

# Model-based estimation of individual fitness

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**ABSTRACT** *Fitness is the currency of natural selection, a measure of the propagation rate of genotypes into future generations. Its various definitions have the common feature that they are functions of survival and fertility rates. At the individual level, the operative level for natural selection, these rates must be understood as latent features, genetically determined propensities existing at birth. This conception of rates requires that individual fitness be defined and estimated by consideration of the individual in a modelled relation to a group of similar individuals; the only alternative is to consider a sample of size one, unless a clone of identical individuals is available. We present hierarchical models describing individual heterogeneity in survival and fertility rates and allowing for associations between these rates at the individual level. We apply these models to an analysis of life histories of Kittiwakes (*Rissa tridactyla*) observed at several colonies on the Brittany coast of France. We compare Bayesian estimation of the population distribution of individual fitness with estimation based on treating individual life histories in isolation, as samples of size one (e.g. McGraw & Caswell, 1996).*

## **1 Introduction: growth rate and fitness**

Evolutionary ecology is the study of the causes and consequences of variation in genetic traits, specifically, of those traits that contribute to variation in the fitness of genotypes. In broadest terms, fitness is the capacity of a given genotype to be propagated into future generations (Fisher, 1930). Thus, the projected growth rate of a genotype is regarded as a reasonable measure of fitness (Lande, 1982, a,b); Danchin *et al.*, 1995; Caswell, 2001). Projected growth rates of genotypes are determined not only by the total numbers of offspring produced by individuals, but also by how early in the lifespan those offspring are produced.

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For populations with overlapping generations, projected growth rate under time invariant conditions is given as the dominant eigenvalue  $\lambda$  of a primitive, non-negative projection matrix (Caswell, 2001). Derivatives of  $\lambda$  with respect to the individual elements of the matrix are compared to determine which aspects of the demography have the largest potential effects on fitness, and are targets for selection. However, natural selection operates at the level of the individual, and analysis of matrix projection models constructed using parameter values calculated from aggregates of individuals may not adequately characterize fitness differences at the individual level (Cooch *et al.*, this issue). Traditional solutions to this problem have involved use of net reproductive rate ( $R_0$ ) and related metrics, which can be calculated on an individual basis (Kalisz, 1986; Stearns, 1992). However, such measures are often poor proxies for fitness, since they do not account for differences in timing of reproduction, and are only reasonable under restrictive assumptions (Stearns, 1992).

## 2 Latent process definition of individual fitness

Given that natural selection occurs at the individual level, and given that individuals are not all the same in their capacity for propagating their genotypes, a suitable measure of fitness at the individual level is desirable. McGraw & Caswell (1996) propose that individual fitness be measured using  $\lambda$ , the unique non-negative eigenvalue of an *individual-specific* Leslie matrix. Individual fitness, as measured by  $\lambda$ , could in theory be related to variation in individual traits (e.g. body size), with the resulting slopes serving as estimates of the selection gradient on that trait (McGraw & Caswell, 1996; Caswell, 2001). This approach has been adopted in a number of studies (cited in Caswell, 2001, p. 297).

However, while the intuitive appeal of this approach is clear, there remains the question of what  $\lambda$  calculated from an 'individual matrix' actually represents? Here, we formally define individual fitness in terms of *latent* breeding and survival rates, as distinguished from *realized* rates. The distinction is an important one, and perhaps most easily understood by consideration at the population level.

Much confusion can be avoided by distinguishing population propensities from finite population rates. Genetically identical populations, under identical conditions, would be anticipated to have slight differences in realized fertility and survival rates, simply due to natural variation and chance events. Even though two such populations would be described by common *latent* survival and fertility rates, *a priori*, the *realized* survival and fertility rates for the two populations would vary. Consequently, the two populations would be described by a common latent value of  $\lambda$ , but would yield distinct realized values. For many applications, we believe that the latent value is of greater interest; realized values are understood as estimates of the latent value.

Extending this distinction to the individual level allows individual fitness to be defined in perfect analogy to population fitness. We may suppose that associated with each individual there are, *a priori*, individual survival probabilities and fecundities. These are latent features, genetically determined and existing regardless of the individual's realized history. Individual fitness is then defined as the unique non-negative eigenvalue of the individual-specific Leslie matrix calculated using the latent rates. McGraw & Caswell's measure of individual fitness is naturally distinguished as *realized* individual fitness, since it is calculated using realized rather than latent individual rates.

Thus we define individual fitness as a latent feature, directly analogous to a latent population feature. This conception of individual fitness is not new; indeed it appears to underlie McGraw & Caswell’s (1996) discussion, and is evident in Fisher (1930). The distinction of realized fitness and latent fitness may not be particularly important in discussion of large populations, averaged over varying environmental conditions. At the individual level, though, the distinction is important, as we demonstrate in Section 4.

### 3 Formal definition of individual fitness

For a species with maximum lifetime  $\mathcal{J}$ , the population Leslie matrix  $\mathbf{M}$  for changes in pre-breeding population size is characterized by two vectors,  $\mathbf{P}$  and  $\mathbf{F}$ , corresponding to age-specific adult survival and fertility rates:  $\mathbf{M}$  is the  $\mathcal{J} \times \mathcal{J}$  matrix with  $\mathbf{F} = (F_1, F_2, \dots, F_{\mathcal{J}})'$  along its first row,  $\mathbf{P} = (P_1, P_2, \dots, P_{\mathcal{J}-1})'$  along the first subdiagonal, and zeros elsewhere. The stable population growth rate associated with  $\mathbf{P}$  and  $\mathbf{F}$  is the unique non-negative eigenvalue of  $\mathbf{M}$ , the existence of which is guaranteed by the Perron-Frobenius theorem (as discussed at length in Caswell, 2001).

