males from the Canary Islands, respectively. Intermediate values were observed in the females

38 from both. This result is probably due to differences in the external factors affecting both

39 populations, essentially predation pressure and competition. The existence of sex-specific costs

40 of reproduction on survival in several populations of this long-lived species, may have important

41 implications for species population dynamics.

42

45   **Introduction**

46

47   Life History Theory (LHT) postulates that individuals need to carefully trade off investment in

48   survival, growth and reproduction to maximize lifetime reproductive success [1–3]. As a result,

49   greater investment in one of these traits may result in reduced investment in others. Under

50   different environmental conditions, species, populations or even groups of individuals within

51   the same population, such as a given sex, may invest in life history traits differently, and

52   therefore face different life history trade-offs [4].

53

54   For example, reproduction trades off with survivorship by reducing the allocation of resources

55   for growth or self-maintenance and, depending on the species, the feeding, rearing, and caring

56   of offspring have important consequences for the physical state of progenitors [5]. In addition,

57   reproduction reduces the survivorship of individuals by increasing their vulnerability and

58   predation risk (*e.g.*, when building or attending nests, or when carrying embryos or eggs [6–8]).

59   In turn, predation can modify individual traits such as reproduction in order to reduce predation

60   risk (*e.g.*, reducing the number of offspring when predation risk is high [9,10]). Other aspects of

61   social interactions between populations and individuals, such as competition, can also alter

62   reproduction (*e.g.*, via competition for food, nesting places or mates [11]) or even increase direct

63   mortality [12]. All these costs may differ between sexes since, for example, females typically

64   take on extra energetic costs with parturition or egg-laying, which may compromise their own

65   body condition [13]; and males are most affected by intra and inter-specific competition for nest

66   sites than females [14,15].

67

68   According to the LHT, the trade-off between reproduction and survival differs between short-

69   and long-lived species. To maximize lifetime reproductive success, short-lived species show

70   higher fecundity and tend to invest in current reproductive events to a greater extent than long-

71   lived species, even when this effort may compromise individual survival and future breeding

72   attempts [1,16]. Contrarily, long-lived species have low fecundity, deferred maturity and high

73   adult survival rates [17–19]. Furthermore, progenitors of long-lived species can reduce their

74   reproductive investment and even skip the current breeding attempt, favouring self-

75   maintenance and survival until the next possible breeding attempt (a phenomenon known as

76   reproductive skipping behaviour, intermittent breeding or sabbatical years [20,21]). However,

77   the extent to which the trade-off between survival and reproduction differs between sexes in

78   long-lived species, which experience very different costs associated with reproduction, has been

79   little studied [22–24].

80

81   In this study, we analysed sex-specific costs of reproduction on survival in a long-lived species,

82   the Bulwer's petrel (*Bulweria bulwerii*), at two breeding colonies from two different populations

83   in the Atlantic Ocean. First, as reproduction may reduce the survivorship of individuals [17], we

84   expected lower survival probabilities in breeders than in non-breeders. Second, *a priori*, we did

85   not expect sex-specific costs of reproduction, since in Procellariiformes, females and males share

86   incubation and chick-rearing duties [25]. Females certainly incur the costs of egg production and

87   laying, but this is believed to be counterbalanced by a higher parental investment of males

88   through longer periods of colony attendance during the pre-laying period, longer incubation

89   shifts and/or higher chick provisioning rates [26–28]. Third, in the event of sex-specific costs of

90   reproduction on survival, we would expect the sex with the highest survival to show the highest

91   probability of skipping reproduction, since (a) sabbatical years are considered to increase adult

92   survival [29] and (b) sex-specific survival could imply a limitation in the availability of potential

93   mates [30,31]. Finally, since the predator density and competition for nest sites differs between

94   our two colonies [32,33], we expected to find different effects on the trade-off between survival

95   and reproduction between both. In the colony with higher competition pressure, we expected

96   a lower survival rate for males due to direct mortality from competition, since males tend to

97   defend their nest more than females [34]; and in the colony with higher predation pressure, we

98   expected a high incidence of skipping behaviour for both sexes as a strategy to reduce predation

99   risk until the next possible breeding attempt.

