S02-3　The trade-off between survival and reproduction in long-lived birds, and the role of individual quality

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Abstract　We tested the influence of individual body mass on survival and reproductive performance in the blue petrel, *Halobaena caerulea*. Body mass varied between and within individuals, as well as between reproductive states: non-breeders were lighter than failed and successful breeders, and failed breeders were lighter than successful breeders. The probability of survival was affected by individual body mass, particularly for first time failed breeders which had a lower probability of survival than experienced breeders. This suggests the existence of a costs-of-first reproduction on survival, and that first reproduction may act as a filter selecting for individuals of intrinsically high quality. Non- and failed breeders had a higher probability of breeding failure in the next years than successful breeders, suggesting that these birds were poor quality individuals. This was reinforced by the fact that non-breeders had a high probability of remaining so, and by the fact that non-breeders and failed breeders had a low probability of becoming successful breeders. The results indicate that body mass is a good indicator of individual quality in blue petrels.

Key words　Blue petrel, Body mass, Reproduction costs, Individual quality, Multistate capture-recapture models, Survival probability, Trade-offs

1　Introduction

Life-history theory predicts that animals balance their investment in young raised against their own chance to survive and reproduce in the future (Williams, 1966; Roff, 1992; Stearns, 1992). This trade-off, referred to as the cost of reproduction, holds a central place in life-history theory. Long-lived seabirds are good candidates for models to detect these costs. They can be expected to be more restrictive than short-lived birds in the degree to which they exhibit increased effort, because even a small reduction in adult survival will reduce the number of subsequent breeding attempts, thereby lowering lifetime reproductive success considerably (Reznick, 1985; Roff, 1992; Stearns, 1992). However, at least two factors are likely to confound measurements of this trade-off in the wild. First, differences can arise in the amount of energy individuals acquire and allocate to various functions. In that case, we might expect some (high quality) individuals to perform well in both reproduction and survival, and other (low quality) individuals to die sooner (Curio, 1983; Reznick, 1992; Viallefont et al., 1995; Cam et al., 1998). Secondly, there can be variation in resource availability affecting energy acquisition and allocation (Erikstad et al., 1998; Orzack and Tuljapurkar, 2001).

Theoretical models examining the optimal phenotypic balance between reproduction and adult survival under variable breeding conditions have recently investigated the second issue (Erikstad et al., 1998). However, very little is known of the influence of individual quality on the costs of reproduction. Here, we use a capture-recapture dataset of blue petrels (*Halobaena caerulea*) to test the influence of body condition, as an indicator of individual quality, on survival and reproductive performance.

2　Materials and methods

This study was conducted on Mayes Island in the Kerguelen group, South Indian Ocean (48°38'S, 68°38'E). Each year between 1987 and 2001, 72 to 233 burrows of blue petrels were monitored (see Chastel et al., 1995a). All birds found in burrows were given individual leg bands and their identity recorded. Burrows were checked a few days after laying to identify the two breeding partners, and after hatching and fledging to record hatching and breeding success respectively. Each bird captured at the colony was classified either as a non-breeder (no egg laid), as a failed breeder (when the bird did not successfully hatch its egg or fledge its chick), or as a successful breeder (when the bird fledged a chick).

Body mass at the onset of the breeding period (measured to the nearest 2 g with a 300 g Pesola balance) was recorded each year from birds caught in their burrows. In this data set we used birds weighed after the pre-laying exodus (Warham, 1990), when birds arrive from the sea to start their first incubation shift. Although body mass is partly the result of structural body size and body fat reserves (Piersma and Davidson, 1991), earlier studies have demonstrated that in the blue petrel, body mass alone is a good indicator of body reserves (Chastel et al., 1995a). Consequently, we used body mass as a surrogate for body condition.