We define a vector  $\mathbf{S} = (S_1, S_2, \dots, S_{\mathcal{J}})'$  of cumulative survival probabilities; here,  $S_1 = 1$  and  $S_k = P_{k-1}S_{k-1}$ , for  $k = 2, 3, \dots, \mathcal{J}$ . It will be convenient to write  $[\mathbf{ab}]$  for the vector formed by element-wise multiplication of  $\mathcal{J}$ -vectors  $\mathbf{a}$  and  $\mathbf{b}$ . For any  $\mathcal{J}$ -vector  $\mathbf{a} = (a_1, a_2, \dots, a_{\mathcal{J}})'$  we define the polynomial

$$h(x; \mathbf{a}) = x^{\mathcal{J}} - \sum_{k=1}^{\mathcal{J}} a_k x^{\mathcal{J}-k} \tag{1}$$

Here and throughout, we assume that  $a_i \geq 0$ , for all  $i$ , with strict inequality for at least one  $i$ ; under these conditions there exists a unique non-negative solution in  $x$  of  $h(x; \mathbf{a}) = 0$ , which we designate as  $\lambda(\mathbf{a})$ . In particular, the stable population growth rate is  $\lambda([\mathbf{SF}])$ : it is the unique non-negative solution in  $x$  of

$$h(x; [\mathbf{SF}]) = x^{\mathcal{J}} - \sum_{k=1}^{\mathcal{J}} (S_k F_k) x^{\mathcal{J}-k} = 0$$

We define individual fitness analogously, supposing that associated with each individual there are, *a priori*, vectors  $\mathbf{s}$  and  $\mathbf{f}$  of cumulative survival probabilities and fecundities. These are latent features, genetically determined and existing regardless of the individual’s realized history. Individual fitness is then also a latent feature, the unique positive solution of  $h(x; [\mathbf{sf}]) = 0$ , denoted by  $\lambda([\mathbf{sf}])$ .

### 4 Realized individual fitness as an estimator of latent individual fitness

Individual fitness, defined as a latent feature, cannot be observed. It is an *a priori* summary of parameters governing potential realizations of an individual’s life history. Putting aside for the moment the possibility of estimating these individual parameters in the context of a model-based analysis of groups of individuals, we here consider what can be done to estimate an individual’s latent fitness using the only data specifically relevant to the individual, the individual’s ‘realized history’. Since the realized history is a sample of size 1 of the potential realizations governed by the parameters determining latent fitness, we might have doubts as to the feasibility of the endeavour. In this section we show that McGraw & Caswell’s

measure of individual fitness can be thought of as an estimator, albeit biased, of individual latent fitness. We demonstrate that the bias can vary among individuals having the same latent fitness, and argue for the need of model-based estimation of individual fitness.

Suppose that we are able to observe the life history of a particular individual described by latent vectors  $\mathbf{s}$  and  $\mathbf{f}$ , and let  $X$  denote the maximum age the individual attains. Let  $\mathbf{1}_k$  denote a vector consisting of  $k$  ones followed by  $\mathcal{J} - k$  zeros; thus the vector  $[\mathbf{1}_k \mathbf{f}]$  consists of the individual's fecundity in years 1 through  $k$ , followed by  $\mathcal{J} - k$  zeros. Replacing  $k$  by  $X$ , the random vector  $[\mathbf{1}_X \mathbf{f}]$  is an unbiased estimator of  $[\mathbf{s} \mathbf{f}]$ , based only on the available information from the realized lifetime. It is natural therefore to describe  $\lambda([\mathbf{1}_X \mathbf{f}])$  as the individual's realized fitness. This is precisely the approach taken by McGraw & Caswell (1996): it can be shown without difficulty that the measure of individual fitness they propose, based on individual Leslie matrices, is equivalent to  $\lambda([\mathbf{1}_X \mathbf{f}])$ .

Realized individual fitness may be of interest in its own right, but the natural question is how realized fitness relates to latent fitness. Since  $[\mathbf{1}_X \mathbf{f}]$  is an unbiased estimator of  $[\mathbf{s} \mathbf{f}]$ , it is natural to ask whether  $\lambda([\mathbf{1}_X \mathbf{f}])$  is also an unbiased estimator of  $\lambda([\mathbf{s} \mathbf{f}])$ ; that is, whether realized individual fitness is an unbiased estimator of latent fitness. This amounts to asking whether

$$E(\lambda([\mathbf{1}_X \mathbf{f}])) = \lambda(E([\mathbf{1}_X \mathbf{f}]))$$

where  $E(\cdot)$  denotes mathematical expectation. Since  $\lambda(\mathbf{a})$  is non-linear, it is not surprising that the question is answered in the negative. In the Appendix we demonstrate that realized fitness always has a negative bias as an estimator of latent fitness. As McGraw & Caswell (1996) point out, bias need not preclude the usefulness of an estimator. Since realized fitness might only be used as an index to individual quality, we might not be concerned with bias: if we could be confident that the amount of bias were reasonably consistent for distinct values of the latent parameters  $\mathbf{p}$  and  $\mathbf{f}$ , realized fitness would serve as a useful index to latent fitness, even though negatively biased.

The performance of realized fitness as an estimator of latent fitness is easily assessed, particularly if we restrict our attention to a special case of a fixed fecundity vector  $\mathbf{f}$ . Under this restriction, there are only  $\mathcal{J}$  distinct life histories, determined by the number of age-classes into which the individual survives. Given the latent vector  $\mathbf{p}$  of survival rates, one may calculate the probability distribution for survival, and directly calculate the expected value of the latent fitness. Figure 1 summarizes 1000 calculations of the expected value of the realized fitness, all for individuals with  $\mathbf{f} = (0, 1, 1, 1, 1, 1, 0, 0)'$ , each having a distinct vector  $\mathbf{p}$ . Each vector  $\mathbf{p}$  consists of seven survival probabilities, chosen at random over the range  $(0.25, 0.75)$ . The median values of latent and average realized fitness were 0.98 and 0.60, respectively. A Loess curve through the cloud of points is roughly parallel to the identity, suggesting that the bias, although consistently negative, is reasonably constant.

In Fig. 2, however, not only is the bias typically greater (median latent and average realized fitnesses are 0.95 and 0.14, respectively), but the magnitude of the bias varies: when the latent fitness is 0.6, the bias is typically about  $-0.55$ ; when the latent fitness is 1.10, the bias is typically about  $-0.84$ . Figure 2 was produced with constant  $\mathbf{f} = (0, 0, 0, 5, 5, 5, 5, 5)'$ , and with individual latent survival rates chosen at random over the range  $(0.10, 0.90)$ .

