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Author for correspondence:
Marta Cruz-Flores
e-mail: martacruzflores@gmail.com

†Present address: 8 Avenue de la Reine Nathalie, 64200 Biarritz, France.

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

Marta Cruz-Flores[1], Roger Pradel[2], Joël Bried[3,†], Jacob González-Solís[1] and Raül Ramos[1]

[1]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal 643, Barcelona 08028, Spain
[2]CEFE UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, Montpellier, France
[3]Departamento de Oceanografia e Pescas, Centro Okeanos, MARE (Marine and Environmental Sciences Centre), IMAR and LARSyS Associated Lab, Universidade dos Açores, 9901-862 Horta, Açores, Portugal

MC-F, 0000-0001-9905-4727; JB, 0000-0001-7377-4304; RR, 0000-0002-0551-8605

Costs of reproduction on survival have captured the attention of researchers since Life History Theory (LHT) was formulated. Adults of long-lived species may increase survival by reducing their breeding effort or even skipping reproduction. In this study, we aimed to evaluate the costs of current reproduction on survival and whether skipping reproduction increases adult survival in a long-lived seabird. We used capture-mark-recapture data (1,450 encounters) from two populations of Bulwer's petrel (*Bulweria bulwerii*), breeding in the Azores and Canary Islands, North Atlantic Ocean. Using a multievent model with two different breeding statuses (breeders versus non-breeders), we calculated probabilities of survival and of transitions between breeding statuses, evaluating potential differences between sexes. Females had lower survival probabilities than males, independent of their breeding status. When considering breeding status, breeding females had lower survival probabilities than non-breeding females, suggesting costs of reproduction on survival. Breeding males had higher survival probabilities than non-breeding males, suggesting that males do not incur costs of reproduction on survival and that only the highest quality males have access to breeding. The highest and the lowest probabilities of skipping reproduction were found in breeding males from the Azores and in breeding males from the Canary Islands, respectively. Intermediate values were observed in the females from both. This result is probably due to differences in the external factors affecting both populations, essentially predation pressure and competition. The existence of sex-specific costs of reproduction on survival in several populations of this long-lived species may have important implications for species population dynamics.

1. Introduction

Life History Theory (LHT) postulates that individuals need to carefully trade-off investment in survival, growth and reproduction to maximize lifetime reproductive success [1–3]. As a result, greater investment in one of these traits may result in reduced investment in others. Under different environmental conditions, species, populations or even groups of individuals within the same population, such as a given sex, may invest in life-history traits differently, and therefore face different life-history trade-offs [4].

For example, reproduction trades off with survivorship by reducing the allocation of resources for growth or self-maintenance and, depending on the species, the feeding, rearing and caring of offspring have important

consequences for the physical state of progenitors [5]. In addition, reproduction reduces the survivorship of individuals by increasing their vulnerability and predation risk (e.g. when building or attending nests, or when carrying embryos or eggs [6–8]). In turn, predation can modify individual traits such as reproduction in order to reduce predation risk (e.g. reducing the number of offspring when predation risk is high [9,10]). Other aspects of social interactions between populations and individuals, such as competition, can also alter reproduction (e.g. via competition for food, nesting places or mates [11]) or even increase direct mortality [12]. All these costs may differ between sexes since, for example, females typically take on extra energetic costs with parturition or egg-laying, which may compromise their own body condition [13]; males are most affected by intra- and interspecific competition for nest sites than females [14,15].

According to the LHT, the trade-off between reproduction and survival differs between short- and long-lived species. To maximize lifetime reproductive success, short-lived species show higher fecundity and tend to invest in current reproductive events to a greater extent than long-lived species, even when this effort may compromise individual survival and future breeding attempts [1,16]. Contrarily, long-lived species have low fecundity, deferred maturity and high adult survival rates [17–19]. Furthermore, progenitors of long-lived species can reduce their reproductive investment and even skip the current breeding attempt, favouring self-maintenance and survival until the next possible breeding attempt (a phenomenon known as reproductive skipping behaviour, intermittent breeding or sabbatical years [20,21]). However, the extent to which the trade-off between survival and reproduction differs between sexes in long-lived species, which experience very different costs associated with reproduction, has been little studied [22–24].

