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Individual Covariation in Life-History Traits: Seeing the Trees Despite the Forest

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ABSTRACT: We investigated the influence of age on survival and breeding rates in a long-lived species *Rissa tridactyla* using models with individual random effects permitting variation and covariation in fitness components among individuals. Differences in survival or breeding probabilities among individuals are substantial, and there was positive covariation between survival and breeding probability; birds that were more likely to survive were also more likely to breed, given that they survived. The pattern of age-related variation in these rates detected at the individual level differed from that observed at the population level. Our results provided confirmation of what has been suggested by other investigators: within-cohort phenotypic selection can mask senescence. Although this phenomenon has been extensively studied in humans and captive animals, conclusive evidence of the discrepancy between population-level and individual-level patterns of age-related variation in life-history traits is extremely rare in wild animal populations. Evolutionary studies of the influence of age on life-history traits should use approaches differentiating population level from the genuine influence of age: only the latter is relevant to theories of life-history evolution. The development of models permitting access to individual variation in fitness is a promising advance for the study of senescence and evolutionary processes.

Keywords: age, bivariate latent factors models, breeding probability, individual heterogeneity, within-cohort phenotypic selection, survival probability.

Individual variation in fitness and its covariance with values of particular phenotypic traits are necessary conditions for natural selection (Endler 1986). Indeed, much of the focus of evolutionary ecology is quantifying and understanding the sources and consequences of individual variation in fitness and trait values. Yet, for the most part, analysis of selection often relies on comparisons among aggregations of individuals. In some cases, this is perhaps quite reasonable. Often, we group individuals based on an a priori expectation that they share a common component (perhaps heritable) for a trait of interest and that the groupings of individuals may successfully account for the major axes of variation in the data (e.g., allowing for differences among age classes).

However, in cases where the groupings based on a priori criteria are orthogonal to or at least covary in unexpected ways with biologically relevant groupings (i.e., pooling individuals of homogeneous fitness), aggregate-based techniques may be inadequate to address individual heterogeneity in fitness and may obscure important patterns. For example, consider a single birth cohort consisting of individuals with different underlying probabilities of survival; some individuals of a given age, perhaps those of better quality, have a higher latent probability of surviving over a given interval than do other individuals of the same age but with lower probabilities of survival. Individuals with lower latent survival probabilities will tend to die earlier (younger; age and time are synonymous within birth cohorts). This results in phenotypic mortality selection within birth cohorts (Curio 1983; Endler 1986; Forslund and Pärt 1995), such that over time, the proportion of individuals with lower survival probability decreases, and the average survival probability among remaining individuals appears to increase. This is likely to result in

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apparent increase in survival with age in the population, when in fact the probability of dying may not vary with age within each individual (Manton and Stallard 1984; Vaupel and Yashin 1985*a*, 1985*b*). Because of individual heterogeneity in fitness, population-level patterns may lead to an erroneous perception of the shape of the relationship between survival and age at the individual level (Vaupel and Yashin 1985*a*, 1985*b*; Service 2000).

The problem created by such individual heterogeneity in fitness affects the study of many subjects in ecology and evolutionary biology (Cooch et al. 2001). The obvious example of this is in studies of senescence (e.g., Carey et al. 1992; Tatar et al. 1993; McDonald et al. 1996; Service 2000). But individual heterogeneity in fitness can have other effects, especially when there are correlations among separate components of fitness, like survival and reproduction. For example, if correlations are positive (e.g., variation in individual quality such as in the good genes hypothesis; Curio 1983), reproductive performance may appear to increase with age at the population level, when in fact it may not at the individual level.

In this study, we considered biologically more realistic models allowing variation among individuals in fitness components, plus variation associated with other factors (e.g., age and time), using data from a long-term study of a long-lived seabird, the kittiwake (*Rissa tridactyla*). Our primary objective was to assess the magnitude of variation and covariation in survival and breeding probability among individuals and to investigate age-related changes in these fitness components within individuals. In addition, we also sought to compare the influence of age on vital rates at the individual level to patterns detected at the population level.

Methods

Data Collection and Selection

We used data from individually marked birds collected in Brittany, France, from 1984 to 1996 (Danchin and Monnat 1992; Danchin et al. 1998). Only data from known-age individuals (i.e., individuals marked as chicks and that returned to the study area to breed) were retained for analyses (e.g., Cam and Monnat 2000*a*, 2000*b*). We restricted analysis and inference to individuals that bred at least once (hereafter referred to as "adults") and excluded data from prebreeders. Each year, adults were categorized as breeders or nonbreeders (Cam et al. 1998) following a criterion specified by Maunder and Threlfall (1972). Recapture probability (i.e., the probability of encountering an individual, given that it is alive and present in the study area) in this population is very close to 1 regardless of breeding activity in adults (Cam et al. 1998). This very high recapture probability in individuals that recruited into the breeding segment of the population permits identification of the first breeding attempt (Cam and Monnat 2000*a*).