Realized fitness is zero for individuals that die before sexual maturity. Their latent fitness, however, may not be zero; *a priori*, such individuals may have a

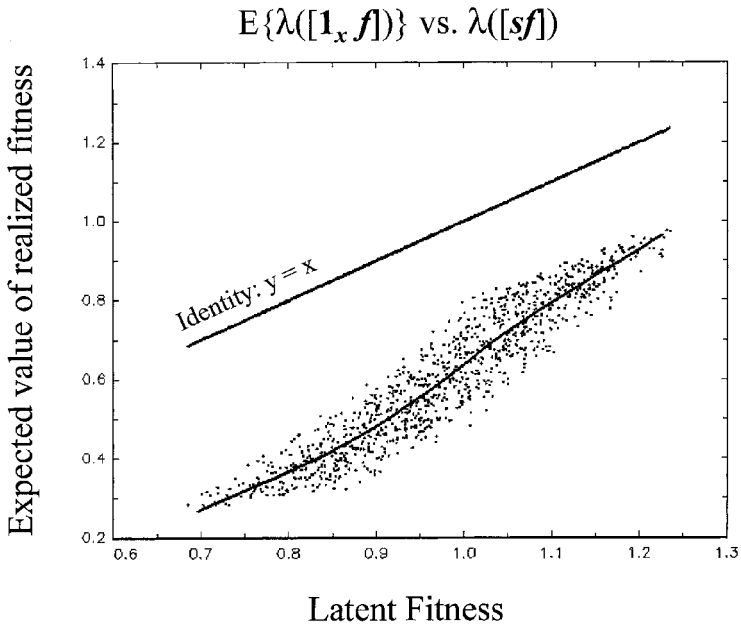


FIG. 1. Expected value of realized fitness compared to latent fitness. 1000 calculations of the expected value of the realized fitness, all for individuals with  $\mathbf{f} = (0,1,1,1,1,1,0,0)'$ , each having a distinct vector  $\mathbf{p}$ . Each vector  $\mathbf{p}$  consists of seven survival probabilities, chosen at random over the range (0.25, 0.75).

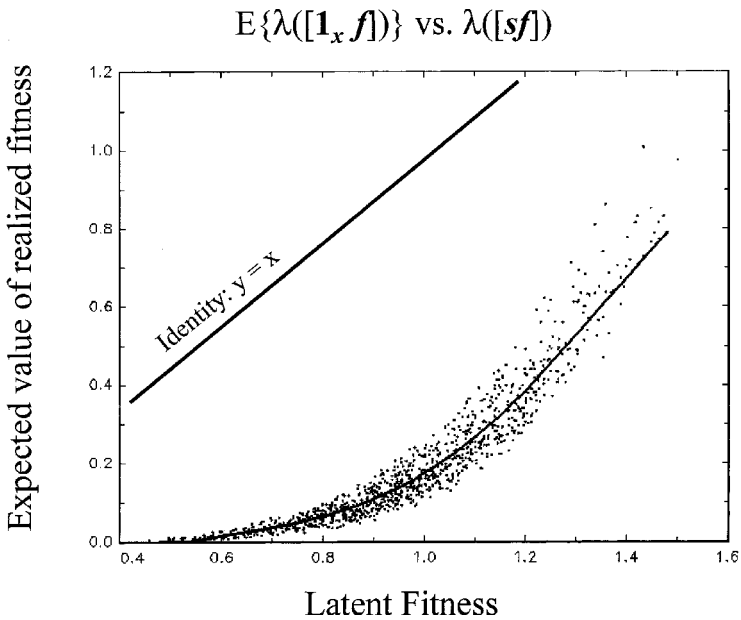


FIG. 2. Expected value of realized fitness compared to latent fitness. 1000 calculations of the expected value of the realized fitness, all for individuals with  $\mathbf{f} = (0,0,0,5,5,5,5,5)'$ , and with individual latent survival rates chosen at random over the range (0.10, 0.90).

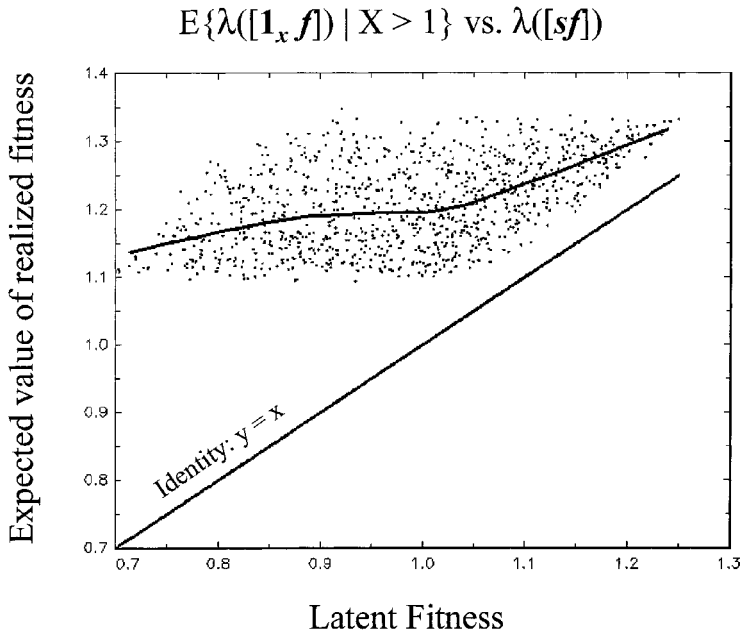


FIG. 3. Expected value of realized fitness, given survival to breeding age, compared to latent fitness. Latent parameters as for Fig. 1.

potential for reaching sexual maturity and breeding. It is interesting to evaluate the relation between latent fitness and realized fitness, conditional on the individual reaching sexual maturity. Under the conditions given for Fig. 1, breeding requires  $X > 1$ ; we thus computed the expected value of the realized fitness conditional on  $X > 1$  for the same 1000 individuals, and plot the results in Fig. 3. There is very little association between these expected realized fitnesses and the corresponding latent fitnesses.