In this study, we analysed sex-specific costs of reproduction on survival in a long-lived species, the Bulwer's petrel (*Bulweria bulwerii*), at two breeding colonies from two different populations in the Atlantic Ocean. First, as reproduction may reduce the survivorship of individuals [17], we expected lower survival probabilities in breeders than in non-breeders. Second, *a priori*, we did not expect sex-specific costs of reproduction, since in Procellariiformes, females and males share incubation and chick-rearing duties [25]. Females certainly incur the costs of egg production and laying, but this is believed to be counterbalanced by a higher parental investment of males through longer periods of colony attendance during the pre-laying period, longer incubation shifts and/or higher chick provisioning rates [26–28]. Third, in the event of sex-specific costs of reproduction on survival, we would expect the sex with the highest survival to show the highest probability of skipping reproduction, since (i) sabbatical years are considered to increase adult survival [29] and (ii) sex-specific survival could imply a limitation in the availability of potential mates [30,31]. Finally, since the predator density and competition for nest sites differs between our two colonies [32,33], we expected to find different effects on the trade-off between survival and reproduction between both. In the colony with higher competition pressure, we expected a lower survival rate for males due to direct mortality from the competition, since males tend to defend their nest more than females [34]; in the colony with higher predation pressure, we expected a high incidence of skipping

behaviour for both sexes as a strategy to reduce predation risk until the next possible breeding attempt.

2. Material and methods

(a) Species and study colonies

Bulwer's petrel is a small (*ca.* 95 g) Procellariiforme whose maximum recorded longevity is 23 years [35]. In the Atlantic Ocean, it breeds on small islets and islands throughout all Macaronesian archipelagos [36]. Like all Procellariiform species, it is socially monogamous and lays a single egg per breeding attempt, and incubation and chick-rearing duties are shared by both sexes [25].

Fieldwork was conducted at two different North Atlantic colonies situated *ca.* 1370 km apart, namely on Vila Islet (hereafter Vila, Azores Islands; 36°55′ N, 25°10′ W; *ca.* 50 breeding pairs; J. Bried unpublished data; [37]), where interspecific competition for nesting places with Cory's shearwaters (*Calonectris borealis*) is the main cause of Bulwer's petrel mortality [12,33], and on Montaña Clara Islet (hereafter M.Clara, Canary Islands; 29°18′ N, 13°32′ W; less than 100 breeding pairs [38]), where the main cause of Bulwer's petrel mortality is presumably predation by Eleonora's falcon (*Falco eleonorae*), which breeds on the islet at high densities (77.7 nests km^{-2} [32,38]).

(b) Capture-mark-recapture sampling strategy

At both colonies, we captured birds in their burrows. Each individual was ringed with a unique stainless-steel ring at its first capture, with every subsequent recapture registered. The dataset considered 1,450 encounters from the two study colonies: Vila ($n = 261$ adults, data from 2007 to 2012 and 2016) and M.Clara ($n = 416$, 2010–2018). The reproductive performance of the individuals was recorded each year during the entire sampling period on Vila, and for 2015–2018 on M.Clara. Forty-five females and 46 males on Vila (17.2 and 17.6% of the total number of adults from Vila, respectively), and 24 females and 46 males on M.Clara (5.8 and 11.1%, respectively) were molecularly sexed following Fridolfsson & Ellegren (1999) [39]. The sex remained unknown for the other individuals. Differences in the sex ratios of sexed individuals are due to different sampling strategies and fieldwork schedules on the two Islets. Capture-mark-recapture (CMR) data are accessible through a public repository [40]. Total numbers of individuals captured at each colony per breeding status, sex and year (and proportion of each combination of breeding status and sex, per year), and M-array summaries by colony and sex are shown in the electronic supplementary material, S1.

(c) Capture-mark-recapture models and statistical analyses

We first evaluated whether the general model for single-state data with only time-dependent parameters (Cormack–Jolly–Seber [CJS] model) was an acceptable starting point for our dataset. To do so, we carried out standard Goodness-Of-Fit (GOF) tests using U-CARE 2.3.4 [41].

Second, to construct our model, we defined five states: breeders and non-breeders, both by sex, and dead birds. After running preliminary models (not shown), we considered that the unsexed individuals were a mixture of 50% females and 50% males when modelling Initial States (IS) probabilities. We modelled survival (Φ, probability that an individual alive at Year t survives until Year $t + 1$) as either constant, conditioned on colony, sex, breeding status (breeders versus non-breeders) or on the breeding status by sex. In addition, we modelled the probability of Transitions between Breeding Statuses (TBS), since we were interested in the proportion of breeding adults that became

Table 1. Modelling Initial States (IS), survival (Φ), Transitions between Breeding Statuses (TBS) and capture (p) probabilities, for Bulwer's petrel on Vila and M.Clara, depending on time (years), sex (without differentiating Breeding Statuses), Breeding Status (breedStatus: breeders and non-breeders, without distinguishing sexes), each combination of breeding status and sex (breedStatus/sex) or colony (colony; while colony means no differences between colonies). 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 previous group. (c) is constant; 'np' number of estimated parameters; 'Dev' deviance; 'QAICc' quasi-likelihood Akaike information criterion values for overdispersion and small samples; 'ΔQAICc' difference 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.