The data consisted of truncated capture-recapture histories (Lebreton et al. 1992) from 845 individuals, starting at first reproduction. These histories included information on breeding activity, as in multistate capture-recapture models (Nichols et al. 1994; Nichols and Kendall 1995; a sample of this data set is available at http://www.esapubs.org/archive/ecol/E079/002, Ecological Archive E079-002). As the recapture probability is very close to 1 (Cam et al. 1998), a "0" in the capture-recapture history corresponds to death (or permanent emigration from the study area). For each pair of years in the history, it is thus possible to extract information on whether an individual aged a in year i survived from year i to year $i+1$ and whether a survivor bred in year $i+1$. The data used consisted of 2,947 survival events and 2,344 breeding events, each event being identified by the individual's number, the year, and the age of the bird in that year. These events are binary variables (Bernoulli trials) and were modeled as a function of year, age, and individual, using a logit link function (Agresti 1990).

Individual Heterogeneity and Random-Effects Models

One obvious approach to accounting for heterogeneity among individuals is to incorporate values for one or more individual characteristics in the analysis. However, in many cases measurable individual characteristics do not adequately reflect heterogeneity (Schoenberg 1985; Trussell and Richards 1985; Hougaard 1991), and use of individual covariates is arguably just a different form of stratification since, in effect, it aggregates individuals as a function of the covariates included in the model (Nichols 2001). Another approach that can be used for traits like reproduction is to consider changes within individuals (e.g., Hamann and Cooke 1987; Cam and Monnat 2000*a*). In such repeated measures analyses, systematic changes with age must reflect true age effects. This approach, however, cannot be used to address mortality because the event occurs only once.

A more general approach is based on models incorporating individual random variables accounting for individual heterogeneity (Hedeker and Gibbons 1994), which are sometimes called latent random variables (Schoenberg 1985; Dupuis-Sammel and Ryan 1996; Spiegelhalter et al. 1996). Lebreton (1995) described these models with random effects as models with an individual covariate of unknown value. In a random-effects context, the focus is on the distribution of the unobservable latent response variable (Hedeker and Gibbons 1996; Hedeker

1999). The term "latent" reflects the fact that one addresses unobserved realizations of an underlying random variable (Steele 1996). For example, in the context of studies of survival, one assumes that each individual has its own mortality risk ("frailty"), which cannot be directly observed. However, it is possible to assess the distribution of this underlying variable and, thus, variation among individuals (Steele 1996), using individual realizations of this probability. Models incorporating random individual effects permit investigation of deviation of subject-specific responses about the response assessed at the level of the overall population (i.e., subject-specific inference as opposed to population-averaged inference; Chan and Kuk 1997; Hu et al. 1997). This type of approach is standard in human demography (e.g., Manton et al. 1981; Hougaard 1984; Vaupel and Yashin 1985*a*, 1985*b*; Hougaard 1986, 1991) and has also been widely used to address individual effects in several areas of research (e.g., numerous examples of biomedical or sociological studies are provided in Littell et al. 1996, or Hedeker and Gibbons 1996 and Hedeker 1999) but is not generally familiar to evolutionary ecologists.

Biological Hypotheses and Modeling

One possible approach to investigating individual variation in fitness components is to fit models including one parameter per component per individual. This approach leads to models with large numbers of parameters and to identifiability problems. Instead, we treated individual factors as random effects in a hierarchical model, more precisely, a generalized linear mixed model with random individual effects (Bryk and Raudenbush 1992; Searle et al. 1992; Littell et al. 1996; Hedeker al. 2000). We modeled survival and breeding probability (ϕ and β, respectively) as satisfying

$$\mathrm{logit}(\phi) = f_\phi(\mathrm{age}) + g_\phi(\mathrm{year}) + \alpha_\phi(\mathrm{individual})$$

and

$$\mathrm{logit}(\beta) = f_\beta(\mathrm{age}) + g_\beta(\mathrm{year}) + \alpha_\beta(\mathrm{individual}), \quad (1)$$

respectively. The components of the equation corresponding to survival and reproduction, respectively, are logit models for discrete-time data (e.g., Allison 1995; Hedeker et al. 2000; see Cam and Monnat 2000*a*, 2000*b* for examples of fixed-effects models in the kittiwake). This approach to modeling of survival and breeding rates is related to the large body of statistical inference methods for estimating survival using capture-recapture data from individually marked animals (Burnham et al. 1987; Lebreton et al. 1992; Nichols 1992; Clobert 1995). However, as the recapture probability is very close to 1 for this study (Cam et al. 1998), this parameter was ignored in our models. Here, $f_\phi(\cdot)$ and $f_\beta(\cdot)$ are specified functions of age, and $g_\phi(\cdot)$ and $g_\beta(\cdot)$ are year effects.