100

101   **Materials and methods**

102   **Species and study colonies**

103   Bulwer's petrel is a small (*ca.* 95 g) Procellariiforme whose maximum recorded longevity is 23

104   years [35]. In the Atlantic Ocean, it breeds on small islets and islands throughout all

105   Macaronesian archipelagos [36]. Like all Procellariiform species, it is socially monogamous, lays

106   a single egg per breeding attempt, and incubation and chick-rearing duties are shared by both

107   sexes [25].

108

109   Fieldwork was conducted at two different North Atlantic colonies situated *ca.* 1370 km apart,

110   namely on Vila Islet (hereafter Vila, Azores Islands; 36°55' N, 25°10' W; *ca.* 50 breeding pairs; J.

111   Bried unpublished data; [37]), where inter-specific competition for nesting places with Cory's

112   shearwaters (*Calonectris borealis*) is the main cause of Bulwer's petrel mortality [12,33]; and on

113   Montaña Clara Islet (hereafter M.Clara, Canary Islands; 29°18' N, 13°32' W; <100 breeding pairs

114   [38]), where the main cause of Bulwer's petrel mortality is presumably predation by Eleonora's

115   falcon (*Falco eleonorae*), which breeds on the islet at high densities (77.7 nests/km² [32,38]).

116

117   **Capture-Mark-Recapture (CMR) sampling strategy**

118   At both colonies, we captured birds in their burrows. Each individual was ringed with a unique

119   stainless-steel ring at its first capture, with every subsequent recapture registered. The dataset

120   considered 1,450 encounters from the two study colonies: Vila (n=261 adults, data from 2007-

121   2012 and 2016) and M.Clara (n=416, 2010-2018). The reproductive performance of the

122   individuals was recorded each year during the entire sampling period on Vila, and for 2015-2018

123   on M.Clara. Forty-five females and 46 males on Vila (17.2 and 17.6% of the total number of

124   adults from Vila, respectively), and 24 females and 46 males on M.Clara (5.8 and 11.1%,

125   respectively) were molecularly sexed following Fridolfsson & Ellegren (1999) [39]. The sex

126   remained unknown for the other individuals. Differences in the sex ratios of sexed individuals

127   are due to different sampling strategies and fieldwork schedules on the two Islets. Capture-

128   mark-recapture data are accessible through a public repository [40]. Total numbers of

129   individuals captured at each colony per breeding status, sex and year (and proportion of each

130   combination of breeding status and sex, per year); and M-array summaries by colony and sex

131   are shown in the ESM 1 in Electronic Supplementary Material.

132

133   **CMR models and statistical analyses**

134   We first evaluated whether the general model for single-state data with only time-dependent

135   parameters (Cormack-Jolly-Seber [CJS] model) was an acceptable starting point for our dataset.

136   To do so, we carried out standard Goodness-Of-Fit (GOF) tests using U-CARE 2.3.4 [41].

137

138   Second, to construct our model, we defined five states: breeders and non-breeders, both by sex,

139   and dead birds. After running preliminary models (not shown), we considered that the unsexed

140   individuals were a mixture of 50% females and 50% males when modelling Initial States (IS)

141   probabilities. We modelled survival (Φ, probability that an individual alive at Year t survives until

142   Year $t+1$) as either constant, conditioned on colony, sex, breeding status (breeders vs. non-

143   breeders), or on the breeding status by sex. In addition, we modelled the probability of

144   Transitions between Breeding Statuses (TBS), since we were interested in the proportion of

145   breeding adults that became non-breeders (*i.e.*, that performed reproductive skipping

146   behaviour). We also checked if differences in TBS occurred between colonies.

147

148   Regarding the detection process, we considered the alternative events of being or not being

149   detected with capture probability (p, probability that a Bulwer's petrel alive and present at the

150   breeding colony at Year t is captured during Year t). We started modelling capture probabilities

151   depending on colony and time to control for the sampling effort and set the years with missing

152   data for each colony. For those individuals detected, we defined six possible events related to

153   their reproductive performance/status and we constructed a multievent model with uncertainty

154   to define how events relate to each of the five states [42]. For more details about the model

155   definition see the ESM 2 in Electronic Supplementary Material.

156

157   CMR models were run using E-SURGE 2.1.4 [43], and model selection was based on the Akaike

158   Information Criterion corrected for overdispersion and small sample sizes (QAICc [44]). The

159   model with the lowest QAICc had the best compromise between bias and variance [45]. In

160   addition, Akaike weights were calculated as an index of the relative plausibility of each model

161   [46]. Following Burnham & Anderson (2002), and once we had selected the best model for IS, Φ,

162   TBS and p (table 1 section A-D), we explored neighbouring models of interest to re-evaluate

163   early-dropped effects (table 1 section E).