From this long-term study we extracted individual capture histories, including information on whether an individual was re-sighted each breeding season, and if so, on its breeding state: 1 = non-breeder, 2 = failed breeder, 3 = successful breeder. Data were analyzed using multistate capture-recapture models (Brownie et al., 1993) and program MARK (White and Burnham, 1999). These models included three kinds of parameters: recapture probability p_{r*t}, survival rate S_{r*t}, and conditional transition probability Ψ_{r*t} (Nichols et al., 1994). In order to draw inferences about the evolutionary consequences of breeding successfully, unsuccessfully or not at all, we first investigated two complementary fitness components, estimating and comparing (1) survival of successful, failed and non-breeders, and (2) the respective probabilities that these three categories of birds would breed again, given their survival. Then, because we wanted to draw inferences on the cost of first reproduction to test the hypothesis that poor quality individuals die sooner, we started our model selection by using a model with two age classes for survival and state transition probabilities: first time breeders *versus* experienced breeders.

For non-breeders, we only considered one age class since there was no cost associated with reproduction. Because we wanted to test for the effect of the mean body mass of individuals on transition and survival probabilities across years, we started with a model where survival and transition probabilities were constant across years but state specific. Capture probabilities were not constrained and were state and time dependent. Thus, we derived our initial model ($S_{r,s*a2}p_{u*t}\Psi_{u*a2}$), where $r = 0$ (not seen) or 1 (non-breeder); $s = 0$ (not seen), 2 (failed breeder), or 3 (successful breeder); $u = 0$ (not seen), 1 (non-breeder), 2 (failed breeder), or 3 (successful breeder); a_2 is the age with two age classes; and t is time. As goodness-of-fit tests suitable for multistate capture-recapture models do not exist, we performed a goodness-of-fit test of the Cormack-Jolly-Seber model with all states pooled using the program U_CARE (Choquet et al., 2001).
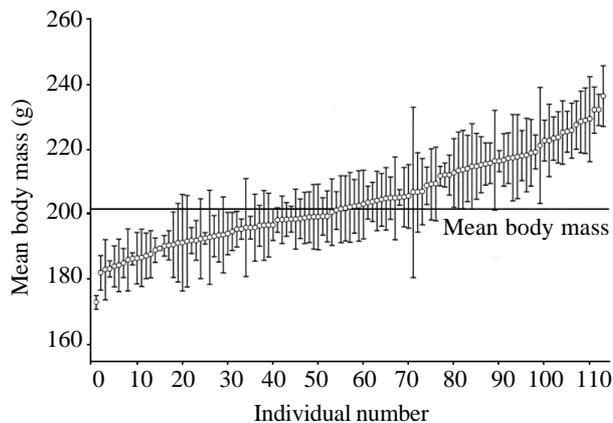
Because we detected dependence in sighting probabilities (see Results: goodness-of-fit tests), we used the modification proposed by Pradel (1993) for trap dependence. However, even when accounting for trap dependence in sighting probabilities, the goodness-of-fit test still indicated significant lack of fit. To account for that extra-binomial variation, we computed a conservative variance inflation factor, $\hat{c}$ (see Lebreton et al., 1992). Consequently, we started our model selection from the general model ($S_{r,s*a2}p_{u*t*m}\Psi_{u*a2}$), where m is trap dependence. We used the quasi-likelihood Akaïke's Information Criterion adjusted for sample size, QAICc (Akaïke, 1973; Lebreton et al., 1992) to select parsimonious models for the data; the model with the lowest QAICc was selected.

A particular kind of model resulted, where state-specific parameters are modeled as a function of mean individual body mass on a logit scale (Lebreton et al., 1992). For each individual we calculated the average body mass across years during the incubation. This mean individual mass was then used as an individual covariate in our modeling. For example, survival was modeled as a function of mean individual body mass using the equation: logit (S_r) = $a + b \times$ *mass*, where a is an intercept parameter, b is a slope parameter and *mass* is the mean individual body mass.