One of the distinguishing features of our approach is that both dependent variables were modeled simultaneously (Link et al. 2001). This approach was required in order to incorporate the possible correlation between individual effects on both survival and reproduction. This was accomplished by incorporating pairs ($\alpha_\phi(\cdot)$, $\alpha_\beta(\cdot)$), which are individual-specific random effects sampled from a bivariate normal distribution (e.g., Chan and Kuk 1997) reflecting the potential correlation between survival and reproduction. Thus, each individual bird is characterized by an unobservable pair of latent effects, a bivariate parameter relating breeding and survival ($\alpha_\phi(\cdot)$, $\alpha_\beta(\cdot)$). These are assumed to have a bivariate normal distribution with mean 0 and variance-covariance matrix Σ. Therefore, the individual effects are described by three parameters: two variances and a correlation.

Calculating the likelihood for such models and estimating parameters using conventional maximum likelihood estimators (MLE) is prohibitively difficult. However, applying an objective Bayesian approach to this analysis was fairly straightforward (Link et al. 2001). The approach we used was based on Markov chain Monte Carlo to fit flat prior Bayesian models (Gilks et al. 1996; Spiegelhalter et al. 1996; Gelman et al. 1997). The analyses were performed using the software program BUGS (Spiegelhalter et al. 1996). Since we desired an objective Bayesian analysis (e.g., Gelman et al. 1997), we used noninformative priors. Concerning individual-specific effects, we used a standard noninformative prior for variances (inverse γ; Spiegelhalter et al. 1996) and a uniform prior on $[-1, 1]$ for the correlation term between latent survival and breeding rates (ρ). For the intercept and the coefficients in the linear model, we specified prior distributions that were normal, with mean 0 and standard deviations of 1,000. These priors are essentially uniform over a large range: the density values on the interval $[-50, 50]$ are always within 99.875% of the maximum value. Values outside of that range are not interpretable on the logit scale. We therefore considered these priors as essentially uniform (that is, noninformative). It follows from Bayes theorem that the maximizer for the posterior distribution of a parameter θ is the same as the maximum likelihood estimator (e.g., Gelman et al. 1997). Thus, the modes of the posterior distributions for the parameters in our models will be equivalent to the MLE in a frequentist analysis.

The correlation term between latent factors governing survival and breeding probabilities permits exploration of covariation between individual fitness components. This is relevant to the predominant theory of life-history evo-

Table 1: Model selection for the variable age and individual effects on survival and breeding probability in the kittiwake

Parametric form of age for breeding probability	Parametric form of age for survival probability	AIC	Model likelihood[a]
Quadratic	Linear	84.98	1.00
Quadratic	Quadratic	85.50	.77
Factor[b]	Constant	85.76	.68
Factor	Linear	86.72	.42
Factor	Quadratic	87.25	.32
Quadratic	Factor[b]	88.14	.21
Quadratic	Constant	88.22	.20

Note: Only models with likelihood >.01 are listed, with the most parsimonious model at the top. All these models included individual effects. Model notation is described in the text.

[a] Model likelihood for a given model, derived as the ratio of the normalized AIC weight (Burnham and Anderson 1998) for that model divided by the AIC weight for the most parsimonious model.

[b] 12 levels (see text).

lution based on trade-offs between fitness components (Roff 1992; Stearns 1992). Previous studies based on nonexperimental data (such as this one) have provided contradictory results concerning the existence and the sign of this correlation (Stearns 1992). If the correlation term differs from 0, a negative sign indicates that trade-offs are expressed at the phenotypic level within individuals (Stearns 1992), such that individuals with higher values of one component tend to have lower values of the other (birds with higher survival probabilities are less likely to attempt breeding, given that they survive). A positive sign indicates that the same individuals have high survival and breeding probabilities, which directly supports the hypothesis of heterogeneity in individual quality (Curio 1983; Forslund and Pärt 1995). These hypotheses are not mutually exclusive (e.g., Van Noordwijk and de Jong 1986), and positive relationships do not provide evidence that there are no trade-offs at the genetic level; they may simply not be detectable at the phenotypic level (Van Noordwijk and de Jong 1986; Stearns 1992). Our objective was not to draw inference about genetic trade-offs between fitness components; the inference we intended to draw concerned the level at which the possible trade-offs in question were addressed. We adopted this terminology to maintain consistency with the literature. Importantly, our motivation for addressing the relationship between survival and breeding rates was elsewhere. We designed our model to account for the possible correlation between fitness components in order to separate the influence of age on reproduction at the individual level from age-specific variation in reproduction linked to within-cohort phenotypic selection at the population level (Forslund and Pärt 1995; Cam and Monnat 2000*a*).