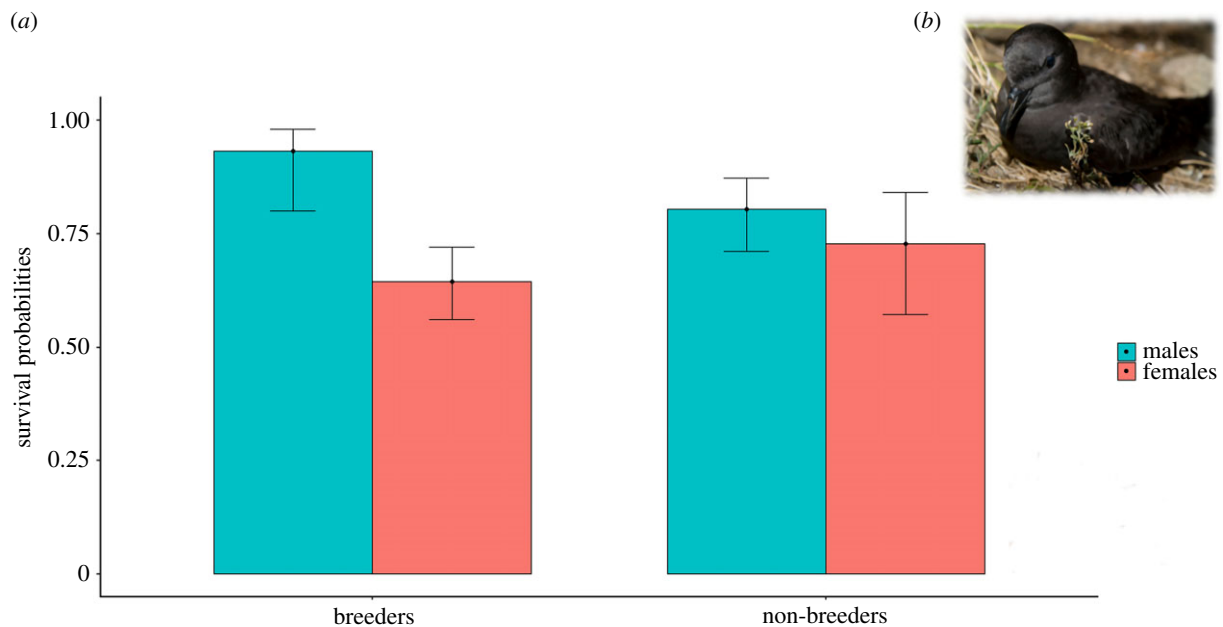| Model				np	Dev	QAICc	ΔQAICc	weight
(A) Modelling Initial States probabilities (IS):								
1. IS(breedStatus/sex*time)	Φ(c)	TBS(colony)	p(colony*time)	67	5883.6	6024.2	42.4	0.000
2. IS(breedStatus/sex)	Φ(c)	TBS(colony)	p(colony*time)	45	5945.5	6038.4	56.5	0.000
(B) Modelling survival probabilities (Φ):								
3. IS(breedStatus/sex*time)	Φ(breedStatus/sex)	TBS(colony)	p(colony*time)	70	5860.6	6007.8	25.9	0.000
4. IS(breedStatus/sex*time)	Φ(sex)	TBS(colony)	p(colony*time)	68	5865.4	6008.2	26.3	0.000
5. IS(breedStatus/sex*time)	Φ(breedStatus/sex*colony)	TBS(colony)	p(colony*time)	74	5855.7	6011.8	29.9	0.000
6. IS(breedStatus/sex*time)	Φ(breedStatus)	TBS(colony)	p(colony*time)	68	5877.5	6020.3	38.4	0.000
7. IS(breedStatus/sex*time)	Φ(colony)	TBS(colony)	p(colony*time)	68	5881.4	6024.2	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	5867.0	6005.4	23.5	0.000
(D) Modelling capture probabilities (p):								
9. IS(breedStatus/sex*time)	Φ(breedStatus/sex)	TBS(colony)	p(colony*time) (breedStatus)	**68**	**5839.1**	**5981.9**	**0.0**	**0.681**
(E) Neighbouring models of model 9:								
10. IS(breedStatus/sex*time)	Φ(breedStatus/sex)	TBS(colony)	p(colony*time) (breedStatus)	**72**	**5832.0**	**5983.6**	**1.7**	**0.285**
11. IS(breedStatus/sex*time)	Φ(breedStatus/sex*colony)	TBS(colony)	p(colony*time) (breedStatus)	72	5836.6	5988.2	6.4	0.028
12. IS(breedStatus/sex*time)	Φ(sex)	TBS(colony)	p(colony*time) (breedStatus)	66	5853.1	5991.5	9.7	0.005
13. IS(breedStatus/sex*time)	Φ(breedStatus)	TBS(colony)	p(colony*time) (breedStatus)	66	5860.6	5999.0	17.1	0.000