3   Results

3.1   Body mass and reproductive success

Body mass was variable both within and between individuals (Fig. 1). Body mass varied between years and reproductive status *GLM* using SAS (2001), with individual number nested within status to account for related samples of birds which have been treated for several years; year:
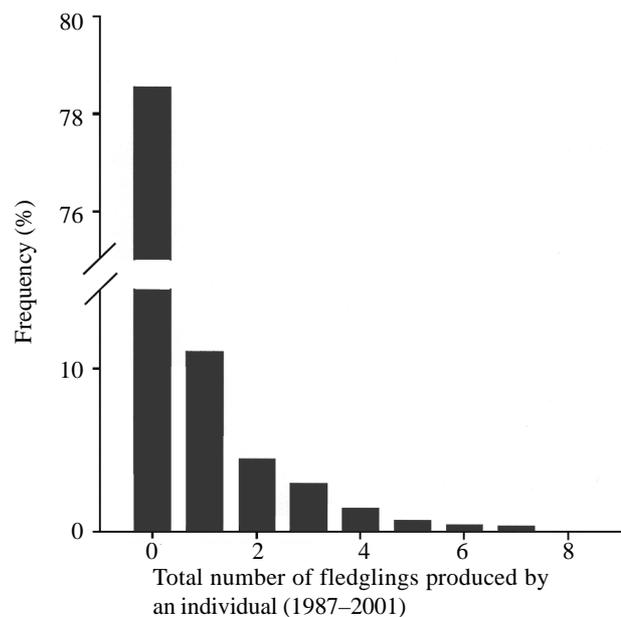

Fig. 1   Mean (± *SD*) body mass for 113 individual blue petrels ranked according to body mass
The plain horizontal line indicates the grand mean body mass for all individuals across years.

Fig. 2   Percentage of individual blue petrels in the studied population that produced from 0 to 8 chicks between 1987 and 2001

$F_{14,957} = 17.73$, $P < 0.0001$; status (individual): $F_{1552,957} = 1.76$, $P < 0.0001$; year*status: $F_{27,957} = 2.12$, $P = 0.0008$. Successful breeders were heavier than failed breeders (post-hoc Tukey test = 2.479, $P = 0.038$) and non-breeders (post-hoc Tukey test = 11.104, $P < 0.001$), and failed breeders were heavier than non-breeders (post-hoc Tukey test = 8.625, $P < 0.001$). During the study period, a high proportion of the population did not produce any chicks (Fig. 2), and the number of chicks produced by individuals was positively correlated with the mean individual body mass (ANOVA: $F_{7,556} = 2.999$, $P = 0.004$).

3.2 Goodness-of-fit tests

The goodness-of-fit test of the initial model ($S_{r,s*a2}p_{u*t}\Psi_{u*a2}$) indicated that this model fitted the data poorly ($\chi^2 = 368.117$, $df = 74$, $P < 0.001$), and that there was trap dependence (see Pradel 1993). After taking into account trap dependence, the goodness-of-fit test of the general model ($S_{r,s*a2}p_{u*t*m}\Psi_{u*a2}$) was still unsatisfactory ($\chi^2 = 104.435$, $df = 62$, $P = 0.0004$). In order to correct for over-dispersion, we used an inflation factor in the remaining analysis, $\hat{c}=1.684$. This inflation factor remained well below 3 as recommended by Lebreton et al. (1992).

3.3 Modeling recapture, survival and transition probabilities

Examination of temporal variation in recapture probabilities suggested that recapture rates varied with year (Table 1, model 4 vs. model 8) and state (model 4 vs. model 5). A model where trap dependent temporal variations of state-specific parameters are parallel on a logit scale (model 6) was not preferred to model 4. We could reduce the number of parameters by setting capture probabilities constant for non-breeders and successful breeders but time dependent for failed breeders (model 3). As we could not reduce further the number of parameters corresponding to recapture probabilities, we continued our modeling with model 3. In this model, recapture probabilities varied between years for failed breeders, but were constant for successful breeders (≈ 1.0) and non-breeders (0.557 ± 0.047).

A model without an age effect on transition probabilities was preferred to a model where transition probabilities

were only state dependent (model 2 vs. model 3). However, transition probabilities were clearly state dependent (model 2 vs. model 7). Consequently, our best model before integrating the effect of body mass was the model ($S_{r,s*a2}p_{NB*m, FB*t*m, SB*m}\Psi_u$), which indicated that blue petrel survival differed between breeding states and the age classes of breeders. Parameter estimates from this model indicate that the survival probabilities of non-breeders (0.863 ± 0.011) are significantly lower than those of failed (0.915 ± 0.021) and successful (0.957 ± 0.020) breeders. Survival probabilities are also lower for first time breeders than for experienced breeders, especially among those that failed (Fig. 3); and survival probabilities for first time failed breeders were lower than for non-breeders (Fig. 3A). The probability of both non-breeders and failed breeders becoming successful breeders was low (Fig. 3B). By contrast, non-breeders and failed breeders had a much higher probability of respectively becoming and remaining failed breeders (Fig. 3B). Successful breeders had a roughly similar chance of remaining successful or failing (and not breeding) (Fig. 3B).

