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 \( p_{rt} \), survival rate \( s_{rt} \), and conditional transition probability \( \psi_{rt} \) (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 \( (s_{rt}, p_{rt}, \psi_{rt}) \), 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); \( a \) 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, \( \ell \) (see Lebreton et al., 1992). Consequently, we started our model selection from the general model \( (s_{rt}, p_{rt}, \psi_{rt}) \), where \( m \) is trap dependence. We used the quasi-likelihood Akaike’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 \( (S) = a + b \times \text{mass} \), where \( a \) is an intercept parameter, \( b \) is a slope parameter and \( \text{mass} \) 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:
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For failed breeders, but were constant for successful breeders but time dependent. The number of parameters for this model was the model \( S_{r, a} \rho_{N, s} \psi_{a, s} \), 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 failure (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 \( S_{r, a} \rho_{N, s} \psi_{a, s} \). 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

<table>
<thead>
<tr>
<th>Model</th>
<th>QAICc</th>
<th>ΔQAICc</th>
<th>#</th>
<th>DEV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) ( S_{r, a} \rho_{N, s} \psi_{a, s} \rho_{N, s} )</td>
<td>5313.18</td>
<td>0.00</td>
<td>45</td>
<td>5221.43</td>
</tr>
<tr>
<td>2) ( S_{r, a} \rho_{N, s} \psi_{a, s} )</td>
<td>5348.28</td>
<td>35.09</td>
<td>54</td>
<td>5237.75</td>
</tr>
<tr>
<td>3) ( S_{r, a} \rho_{N, s} \psi_{a, s} \rho_{N, s} \psi_{a, s} )</td>
<td>5358.74</td>
<td>45.55</td>
<td>60</td>
<td>5235.61</td>
</tr>
<tr>
<td>4) ( S_{r, a} \rho_{N, s} \psi_{a, s} \rho_{N, s} )</td>
<td>5386.64</td>
<td>73.46</td>
<td>98</td>
<td>5182.23</td>
</tr>
<tr>
<td>5) ( S_{r, a} \rho_{N, s} \psi_{a, s} \rho_{N, s} )</td>
<td>5414.45</td>
<td>101.26</td>
<td>44</td>
<td>5324.77</td>
</tr>
<tr>
<td>6) ( S_{r, a} \rho_{N, s} \psi_{a, s} \rho_{N, s} \psi_{a, s} )</td>
<td>5425.70</td>
<td>112.52</td>
<td>37</td>
<td>5350.51</td>
</tr>
<tr>
<td>7) ( S_{r, a} \rho_{N, s} \psi_{a, s} \psi_{a, s} )</td>
<td>5431.52</td>
<td>118.34</td>
<td>49</td>
<td>5331.44</td>
</tr>
<tr>
<td>8) ( S_{r, a} \rho_{N, s} \psi_{a, s} \psi_{a, s} )</td>
<td>5452.49</td>
<td>139.30</td>
<td>23</td>
<td>5406.03</td>
</tr>
</tbody>
</table>

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 $\psi_{u} = \frac{\psi_{u}}{\psi_{s\tau a2}}p_{NB}m, FBr*t*m, SB*m$; bars indicate $\pm SE$. In subfig. B: NBr = non-breeder, FBr = failed breeder, SBr = successful breeder. Estimates are from model $\psi_{u} = \frac{\psi_{u}}{\psi_{s\tau a2}}p_{NB}m, FBr*t*m, SB*m$; bars indicate $\pm SE$. In subfig. C: estimates are from model $\psi_{u} = \frac{\psi_{u}}{\psi_{s\tau a2}}p_{NB}m, FBr*t*m, SB*m$.
they fall below a threshold body mass (Chaurand and
of energy that would otherwise allocated to maintenance.
individuals, pay less in first reproduction. First reproduc-
tivity hypothesis: successful breeders, being higher quality
among successful breeders reinforces the individual qual-
tion on survival. The fact that this cost was less pronounced
among failed breeders, suggesting a cost of first reproduc-
tion between years (Barbraud and Weimerskirch, unpub-
ished 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., indi-
vidual 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 Sandercoc 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 inter-
pret non-breeding as a means for preserving residual repro-
ductive value (Coulson, 1984; Wooler et al., 1989; Aebischer
and Wanless, 1992; Pugeseck 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 reproduc-

tion on survival. The fact that this cost was less pronounced
among successful breeders reinforces the individual quali-

ty hypothesis: successful breeders, being higher quality
individuals, pay less in first reproduction. First reproduc-
tion costs may be particularly high for failed breeders be-
cause 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 prob-
ability of remaining non-breeders, and by the fact that non-
breeders and failed breeders had a low probability of be-
coming 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 suc-
cessful breeders had nearly the same probability of becom-
ing 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 es-


timates indicate.
This, however, does not refute the individual quality

hypothesis because it is the relative estimates of the breed-
ing 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 indi-


dual quality, but these states probably partly reflect inter-
dividual body mass variations, which is the major deter-

minant 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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References
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