164

165   **Results**

166   The overall GOF test for the CJS model was not significant, making it an acceptable point of

167   reference for further models (see the ESM 3 in Electronic Supplementary Material).

168

169   According to the best-supported models (models 9 and 10, table 1), survival probabilities

170   differed for each combination of breeding status and sex, but not between colonies; and capture

171   probabilities varied among colonies, years, and between breeding statuses. ΔQAICc of these two

172   models did not allow ruling out either of them. The main difference between models 9 and 10

173   was in TBS, identical or different between colonies, respectively. Model 10 made more sense

174   from a biological point of view due to the differences between the two islets in habitat

175   availability for Bulwer's petrel and predation pressure (both lower on Vila than on M.Clara; see

176   Discussion). Model 10 considered that breeding females had lower survival probabilities than

177   non-breeding females (mean ± SE: 0.64 ± 0.04 and 0.73 ± 0.07, respectively), whereas breeding

178   males had higher survival probabilities than non-breeding males (0.93 ± 0.04 and 0.80 ± 0.04,

179   respectively; figure 1). Thus, breeding females had the lowest survival rate while breeding males

180   had the highest survival rate (figure 1). Concerning TBS, breeding individuals were more likely to

181   breed again the next year than to take a sabbatical year. The probability of skipping reproduction

182   the next year was highest in the breeding males from Vila and lowest in the breeding males from

183   M.Clara (figure 2; see ESM 4 in Electronic Supplementary Material for more details). Despite

184   differences in TBS and in predation pressures between Vila and M.Clara, the model considering

185   inter-colony differences in survival was not a competitive model (model 11, table 1).

186

187   **Discussion**

188   Contrary to our expectations, survival probabilities varied in an opposite manner between

189   breeders and non-breeders when considering sex, highlighting sex-biased costs of reproduction

190   on survival. The lower survival rate observed in breeding females compared to non-breeding

191   females suggests that the former incur costs of reproduction in terms of survival. These costs

192   may arise from egg production and laying, which implies a higher energetic expense than for

193   males. They have been observed in many other species including Procellariiformes [13,24]. The

194   higher survival of breeding males compared to non-breeding males suggests that high quality

195   males are more likely to obtain mates, and less affected by the trade-off between reproduction

196   and survival than low quality males. Similar results were found in related species, including the

197   Monteiro's storm petrel (*Hydrobates monteiroi*), in which breeders (successful or failed,

198   regardless of sex) had higher survival probabilities than non-breeders [47]. High-quality males

199   may be older or more experienced, since individual quality and breeding performance of males

200   in long-lived species are often related to age or experience [48,49]. However, we were unable

201   to address this question. As in most Procellariiform species, Bulwer's petrels cannot be aged

202   using plumage [25], and during our study very few birds ringed as chicks, and therefore of known

203   age, have returned to breed. Overall, the costs of reproduction that breeding males face, from

204   the pre-laying stage until the end of the chick-rearing period, seem to be lower than those faced

205   by breeding females during the same period. Nevertheless, males are supposed to spend more

206   time ashore than females during the pre-laying period, when they have to defend their burrows

207   against conspecifics [34], making them more vulnerable to injuries or predation. They also invest

208   more time and/or resources than females into incubation and chick-rearing [26–28]. Since

209   predators mainly prey on poor-condition individuals [50], a higher exposure of breeding males

210   to predation could imply a selection against low-quality males, which would ultimately explain

211   the high survival of breeding males.

212

213   The sex bias we found in survival rates can affect the adult sex ratio in favour of males [51],

214   resulting in a reduction of the effective population size with respect to census size that assumes

215   sex parity [30,31]. This male-biased sex ratio would imply a higher number of sabbatical males

216   than females due to a lack of potential mates. As expected, we found this result on Vila, where

217   the higher proportion of sabbatical individuals compared to M.Clara, particularly in males (figure

218   2), is probably favoured by a shortage of suitable nesting places and a negligible predation

219   pressure. On Vila, inter-specific competition with Cory's shearwaters for nesting places

220   represents the main cause of Bulwer's petrel mortality [12,33]. This competition might explain

221   the high proportion of breeders skipping breeding the next year and the low proportion of non-

222   breeding individuals resuming breeding on Vila. In contrast, on M.Clara, the proportion of

223   sabbatical males resuming breeding was higher than the proportion of breeding males becoming

224   sabbatical. This result is possibly related to the presumably higher predation pressure on

225   M.Clara [38], to which males would be more exposed, and which results in new vacancies year

226   after year.