We then examined the effect of individual body mass on survival and transition probabilities. Incorporating body mass as a covariate in our best QAICc model greatly improved the fit of the model (model 1 vs model 2; Table 1). This indicated a strong effect from individual mass on both survival probabilities and breeding state transition probabilities. In our attempts to reduce the number of parameters, we tried to eliminate the interactions between breeding status and body mass. The best model retained was $S_{r*mass, s+a2+mass}p_{NB*m, FB*t*m, SB*m}\Psi_{u*mass}$. Slope estimates from this model indicated that the survival probability of first time failed breeders was related to body mass almost significantly (slope = 9.525 ± 8.525), but that the survival probability of non-breeders and experienced breeders was not related to body mass (slope = 0.795 ± 0.609 and -0.823 ± 1.425, respectively). Slope estimates between state transition probabilities and body mass indicated that the probability of a non-breeder or a failed breeder breeding successfully increased with body mass (Fig. 3C; slope = 2.604 ± 0.932 and 1.598 ± 1.260, respectively). By contrast, the probability of being a non- or a failed breeder tended to decrease with body mass for failed breeders (slope =

Table 1 Modeling recapture, survival and transition probabilities between states for blue petrels at Mayes Island, Kerguelen Archipelago, between 1987 and 2001

Model	QAICc	ΔQAICc	#	DEV
1) ($S_{r*mass, s+a2+mass}p_{NB*m, FB*t*m, SB*m}\Psi_{u*mass}$)	**5 313.18**	**0.00**	**45**	**5 221.43**
2) ($S_{r, s*a2}p_{NB*m, FB*t*m, SB*m}\Psi_u$)	5 348.28	35.09	54	5 237.75
3) ($S_{r, s*a2}p_{NB*m, FB*t*m, SB*m}\Psi_{u*a2}$)	5 358.74	45.55	60	5 235.61
4) ($S_{r,s*a2}p_{u*t*m}\Psi_{u*a2}$)	5 386.64	73.46	98	5 182.23
5) ($S_{r,s*a2}p_{t*m}\Psi_{u*a2}$)	5 414.45	101.26	44	5 324.77
6) ($S_{r,s*a2}p_{u+t+m}\Psi_{u*a2}$)	5 425.70	112.52	37	5 350.51
7) ($S_{r, s*a2}p_{NB*m, FB*t*m, SB*m}\Psi$)	5 431.52	118.34	49	5 331.44
8) ($S_{r,s*a2}p_{u*m}\Psi_{u*a2}$)	5 452.49	139.30	23	5 406.03