3

4

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

non-breeders (i.e. that performed reproductive skipping behaviour). We also checked if differences in TBS occurred between colonies.

Regarding the detection process, we considered the alternative events of being or not being detected with capture probability (*p*, probability that a Bulwer's petrel alive and present at the breeding colony at Year *t* is captured during Year *t*). We started modelling capture probabilities depending on colony and time to control for the sampling effort and set the years with missing data for each colony. For those individuals detected, we defined six possible events related to their reproductive performance/ status and we constructed a multievent model with uncertainty to define how events relate to each of the five states [42]. For more details about the model definition see the electronic supplementary material, S2.

CMR models were run using E-SURGE 2.1.4 [43], and model selection was based on the Akaike Information Criterion corrected for overdispersion and small sample sizes (QAICc [44]). The model with the lowest QAICc had the best compromise between bias and variance [45]. In addition, Akaike weights were calculated as an index of the relative plausibility of each model [46]. Following Burnham & Anderson [44], and once we had selected the best model for IS, Φ, TBS and *p* (table 1 section A-D), we explored neighbouring models of interest to re-evaluate early dropped effects (table 1 section E).

3. Results

The overall GOF test for the CJS model was not significant, making it an acceptable point of reference for further models (see the electronic supplementary material, S3).

According to the best-supported models (models 9 and 10, table 1), survival probabilities differed for each combination of breeding status and sex, but not between colonies; capture probabilities varied among colonies, years and between breeding statuses. ΔQAICc of these two models did not allow ruling out either of them. The main difference between models 9 and 10 was in TBS, identical or different between colonies, respectively. Model 10 made more sense from a biological point of view due to the differences between the two islets in habitat availability for Bulwer's petrel and

predation pressure (both lower on Vila than on M.Clara; see Discussion). Model 10 considered that breeding females had lower survival probabilities than non-breeding females (mean ± s.e.: 0.64 ± 0.04 and 0.73 ± 0.07, respectively), whereas breeding males had higher survival probabilities than non-breeding males (0.93 ± 0.04 and 0.80 ± 0.04, respectively; figure 1). Thus, breeding females had the lowest survival rate while breeding males had the highest survival rate (figure 1). Concerning TBS, breeding individuals were more likely to breed again the next year than to take a sabbatical year. The probability of skipping reproduction the next year was highest in the breeding males from Vila and lowest in the breeding males from M.Clara (figure 2; see electronic supplementary material, S4, for more details). Despite differences in TBS and in predation pressures between Vila and M.Clara, the model considering inter-colony differences in survival was not a competitive model (model 11, table 1).