227

228   Studies evaluating the effects of predation on reproductive strategies, both in short- and long-

229   lived species, found decreases in breeding propensity or in investment into rearing duties to

230   ultimately reduce predation risk [10,52,53]. However, the Transitions between Breeding

231   Statuses (TBS) we found on M.Clara (with lower probabilities of skipping reproduction than on

232   Vila) may be also influenced by the effect of predation, which could reduce the intra-specific

233   competition for mates and nesting places on M.Clara [54], allowing birds to breed year after

234   year. Consequently, predation would be playing a key role in shaping life-history traits at this

235   locality (*i.e.*, reproductive investment / skipping reproduction). In addition, under high predation

236   pressure, reducing investment in breeding or skipping reproduction might not necessarily result

237   in higher survival probabilities and future opportunities for reproduction, and the fact that the

238   breeding individuals on M.Clara repeat breeding more often than those individuals from Vila

239   may support this hypothesis. Therefore, predation could explain why life-history traits can vary

240 among conspecific populations, and sometimes in a manner that is not expected under Life-

241 History Theory.

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253

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389

Table 1. Modelling Initial States (IS), survival (Φ), Transitions between Breeding Statuses (TBS) and capture (*p*) probabilities, for Bulwer's petrel on Vila and

391   M.Clara, depending on time (years), sex (without differentiating breeding statuses), breeding status (breedStatus: breeders and non-breeders, without

392   distinguishing sexes), each combination of breeding status and sex (breedStatus/sex) or colony (colony; while ~~colony~~ means no differences between colonies).

393   Within each group of models (A-D), we provide QAICc values in ascending order. For groups B-E, we started to model from the best model obtained in the

394   previous group.

				np	Dev	QAICc	ΔQAICc	Weight
A) Modelling Initial States probabilities (IS):								
1. IS(breedStatus/sex*time)	Φ(c)	TBS(colony)	*p*(colony*time)	67	5,883.6	6,024.2	42.4	0.000
2. IS(breedStatus/sex)	Φ(c)	TBS(colony)	*p*(colony*time)	45	5,945.5	6,038.4	56.5	0.000
B) Modelling survival probabilities (Φ):								
3. IS(breedStatus/sex*time)	Φ(breedStatus/sex)	TBS(colony)	*p*(colony*time)	70	5,860.6	6,007.8	25.9	0.000
4. IS(breedStatus/sex*time)	Φ(sex)	TBS(colony)	*p*(colony*time)	68	5,865.4	6,008.2	26.3	0.000
5. IS(breedStatus/sex*time)	Φ(breedStatus/sex*colony)	TBS(colony)	*p*(colony*time)	74	5,855.7	6,011.8	29.9	0.000
6. IS(breedStatus/sex*time)	Φ(breedStatus)	TBS(colony)	*p*(colony*time)	68	5,877.5	6,020.3	38.4	0.000
7. IS(breedStatus/sex*time)	Φ(colony)	TBS(colony)	*p*(colony*time)	68	5,881.4	6,024.2	42.3	0.000
C) Modelling Transitions between Breeding Statuses probabilities (TBS):								
8. IS(breedStatus/sex*time)	Φ(breedStatus/sex)	TBS(~~colony~~)	*p*(colony*time)	66	5,867.0	6,005.4	23.5	0.000
D) Modelling capture probabilities (*p*):								
9. IS(breedStatus/sex*time)	Φ(breedStatus/sex)	TBS(~~colony~~)	*p*(colony*time) (breedStatus)	**68**	**5,839.1**	**5,981.9**	**0.0**	**0.681**
E) Neighboring models of model 9:								
10. IS(breedStatus/sex*time)	Φ(breedStatus/sex)	TBS(colony)	*p*(colony*time) (breedStatus)	**72**	**5,832.0**	**5,983.6**	**1.7**	**0.285**
11. IS(breedStatus/sex*time)	Φ(breedStatus/sex*colony)	TBS(~~colony~~)	*p*(colony*time) (breedStatus)	72	5,836.6	5,988.2	6.4	0.028
12. IS(breedStatus/sex*time)	Φ(sex)	TBS(~~colony~~)	*p*(colony*time) (breedStatus)	66	5,853.1	5,991.5	9.7	0.005
13. IS(breedStatus/sex*time)	Φ(breedStatus)	TBS(~~colony~~)	*p*(colony*time) (breedStatus)	66	5,860.6	5,999.0	17.1	0.000