The sign # indicates the number of parameters of the model, and DEV is the model deviance. For model notations, see Methods. The selected model is indicated in bold characters.
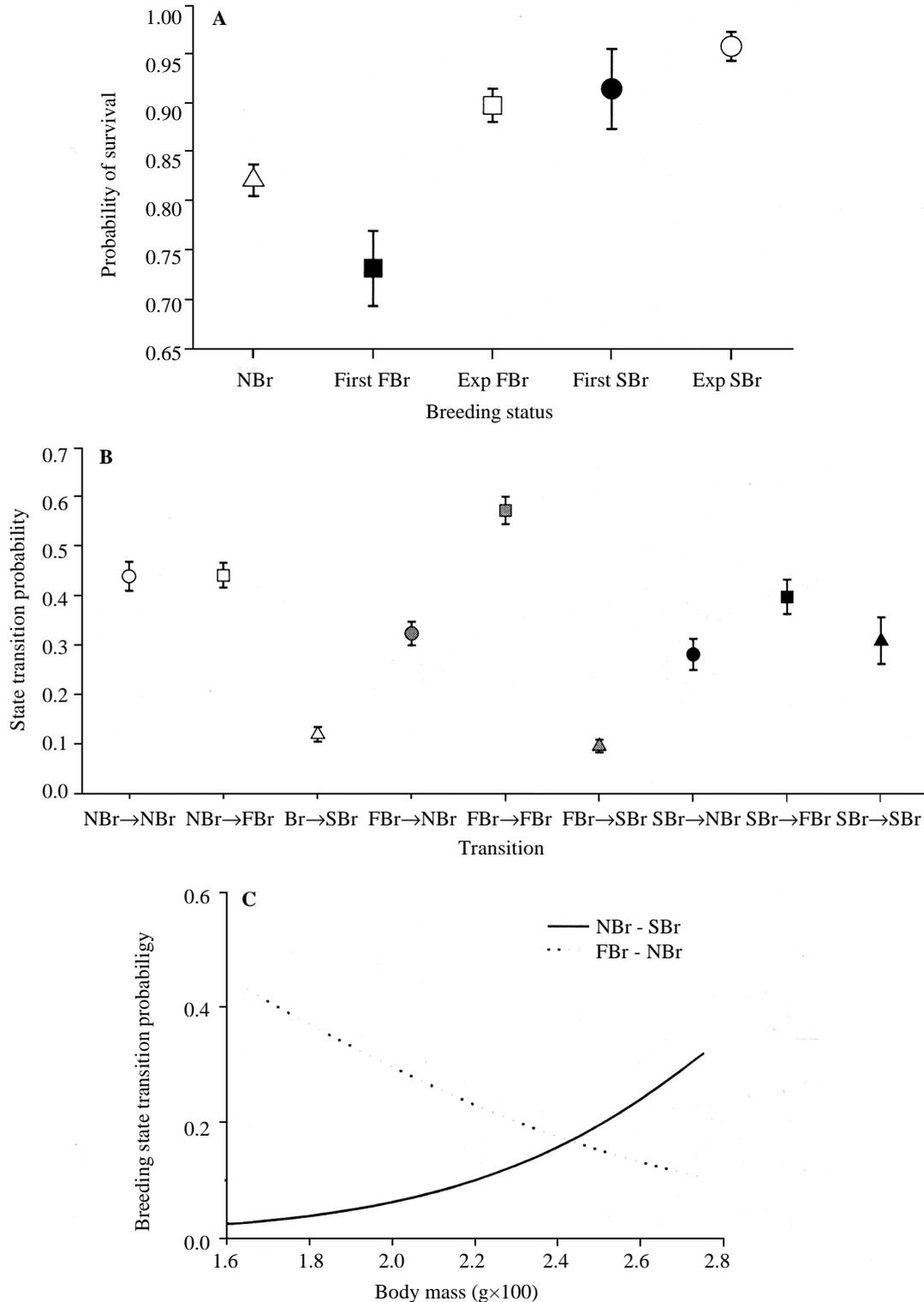
Fig. 3 A: Adult survival probability estimates as a function of the breeding status of blue petrels at Kerguelen Islands; B: Annual state transition probability estimates for blue petrels at Kerguelen Islands; C: Breeding state transition probabilities modeled as a function of body mass

In subfig. A: NBr = non-breeders (open triangle), First FBr = first time failed breeders (filled square), Exp FBr = experienced failed breeders (open square), First SBr = first time successful breeders (open circle), Exp SBr = experienced successful breeders (filled circle). Estimates are from model $S_{r,\ s*a2}\,p_{NB*m,\ FB*t*m,\ SB*m}\,\Psi_u$; bars indicate ± *SE*. In subfig. B: NBr = non-breeder, FBr = failed breeder, SBr = successful breeder. Estimates are from model ($S_{r,\ s*a2}\,p_{NB*m,\ FB*t*m,\ SB*m}\,\Psi_u$); bars indicate ± *SE*. In subfig. C: estimates are from model ($S_{r*mass,\ s+a2+mass}\,p_{NB*m,\ FB*t*m,\ SB*m}\,\Psi_{u*mass}$).

−1.669±1.352). No other relationship between state transition probabilities and body mass was significant.