In Figs 1 and 2 it is apparent that two individuals having approximately the same latent fitness can have distinct average expected fitnesses. In fact, it is easy to construct examples of latent parameter vectors corresponding to equal latent fitness, but with substantially different average realized fitnesses. Suppose  $\bar{y} = 5$ , and start with latent vectors  $\mathbf{p}_1 = (0.8, 0.8, 0.8, 0.8)'$  and  $\mathbf{f}_1 = (0, 1, 2, 3, 2)'$ . Halving the first survival rate and doubling subsequent fecundities yields vectors  $\mathbf{p}_2 = (0.4, 0.8, 0.8, 0.8)'$  and  $\mathbf{f}_2 = (0, 2, 4, 6, 4)'$ . Both pairs result in the same value for  $[\mathbf{s}\mathbf{f}]$  and consequently have equal latent fitnesses,  $\lambda([\mathbf{s}\mathbf{f}]) = 1.56$ ; however, the realized fitness (a random variable) has mean of 1.28 (SD = 0.70) in the first case and mean of 0.82 (SD = 1.03) in the second. Repeating the process twice more, the latent fitness remains unchanged, but the average expected fitness drops first to 0.54 (SD = 1.08), then to 0.35 (SD = 1.07). Such inconsistencies diminish the value of realized fitness as an index to latent fitness. The magnitude of the variability in the realized fitness is also cause for concern, especially if realized fitness is to be used as an explanatory variable in subsequent analyses.

Based on a single life history, viewed in isolation, realized fitness may be the only reasonable estimate of latent fitness. Fortunately, it would be an unusual circumstance in which only a single life history were available, without any other data. In the next sections we investigate model-based estimation of latent fitness.

**5 Modelling individual fitness—a sample population**

Suppose that individual survival and fertility rates are described by parametric models at the population level. It is then possible to obtain better estimates of [sf] than [ $1_x f$ ] and, consequently, to improve estimation of individual fitness.

We begin by describing such a model, which we will then use to illustrate techniques for estimating individual fitness, and as the basis of simulations comparing the *population* distribution of *latent* fitness with the *population* distribution of expected values of *realized* individual fitness. The model we describe is based on analyses of data for Kittiwakes (*Rissa tridactyla*) observed at several colonies on the Brittany coast of France by Jean-Yves Monnat, Etienne Danchin and a team of collaborators (Danchin & Monnat, 1992; Danchin *et al.*, 1998).

The model we describe here includes individual-specific covariation in breeding and survival rates, leading to variation in latent fitness among individuals. At present, we have only estimated these components of variation for birds that have attempted breeding at least once, and must use population average values up to and including the age of first breeding. Thus, our parameterization of life histories has two parts, the first (up to age of first breeding attempt) without individual-specific variation, the second (after first breeding attempt) including individual-specific variation.

In our investigations of the population distribution of individual fitness, the age of first breeding attempt (AFBA) was treated as a latent feature; individuals could die prior to attempting breeding. The probability distribution for age of first breeding attempt is given in Table 1, and was obtained using transition probabilities obtained by Cam *et al.* (in Press, a).

Parameter values used for the first part of the model (up to age at first breeding attempt, AFBA) are given in Table 1. Yearly survival rates up to AFBA were obtained using multistate capture-recapture models (Nichols & Kendall, 1995; Cam *et al.*, in Press, a). Estimates of fertility at AFBA were obtained through analysis of complete life histories of 423 Kittiwakes of known age, the only

TABLE 1. Kittiwake survival and breeding rates up to age of first breeding attempt (AFBA)

<b>Rates by age, through AFBA</b>						
Individual survival rates, age $t - 1$ to $t$ , prior to AFBA:						
$t$	1	2	3	4	5	$\geq 6$
$\phi_t$	0.605	0.600	0.808	0.717	0.704	0.551
Fertility, age of first breeding attempt:						
Age/ Young	0	1	2			
3	0.784	0.183	0.033			
4	0.669	0.280	0.051			
5	0.557	0.375	0.068			
6	0.697	0.257	0.046			
7	0.774	0.191	0.035			
<b>Age of first breeding attempt (AFBA)</b>						
Age	3	4	5	6	7	
Prob	0.221	0.403	0.219	0.099	0.058	

restriction being that selected birds attempted breeding at least once. All were born before 1987, and died before 1999; only eight of the 423 survived more than 15 years, with 20 years as the maximum.

We used the life histories of these 423 Kittiwakes for our modelling of life history parameters after AFBA. We supposed that once an individual bird becomes a breeder, its annual cycle could be described by a sequence of Bernoulli trials. The first, with success probability  $\phi$ , is an indicator of survival from year  $t - 1$  to  $t$ . Given that the individual survives, a second Bernoulli trial has parameter  $\beta$ , the conditional probability of successful breeding. Given that the individual breeds successfully, a third Bernoulli trial with parameter  $\delta$  determines whether the individual produces 1 or 2 chicks. Nests producing three or more chicks are sufficiently uncommon that we omit them from this simple model. The expected number of chicks produced, given survival, is  $\beta + \beta\delta$ .

We fitted linear models for the logits of the rate parameters; these all included additive, mean zero normal random year effects. We informally examined the effects of AFBA and aging, using quadratic, linear, and factor models; we also examined individual-specific variation and covariation in rates; our final selection of models was guided by results presented in Cam *et al.* (in Press, *b*). The data appear to be satisfactorily described by models including linear effects of aging on  $\phi$  and  $\psi$ , with correlated individual effects on  $\phi$  and  $\beta$ . Successful breeding rates  $\beta$  varied among, but not within, individuals. On the other hand, the conditional probability of producing a second chick,  $\psi$ , appeared to vary within individuals (increasing with age) but not among individuals.

Thus the second part of our model, that dealing with life histories after AFBA, was described by survival rates  $\phi_t$  (age  $t - 1$  to  $t$ ), successful breeding rates  $\beta_t$  (one or more young at age  $t$ , given that it survived to age  $t$ ), and multiple breeding rates  $\delta_t$  (two young at age  $t$ , given successful breeding at age  $t$ ). These are given by

$$\text{logit}(\phi_t) = \alpha_\phi + B_\phi t$$

$$\text{logit}(\beta_t) = \alpha_\beta$$

and

$$\text{logit}(\delta_t) = \mu_\delta + B_\delta t$$

here,  $\alpha = (\alpha_\phi, \alpha_\beta)$  is a bivariate normal random variable with mean vector  $(\mu_\phi, \mu_\beta)'$  and covariance matrix described by standard deviations  $\sigma_\phi$  and  $\sigma_\beta$  and correlation  $\rho$ . We describe estimation techniques in the next section.

