

Modelling the effects of environmental and individual variability when measuring the costs of first reproduction

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Extended abstract

Modelling the effects of environmental and individual variability when measuring the costs of first reproduction.— How do animals balance their investment in young against their own chances to survive and reproduce in the future? This life–history trade–off, referred to as the cost of reproduction (Williams, 1966), holds a central place in life–history theory (Roff, 1992; Stearns, 1992; McNamara & Houston, 1996). Because individuals can only acquire a limited amount of energy, reproduction and survival as well as current and future reproduction are considered as functions competing for the same resources. In this framework, individuals may optimise life–history decisions. If the reproductive effort in one year leads to a loss in future reproductive output through decreased adult survival or reduced fecundity, then the optimal effort in the current season is less than the effort that would maximize the number of offspring produced in that season (Charnov & Krebs, 1974). There are at least two kinds of factors likely to confound the measurement of the costs of reproduction in the wild. First, there could be differences in the amount of energy individuals acquire and allocate to various functions. This phenotypic heterogeneity can mask or exacerbate individual allocation patterns when trends are averaged across a population (Vaupel & Yashin, 1985; McDonald et al., 1996; Cam & Monnat, 2000). Second, there could be variations in resource availability affecting energy acquisition and allocation. Theoretical models examining the optimal phenotypic balance between reproduction and survival under variable breeding conditions have investigated the influence of environmental stochasticity on the cost of reproduction in birds (Erikstad et al., 1998; Orzack & Tuljapurkar, 2001). However, there is little empirical evidence supporting these theoretical models. Here, we present analysis of the influence of experience, but also of the differential effects of environmental and individual variation on survival and future breeding probability. We address the question of the costs of reproduction using data from a 17–year study of individually marked blue petrels (*Halobaena caerulea*), a small (190 g) long–lived seabird breeding on sub–Antarctic islands.

Data were analysed using multistate capture–recapture models (Brownie et al., 1993; Schwarz et al., 1993; Nichols et al., 1994). The most general model we started with was the conditional Arnason–Schwarz model (Schwarz et al., 1993). We used the following notation for states: 1. Nonbreeder that never previously bred; 2. First–time breeder; 3. Experienced breeder; and 4. Nonbreeder that previously bred. This general model was constrained since some parameters were not defined, given our definition of individual states. Using matrix notation, the parameters defined above can be summarized in matrices of survival, transition and capture probabilities:

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$$\mathbf{S}_t^r = \begin{pmatrix} S_t^1 \\ S_t^2 \\ S_t^3 \\ S_t^4 \end{pmatrix}, \quad \Psi_t^{rs} = \begin{pmatrix} \Psi_t^{11} & \Psi_t^{12} & 0 & 0 \\ 0 & 0 & \Psi_t^{23} & \Psi_t^{24} \\ 0 & 0 & \Psi_t^{33} & \Psi_t^{34} \\ 0 & 0 & \Psi_t^{43} & \Psi_t^{44} \end{pmatrix}, \quad \text{and } \mathbf{P}_t^r = \begin{pmatrix} p_t^1 \\ p_t^2 = p_t^3 \\ p_t^3 \\ p_t^4 \end{pmatrix}$$

We examined the effect of two covariates that were suspected to affect survival and breeding probabilities: sea surface height representing oceanographic conditions at a regional scale, and body mass of birds during breeding. Covariates were tested through ultrastructural models in which survival probability is a function of sea surface height and/or body mass, following a linear–logistic function:

$$\text{logit}(\phi) = \log\left(\frac{\phi}{1-\phi}\right) = \alpha + \beta \times \text{covariate},$$

where α is the intercept parameter, and β is a slope parameters. Our selection of models for estimation was based on model goodness–of–fit (GOF) tests and a modified Akaike's Information Criterion that takes into account sample sizes (AICc; see Akaike, 1973; Lebreton et al., 1992; Burnham & Anderson, 2002). We used program U–CARE (Choquet et al., 2003a) for GOF testing, and M–SURGE (Choquet et al., 2003b) for model selection and parameter estimation.

The GOF test of our general model indicated a lack of fit and we used a variance inflation factor ($\hat{C} = 1.336$) in the remaining analysis. Recapture probabilities varied with state. Recapture probability for breeders was extremely close to one. Experienced nonbreeders had higher recapture probabilities (0.528 ± 0.033) than inexperienced breeders (0.364 ± 0.019). First–time breeders had the lowest mean survival probabilities (0.775 ± 0.035), and experienced breeders had the highest mean survival probabilities (0.882 ± 0.035). Inexperienced and experienced nonbreeders had intermediate mean survival probabilities, indicating a cost of first reproduction for first time breeders. First–time breeders had a lower probability of breeding in the following year than experienced breeders, and nonbreeders had a lower probability of breeding in the following year than breeders. Among nonbreeders, inexperienced nonbreeders had a lower probability of breeding in the following year than experienced nonbreeders. A model where state survival probabilities were a function of sea surface height had the lowest QAICc. Survival of inexperienced individuals (both breeders and nonbreeders) was negatively affected by poor oceanographic conditions, whereas experienced birds seem to be only weakly affected by similar conditions. The costs of reproduction for first–time breeders were particularly marked during harsh climatic conditions. Body condition of experienced breeders was higher than the body condition of first–time and nonbreeders. Body condition of individuals seen only once was lower than body condition of those seen at least twice. At the individual level, there was no clear evidence for an increase in body condition across years.

These results can be interpreted in the light of the selection hypothesis (Curio, 1983; Forslund & Pärt, 1995). The inferiority of inexperienced breeders may be linked to a higher proportion of lower–quality individuals in younger age classes. First reproduction may act as a filter selecting individuals of higher quality/body mass. The improvement of performance within individuals may contribute marginally to the observed patterns at the population level. Environmental stochasticity, and more particularly the variation in sea surface height reflecting resource availability is probably a major factor of selection.

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