4. Discussion

Contrary to our expectations, survival probabilities varied in an opposite manner between breeders and non-breeders when considering sex, highlighting sex-biased costs of reproduction on survival. The lower survival rate observed in breeding females compared to non-breeding females suggests that the former incur costs of reproduction in terms of survival. These costs may arise from egg production and laying, which implies a higher energetic expense than for males. They have been observed in many other species including Procellariiformes [13,24]. The higher survival of breeding males compared to non-breeding males suggests that high-quality males are more likely to obtain mates, and less affected by the trade-off between reproduction and survival than low-quality males. Similar results were found in related species, including the Monteiro's storm petrel (*Hydrobates monteiroi*), in which breeders (successful or failed, regardless of sex) had higher survival probabilities than non-breeders [47]. High-quality males may be older or more experienced, since individual quality and breeding performance of males
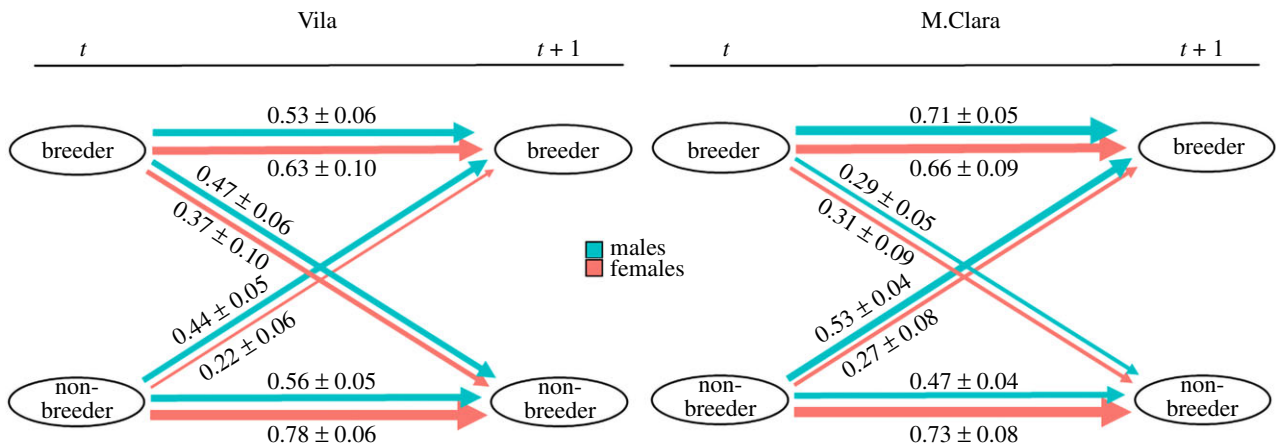
Figure 2. Transition probabilities among breeding statuses (±s.e.) for Vila and M.Clara obtained from the best-supported model (model 10, table 1). Arrow width is proportional to probability estimates.

in long-lived species are often related to age or experience [48,49]. However, we were unable to address this question. As in most Procellariiform species, Bulwer's petrels cannot be aged using plumage [25], and during our study, very few birds ringed as chicks, and therefore of known age, have returned to breed. Overall, the costs of reproduction that breeding males face, from the pre-laying stage until the end of the chick-rearing period, seem to be lower than those faced by breeding females during the same period. Nevertheless, males are supposed to spend more time ashore than females during the pre-laying period, when they have to defend their burrows against conspecifics [34], making them more vulnerable to injuries or predation. They also invest more time and/or resources than females into incubation and chick-rearing [26–28]. Since predators mainly prey on poor-condition individuals [50], a higher exposure of breeding males to predation could imply a selection against low-quality males, which would ultimately explain the high survival of breeding males.

The sex bias we found in survival rates can affect the adult sex ratio in favour of males [51], resulting in a reduction of the effective population size with respect to census size that assumes sex parity [30,31]. This male-biased sex ratio would imply a higher number of sabbatical males than females due to a lack of potential mates. As expected, we found this result on Vila, where the higher proportion of sabbatical individuals compared to M.Clara, particularly in males (figure 2), is probably favoured by a shortage of suitable nesting places and a negligible predation pressure. On Vila, interspecific competition with Cory's shearwaters for nesting places represents the main cause of Bulwer's petrel mortality [12,33]. This competition might explain the high proportion of breeders skipping breeding the next year and the low proportion of non-breeding individuals resuming breeding in Vila. By contrast, on M.Clara, the proportion of sabbatical males resuming breeding was higher than the proportion of breeding males becoming sabbatical. This result is possibly related to the presumably higher predation pressure on M.Clara [38], to which males would be more exposed, and which results in new vacancies year after year.

Studies evaluating the effects of predation on reproductive strategies, both in short- and long-lived species, found decreases in breeding propensity or in investment into rearing duties to ultimately reduce predation risk [10,52,53]. However, the TBS we found on M.Clara (with lower

probabilities of skipping reproduction than on Vila) may be also influenced by the effect of predation, which could reduce the intra-specific competition for mates and nesting places on M.Clara [54], allowing birds to breed year after year. Consequently, predation would be playing a key role in shaping life-history traits at this locality (i.e. reproductive investment/skipping reproduction). In addition, under high predation pressure, reducing investment in breeding or skipping reproduction might not necessarily result in higher survival probabilities and future opportunities for reproduction, and the fact that the breeding individuals on M.Clara repeat breeding more often than those individuals from Vila may support this hypothesis. Therefore, predation could explain why life-history traits can vary among conspecific populations, and sometimes in a manner that is not expected under LHT.

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