Of special interest in the model are the individual effects. Individual heterogeneity is described by individual-specific effects  $\alpha_\phi$  and  $\alpha_\beta$ , which are additive on the logit scale. Fairly strong positive correlation was in evidence: birds more likely to survive also had greater conditional probabilities of breeding, given that they survived.

## 6 Estimation

Our analysis was Bayesian; model fitting was done using Markov chain Monte Carlo, implemented using program BUGS (Spiegelhalter *et al.*, 1995, software available for free; download from <http://www.mrc-bsu.cam.ac.uk/bugs/>). Prior distributions for  $\mu_\phi, \mu_\beta, \mu_\delta, B_\phi$  and  $B_\delta$  were specified as mean zero normal, with large variances corresponding to vague prior knowledge. Variances were given



diffuse inverse gamma priors, and the prior distribution of the correlation parameter  $\rho$  was uniform on  $(-1, 1)$ .

The bivariate normal individual effects  $\alpha = (\alpha_\phi, \alpha_\beta)$  were modelled as  $\alpha_\phi = \sigma_\phi Z_1$  and  $\alpha_\beta = \sigma_\beta(\rho Z_1 + \sqrt{1 - \rho^2} Z_2)$ , where  $Z_1$  and  $Z_2$  are independent standard normal random variables.

Bayesian inference about a parameter  $\psi$  is based on the posterior distribution of  $\psi$ . Markov chain Monte Carlo (MCMC) is a useful technique for evaluating this distribution, which usually cannot be calculated in closed form: several realizations of a Markov chain with stationary distribution equal to the posterior are generated, initial values possibly not representative of the stationary distribution are discarded, and a subset of the remaining values are treated as (dependent) samples of the posterior distribution. For an introduction to MCMC see Gilks *et al.* (1996).

Our MCMC implementation consisted of generating five realizations of a Markov chain for the posterior distribution of  $\psi = (\mu_\beta, \mu_\phi, \mu_\delta, B_\phi, B_\delta, \tau_\beta, \tau_\phi, \sigma_\beta, \sigma_\phi, \rho)'$ ; here,  $\tau_\phi$  and  $\tau_\beta$  are the standard deviations of the year effects on survival and successful breeding rates. The Markov chains we generated were of length 7500; we discarded the first 500 observations from each chain, and assessed convergence to the stationary distribution by applying the Gelman-Rubin diagnostic (Gelman, 1996) to the remaining 7000 observations. We combined the last 2000 observations from each of the five chains, and based our evaluations of posterior distributions on these sets of 10 000 values. Summaries for  $\psi$  are given in Table 2.

It is helpful to recall that if  $\mathbf{X}^*$  is sampled from the distribution of  $\mathbf{X}$ , then  $q(\mathbf{X}^*)$  has the same distribution as  $q(\mathbf{X})$ . Thus, if a particular individual's fitness is desired, one may simply include the pair individual's parameters  $\alpha = (\alpha_\phi, \alpha_\beta)$  in the vector  $\psi$ , then calculate vectors of survival, breeding, and multiple breeding rates ( $\phi_t$ ,  $\beta_t$ , and  $\delta_t$ ) for each of the 10 000 observations produced by the MCMC sample of values. Using these and the pre-breeding survival rates of Table 1, one could produce MCMC samples of individual specific latent survival and fecundity vectors  $\mathbf{s}$  and  $\mathbf{f}$ , and latent fitness  $\lambda([\mathbf{sf}])$ . The posterior distribution of the individual's latent fitness could then be examined; in particular, the posterior mean might be taken as a Bayesian point estimate. This approach might be of value if individual specific values of latent fitness were to be used as explanatory variables in subsequent investigation.

We suggest that interest will generally focus on the population distribution of latent fitness, rather than on the individual latent fitnesses. Features of this distribution are simply functions  $q(\psi)$  of the parameter vector  $\psi = (\mu_\beta, \mu_\phi, \mu_\delta, B_\psi, B_\delta, \tau_\beta, \tau_\phi, \sigma_\beta, \sigma_\phi, \rho)'$ ; we need not (nor should we) obtain estimates of the individual latent fitnesses to estimate such values  $q(\psi)$ . The only difficulty is that the function values  $q(\psi)$  cannot be calculated analytically, and must themselves be computed by simulation. We describe this procedure in the next section.

## 7 Evaluation of population distribution of individual fitness

Even if  $\psi = (\mu_\beta, \mu_\phi, \mu_\delta, B_\psi, B_\delta, \tau_\beta, \tau_\phi, \sigma_\beta, \sigma_\phi, \rho)'$  were known, computation of the population distribution of  $\lambda([\mathbf{sf}])$  would be analytically intractable. Given a specified value  $\psi$ , the best we can do is to decide which features of this distribution we are interested in (e.g. mean, standard deviation, percentiles), and to approximate these features through simulation. We sample one set of individual effects  $\alpha = (\alpha_\phi, \alpha_\beta)$  from the specified bivariate normal distribution, and calculate a corresponding value of latent fitness  $\lambda([\mathbf{sf}])$ . Pre-breeding survival rates are obtained by

TABLE 2. Posterior distributions of parameters in Kittiwake model

Parameters of Kittiwake model										
	$\sigma_\phi$	$\sigma_\rho$	$\rho$	$\mu_\phi$	$\mu_\rho$	$\mu_\phi$	$B_\phi$	$\beta_\phi$	$\tau_\phi$	$\tau_\rho$
Posterior percentiles										
2.5	0.3383	0.6205	0.2912	1.0327	-0.9113	-2.8118	-0.3417	0.0984	0.3366	0.2664
50	0.7679	0.8488	0.6776	1.9754	-0.5651	-2.2222	-0.1459	0.1659	0.6181	0.4344
97.5	1.5004	1.0923	0.9767	3.3334	-0.2462	-1.6419	-0.0374	0.2343	1.1885	0.7272
Posterior summaries										
Mean	0.8123	0.8510	0.6668	2.0403	-0.5682	-2.2265	-0.1593	0.1663	0.6542	0.4498
SD	0.3080	0.1196	0.1858	0.5836	0.1699	0.2997	0.0807	0.0347	0.2187	0.1180

adding  $\alpha_\phi$  to the logit of pre-breeding survival rates given in Table 1; survival and breeding rates are averaged against the distribution of AFBA given there.