395 (c) is constant; 'np' number of estimated parameters; 'Dev' deviance; 'QAICc' quasi-likelihood Akaike information criterion values for overdispersion and small samples; 'ΔQAICc' difference

396 between a specific model and the model with the lowest QAICc value (in bold). Weight is the probability that a model is the expected best model based on QAICc.

397   **Figure 1.** Adult survival probabilities (± 95% CI) of breeding and non-breeding Bulwer's petrels

398   obtained from the best-supported model (model 10, table 1). Photo credit: Raül Ramos.

399   **Figure 2.** Transition probabilities among breeding statuses (± SE) for Vila and M.Clara obtained

400   from the best-supported model (model 10, table 1). Arrow width is proportional to probability

401   estimates.
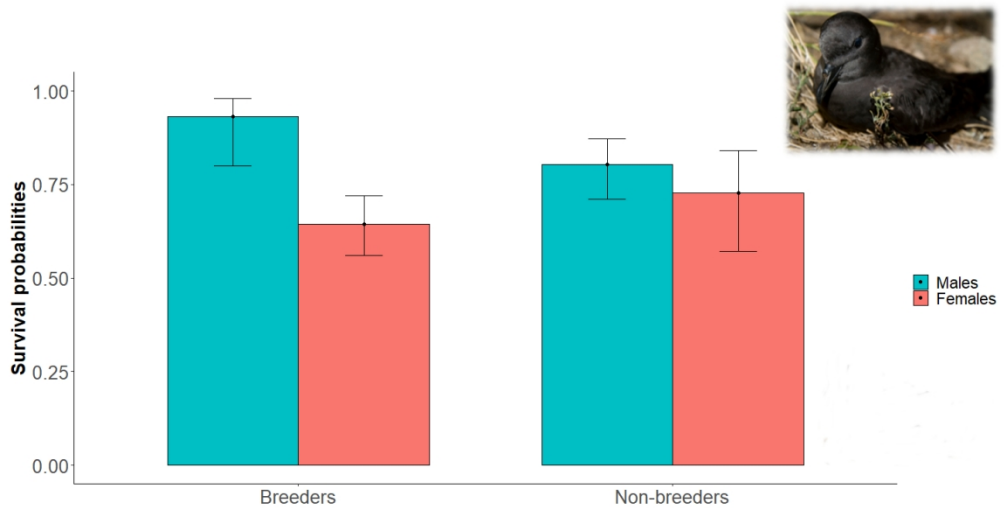
Adult survival probabilities (± 95% CI) of breeding and non-breeding Bulwer's petrels obtained from the best-supported model (model 10, table 1). Photo credit: Raül Ramos.

508x302mm (72 x 72 DPI)
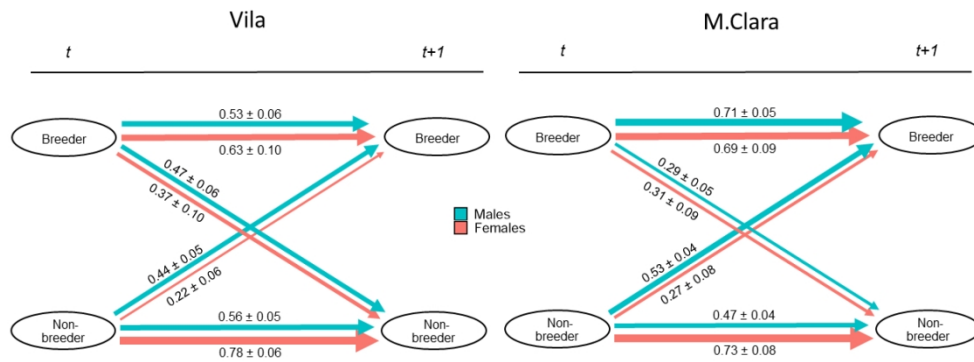
Transition probabilities among breeding statuses (± SE) for Vila and M.Clara obtained from the best-supported model (model 10, table 1). Arrow width is proportional to probability estimates.

338x190mm (96 x 96 DPI)