4 Discussion

In blue petrels, individual body mass varies significantly between individuals. Interestingly, we recorded heavier individuals producing more fledglings during their breeding life than lighter birds. Previous work on blue petrels has revealed that body mass is a major factor affecting the decision to breed and the breeding output of individuals, heavier individuals having a higher probability of breeding successfully than lighter ones (Chaurand and Weimerskirch, 1994; Chastel et al., 1995a, 1995b). Here we have shown that mean individual body mass measured over several years, although variable from year to year, may be used as a surrogate of individual quality since it partly reflects the probability of breeding and the breeding output of an individual during its breeding life. This is an important finding because it is often difficult to identify a state variable reflecting individual quality. Although body mass is a dynamic variable (McNamara and Houston, 1996), in blue petrels it can be viewed as good an indicator of individual quality as in common terns, *Sterna hirundo* (Wendeln and Becker, 1999). Furthermore, there is evidence that some individuals are consistently heavier than others, notwithstanding variation between years (Barbraud and Weimerskirch, unpublished data).

Survival in non-breeders averaged lower than in failed breeders, which in turn was lower than in successful breeders. Because of the influence of body mass (i.e., individual quality) on reproductive status, we suspect that these differences are linked to differences in individual quality, as suggested by Mills (1989), Harris and Wanless (1995), Cam et al. (1998) and Sandercock et al. (2000) for red-billed gulls (*Larus novaehollandiae*), common guillemots (*Uria aalge*), kittiwakes (*Rissa tridactyla*) and green-rumped parrotlets (*Forpus passerinus*), respectively. These studies and ours are not in line with the hypothesis that non-breeding leads to an increase in survival, and provide no reason to interpret non-breeding as a means for preserving residual reproductive value (Coulson, 1984; Wooller et al., 1989; Aebischer and Wanless, 1992; Pugesek and Wood, 1992). Rather they suggest that a significant proportion of the non-breeders in any year might be low quality individuals, the remainder being individuals that skip reproduction for a year.

First time breeders had low survival, particularly among failed breeders, suggesting a cost of first reproduction on survival. The fact that this cost was less pronounced among successful breeders reinforces the individual quality hypothesis: successful breeders, being higher quality individuals, pay less in first reproduction. First reproduction costs may be particularly high for failed breeders because they engage those breeders in the novel investment of energy that would otherwise allocated to maintenance. Because blue petrels spontaneously desert their nests if they fall below a threshold body mass (Chaurand and

Weimerskirch, 1994), failed breeders are probably in poor condition at desertion, and thus may experience survival costs, particularly when environmental conditions are bad. Such first reproduction costs have recently been found in other long-lived species: the greater flamingo, *Phoenicopterus ruber roseus* (Tavecchia et al., 2001) and western gull, *Larus occidentalis* (Pyle et al., 1997).

Further insights into individual quality are revealed in breeding state transition probabilities. The fact that non-breeders and failed breeders had a higher probability of breeding failure than successful breeders strongly suggests that these birds were poor quality individuals. This is also reinforced by the fact that non-breeders had a high probability of remaining non-breeders, and by the fact that non-breeders and failed breeders had a low probability of becoming successful breeders, thereby suggesting that both had difficulties in attaining sufficient body mass to begin nesting. One may argue that there is a paradox in that successful breeders had nearly the same probability of becoming non-, failed or successful breeders. Indeed, according to the individual quality hypothesis and our previous results, one may expect that successful breeders should have a much higher probability of staying successful than our estimates indicate.

This, however, does not refute the individual quality hypothesis because it is the relative estimates of the breeding state transition probabilities, not their absolute values, that are important. Moreover, we suspect that successful breeders may skip breeding in some years (which may also reflect some costs of reproduction), thereby decreasing the average probability of remaining a successful breeder. In that perspective, this reinforces the individual quality hypothesis, because successful breeders that skip a year may be prudent parents (Drent and Daan, 1980). This idea could be tested further by investigating the influence of environmental conditions on breeding decisions and costs of reproduction with multistate time dependent models.

Overall, the results of this study indicate that body mass is a good surrogate of individual quality in blue petrels. The breeding states that were used appear to reflect individual quality, but these states probably partly reflect interindividual body mass variations, which is the major determinant of breeding state in small procellariiform species (Chastel et al., 1995a). In other words, our results suggest that the relative quality of an individual, although measured with a dynamic state variable such as body mass (McNamara and Houston, 1996), is fairly constant over time.

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