This procedure is then repeated for a large number of individual effects  $\alpha = (\alpha_\phi, \alpha_\beta)$  sampled from the distribution determined by the same  $\psi$ . Moments and percentiles of the population distribution of  $\lambda([\mathbf{sf}])$ , for the fixed value of  $\psi$ , are approximated to any desired precision by repeating the simulation. We have ‘computed’  $q(\psi)$  from  $\psi$ .

Since  $\psi$  is unknown, we repeat this simulation for a sample of values  $\psi^*$  sampled from the posterior distribution of  $\psi$ . Each simulation summary is then, to arbitrarily close approximation, a sample  $q(\psi^*)$  from the posterior distribution of  $q(\psi)$ .

Here is how we applied the procedure to the kittiwake data. We conducted 1000 simulations, one simulation for every 10th value  $\psi^*$  among the 10 000 values from the MCMC analysis. Using a subset of the sampled values  $\psi^*$  reduces the computational burden without too much loss of efficiency, since it also reduces the within chain autocorrelation. Each simulation consisted of 399 replications. The 2.5th, 10th, 25th, 50th, 75th, 90th and 97.5th percentiles were estimated by the 10th, 40th, 100th, 200th, 300th, 360th and 390th order statistics respectively; we also recorded the mean and standard deviation among the 399 values. These values are summarized in Table 3. For example, a Bayesian point estimate of the 90th percentile of latent fitnesses is its posterior mean (0.9393), with 95% credible interval (0.8794, 0.9853). Similarly, a Bayesian estimate of the proportion of individuals with  $\lambda > 1$  is 0.0309, with 95% credible interval (0.0000, 0.0777). Table 3 also includes a population level estimate of fitness, denoted by  $\Lambda$ , computed using the average survival and fecundity vectors for each set of 399 simulated individuals.

## 8 Evaluation of realized fitness

For each of the  $1000 \times 399$  parameter sets generated in the analysis described in the previous section, we generated two random life histories, and calculated the corresponding realized fitnesses. This allows evaluation of sources of variation in realized fitness, and consideration of the relation between realized and latent fitness. In particular, it allows an evaluation of the anticipated performance of latent fitness were it possible to obtain complete life histories of the entire population of Kittiwakes, as we have modelled it.

We refer to the variation within the  $1000 \times 399$  pairs of realized fitnesses as realization variation. This quantity, which cannot be measured using the data provided by a single life history, accounted for 47% [95% credible interval: (40%, 53%)] of the total variance among each set of 399 individuals. The magnitude of realization variation accounts, in part, for its poor performance as a surrogate for latent fitness: the correlation between latent and realized fitness is only 0.23 (0.12, 0.32).

Realized fitness is zero for 89% of the individuals (85%, 92%) and takes values greater than 0.79 for all others. The (population) mean realized fitness was 0.107 (0.073, 0.148), considerably lower than the mean latent fitness of 0.749 (0.684, 0.812).

## 9 Discussion

We regard individual fitness as a latent characteristic, of individuals. Unlike population fitness, individual fitness cannot be consistently estimated, in the

TABLE 3. Posterior distributions of features of population distribution of latent fitness

	Features of population distribution of latent fitness										Population fitness	
	Percentiles											Summaries
	2.5	10	25	50	75	90	97.5	Mean	SD	$\Pr(\lambda > 1)$		
Posterior percentiles	2.5	0.2005	0.3629	0.5317	0.7007	0.8138	0.8794	0.9289	0.6832	0.0909	0.0000	0.7777
	50	0.4211	0.5407	0.6514	0.7654	0.8679	0.9422	1.0055	0.7497	0.1524	0.0276	0.8314
	97.5	0.6067	0.6836	0.7480	0.8218	0.9049	0.9853	1.0511	0.8121	0.2216	0.0777	0.8654
Posterior summaries	Mean	0.4121	0.5323	0.6462	0.7642	0.8658	0.9393	1.0026	0.7485	0.1547	0.0309	0.8294
	SD	0.1047	0.0818	0.0548	0.0306	0.0234	0.0267	0.0307	0.0330	0.0348	0.0212	0.0220

probabilistic sense; there is a sample of size 1 (the individual life history) and no prospect of replication.

The only exception to this rule is when the individual is a member of a clone, in which case individual and population survival and breeding rates coincide. From a mathematical perspective, a consistent estimator has been obtained by a strong model assumption (that individuals within the clone are replicates), so that data from other individuals provide the requisite replication.

McGraw & Caswell (1996) describe their measure of individual fitness (which we have distinguished as ‘realized fitness’) as a ‘consistent’ estimator; their use of the term surely being in the colloquial sense, rather than in the sense relating to replication. That is, individuals with similar latent fitnesses should have similar realized fitnesses. We have demonstrated that this is not the case. Even without this inconsistency, the large variability in realized fitness about its expected value mitigates its value as an estimator, especially if realized fitness is to be used as an explanatory variable in subsequent analyses. These comments are not to say that realized fitness is of no value, but to highlight the limitations imposed by attempting to estimate an individual’s fitness using only the sample of size 1 that the individual life history provides, alone.

Fortunately, the strong model assumption associated with using a clone can be relaxed, and replication, of a sort, can be obtained. We suggest that improved estimators of individual fitness can be reasonably obtained under specific models of individual heterogeneity in survival and breeding rates.

Our model for the Kittiwake data incorporates individual heterogeneity through additive random effects on the logits of survival and breeding; these effects have a bivariate normal distribution. The correlation coefficient in these individual effects is certainly positive: the estimate was 0.670, with 95% credible interval (0.282, 0.978), thus birds with higher survival probabilities also have higher probabilities of breeding, given that they survive.

An estimate of the population density for individual fitness is displayed in Fig. 4; this was calculated using a kernel density smoother on a sample of the  $399 \times 1000$  values obtained in the simulations described in Section. There is some indication of a negative skew in the distribution: the posterior probability that the median exceeds the mean was 0.986, although the estimate of the difference was only 0.016 (0.001, 0.039). However, Fig. 5 shows that the difference between the cumulative distribution of latent fitness (solid central line) and an approximating normal distribution (dashed line) is not large. Our estimates of the cumulative distribution of latent fitness, pointwise 95% credible intervals and estimators of difference between median and mean were obtained by the methods of Section 5; the approximating normal distribution is based on the posterior means for the mean and standard deviation of latent fitness.

Interest naturally focuses on the proportion of individuals with latent fitness exceeding 1 and on whether mean individual fitness is greater than 1, because of the implications for population growth associated with population fitness exceeding 1. It is always the case that the average individual fitness is smaller than the population fitness (e.g. 0.7485 versus 0.8294 in Table 3); this is demonstrated using the same reasoning that proves realized fitness to be negatively biased as an estimator of latent fitness, at the individual level. Thus, the interpretation of mean latent fitness, and indeed, of individual fitnesses themselves must be approached with caution. In the case of the Kittiwake data described herein, the pre-breeding survival rates are 1 minus the probability of death or permanent emigration. While

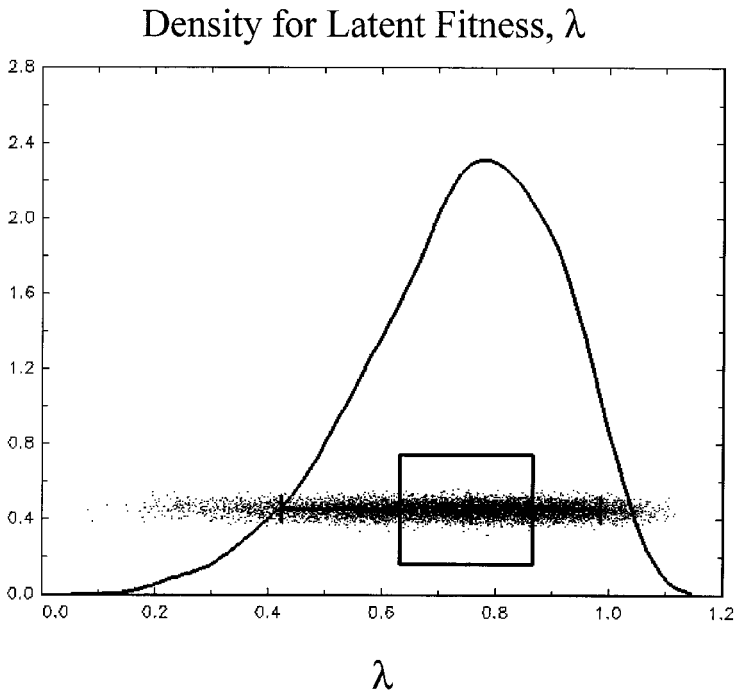


FIG. 4. Estimated population density function for individual latent fitness. Box plot highlights 5th, 25th, 50th, 75th, and 95th percentiles.

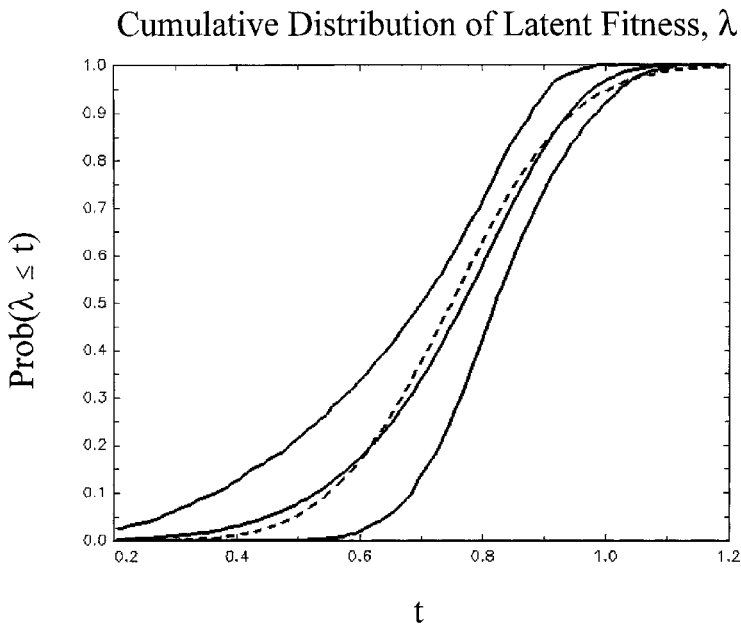


FIG. 5. Cumulative distribution of latent fitness (posterior mean, with pointwise 95% credible intervals). Dashed line is cumulative distribution function based on estimated mean and variance, and assuming normality.

### Density for Latent Fitness, $\lambda$

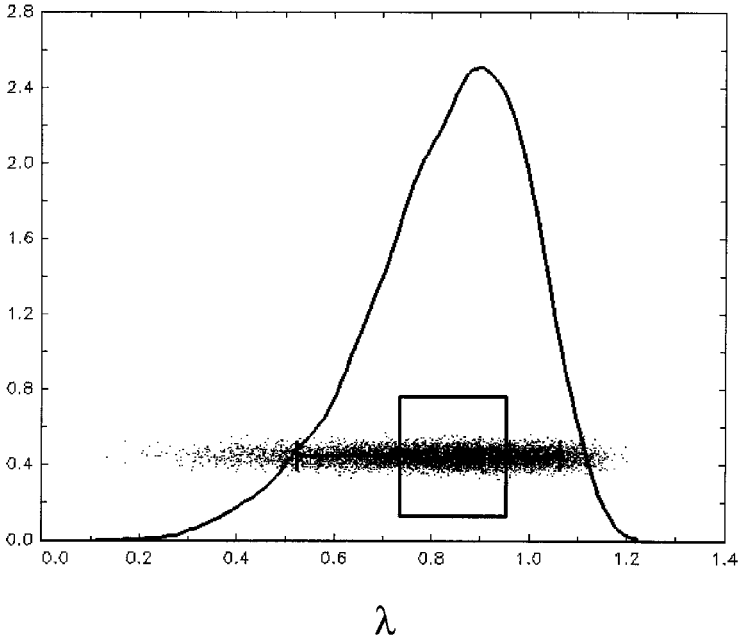


FIG. 6. Estimated population density function for individual latent fitness. Pre-breeding survival rates adjusted to reflect 50% loss due to permanent emigration. Box plot highlights 5th, 25th, 50th, 75th, and 95th percentiles.

### Cumulative Distribution of Latent Fitness, $\lambda$

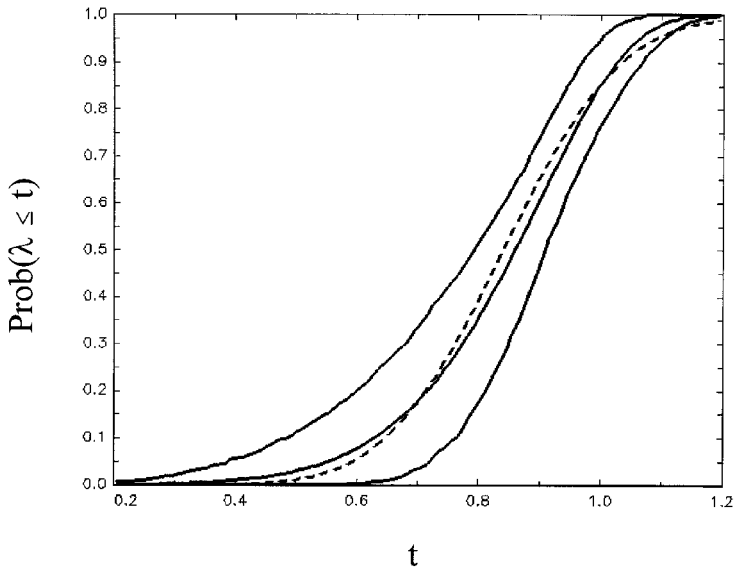


FIG. 7. Cumulative distribution of latent fitness (posterior mean, with pointwise 95% credible intervals). Pre-breeding survival rates adjusted to reflect 50% loss due to permanent emigration. Dashed line is cumulative distribution function based on estimated mean and variance, and assuming normality.

TABLE 4. Posterior distributions of features of population distribution of latent fitness, assuming 50% of pre-breeder loss due to permanent emigration

	Features of population distribution of latent fitness											Population fitness
	Percentiles										Summaries	
	2.5	2.5	10	25	50	75	90	97.5	Mean	SD		
Posterior percentiles	2.5	0.3067	0.4764	0.6389	0.7915	0.9030	0.9692	1.0225	0.7741	0.0948	0.0501	0.8561
	50	0.5154	0.6395	0.7445	0.8566	0.9562	1.0252	1.0877	0.8407	0.1482	0.1454	0.9029
	97.5	0.6778	0.7596	0.8319	0.9088	0.9940	1.0669	1.1311	0.8981	0.2146	0.2331	0.9391
Posterior summaries	Mean	0.5062	0.6305	0.7423	0.8571	0.9540	1.0240	1.0848	0.8403	0.1508	0.1466	0.9014
	SD	0.0992	0.0726	0.0479	0.0288	0.0231	0.0250	0.0268	0.0304	0.0314	0.0477	0.0207



it is known that there is a high degree of site fidelity among adults, it may be that some of the loss among pre-breeders is due to permanent emigration. Latent fitness estimates will obviously be negatively biased when survival rates estimates for pre-breeders are too low.

Coulson & Nève de Mévergnies (1992) estimated that 36% of young kittiwakes are faithful to the natal colony, and that 21% move more than 100 km away. Taking these numbers as rough guides, we repeated the analyses of Section 5, under the assumption that half of the pre-breeding loss was due to permanent emigration. Our results are summarized in Table 4, and Figs 6 and 7. We regard the larger estimates of fitness provided there as our most credible estimates of population values for the kittiwakes.

Finally, we reiterate that the Bayesian approach to analysis of individual heterogeneity in survival and breeding rates presented in this paper is appropriate for other definitions of individual fitness (e.g. net reproductive rate) as well.

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**Appendix**

To show that

$$\begin{aligned} \lambda(\mathbf{1}[\mathbf{s}\mathbf{f}]) &= \lambda(\mathbf{E}(\mathbf{1}_X\mathbf{f})) = \lambda\left(\sum_{k=1}^J \Pr(X = k) \mathbf{1}_k\mathbf{f}\right) \\ &\geq \sum_{k=1}^J \Pr(X = k)\lambda(\mathbf{1}_k\mathbf{f}) = \mathbf{E}(\lambda(\mathbf{1}_X\mathbf{f})) \end{aligned}$$

it suffices to demonstrate that for any vectors **a** and **b** satisfying  $\lambda(\mathbf{a}) \leq \lambda(\mathbf{b})$ , and  $p \in (0, 1)$ ,

$$\lambda(p\mathbf{a} + (1 - p)\mathbf{b}) \geq p\lambda(\mathbf{a}) + (1 - p)\lambda(\mathbf{b}) \tag{A1}$$

Fix **a** and **b**, and define the following notation:

- $\Lambda(p) = \lambda(p\mathbf{a} + (1 - p)\mathbf{b})$ ,  $0 \leq p \leq 1$
- $\mathbf{c}_p = p\mathbf{a} + (1 - p)\mathbf{b}$
- $h'(x; \mathbf{a}) = dh(x; \mathbf{a})/dx$ ;  $h''(x; \mathbf{a}) = d^2h(x; \mathbf{a})/dx^2$ ;  $\Lambda'(p) = d\Lambda(p)/dp$

The following facts are easily verified:

- (F1)  $h(x; \mathbf{c}_p) = ph(x; \mathbf{a}) + (1 - p)h(x; \mathbf{b})$
- (F2)  $h'(\lambda(\mathbf{a}); \mathbf{a}) \geq 0$ ;  $h''(\lambda(\mathbf{a}); \mathbf{a}) \geq 0$
- (F3)  $\Lambda'(p) \leq 0$
- (F4)  $h'(\Lambda(p); \mathbf{a}) - h'(\Lambda(p); \mathbf{b}) \leq 0$

By definition,  $h(\Lambda(p); \mathbf{c}_p) = 0$ . Expanding this using (F1), and taking second derivatives with respect to  $p$ , we establish that

$$2\Lambda'(p)[h'(\Lambda(p); \mathbf{a}) - h'(\Lambda(p); \mathbf{b})] + h''(\Lambda(p); \mathbf{c}_p)[\Lambda'(p)]^2 + h'(\Lambda(p); \mathbf{c}_p)\Lambda''(p) = 0$$

Using (F2), (F3) and (F4), the signs of the terms are summarized as

$$(\leq 0)(\leq 0) + (\geq 0)(\geq 0) + (\geq 0)\Lambda''(p) = 0$$

from which it follows that  $\Lambda''(p) \leq 0$ ; (A1) follows as an immediate consequence.