We considered a cross-classified model set of 32 models, which differed in terms of the type of age effect (constant, linear, or quadratic functions or factors) specified for survival and conditional breeding probabilities (i.e., the probability of breeding given that the individual survived). Incorporation of age effects as factors or quadratic functions permits investigation of accelerating changes in vital rates with age, or even inversion of trends with age. All these models included year effects as factors, and they were considered with and without individual effects. Model selection was based on Akaike's information criterion (AIC; Akaike 1973; Sakamoto et al. 1986; Burnham and Anderson 1998).

Results

Comparisons between models with and without individual effects provided unequivocal evidence that incorporation of individual factors improves our ability to describe the process that gave rise to the data. No model that did not include individual effects was supported by the data (table 1). The fits (likelihoods) of the best three models were essentially equivalent. In the absence of a priori knowledge of age-specific patterns of variation in survival within individuals, and since each of the three best models are biologically reasonable, we retained the model with minimum AIC (Burnham and Anderson 1998), which corresponds to a linear effect of age on survival, and a quadratic effect of age on breeding probability (fig. 1).

Our modeling is expressed in terms of individual-specific rather than group-specific breeding and survival rates (Chan and Kuk 1997). The distinction is subtle but critical. Individual-specific rates are latent values, which were ob-

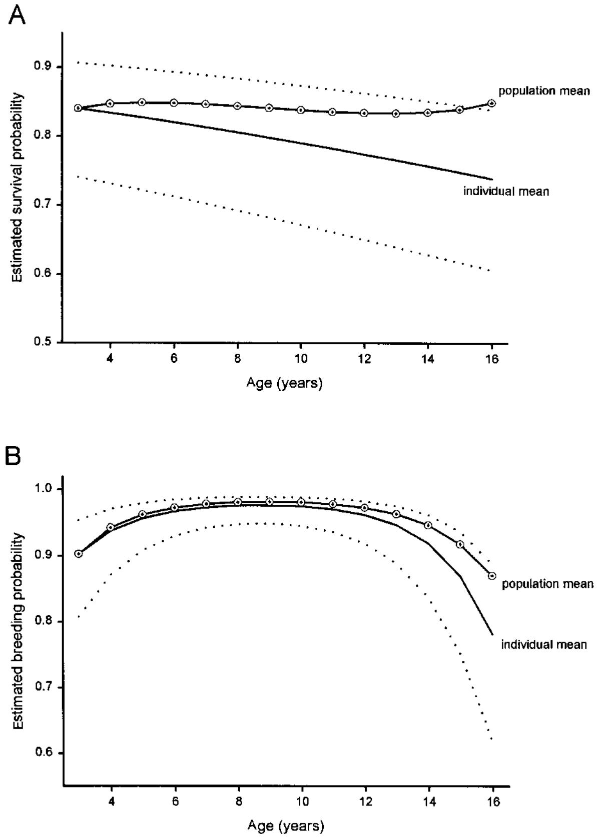

Figure 1: Influence of age on survival probability (*A*) and breeding probability (*B*). Estimates are scaled to median year effect. Group-specific rates (*circled data points*) correspond to the pattern at the observed population level. Individual-specific rates (the mean is indicate by the solid line and the quartiles by the dashed lines) describe the influence of age within individuals. There is evidence of decline in survival with age within individuals (*A*); this is undetectable at the population level. Breeding probability (after recruitment) increases in younger individuals (*B*), levels off, and declines at advanced ages. The population-level breeding rate underestimates the decline in older age classes expressed at the individual level.

tained by substituting fixed values for the individual effect in equation (1). Group-specific rates are those that would be estimated by random sampling of birds from a specified age-class and correspond to the pattern perceptible at the population level. They correspond to the pattern resulting from within-cohort phenotypic selection described by Curio (1983) or Forslund and Pärt (1995). The vast majority of previous studies of the influence of age on life-history traits in wild animal populations have focused on population-level rates (i.e., those estimated using fixed-effects models), rather than individual-specific latent rates (i.e., those estimated using random-effects models).

Figure 1 shows the influence of age on survival and breeding rates within individuals (i.e., latent rates) and contrasts these rates with population-level rates. Survival decreases with age within individuals but is constant at the population level (fig. 1*A*). The model with a quadratic survival term (not presented here) also shows a decline in survival within individuals, but it is delayed and detectable exclusively among older individuals. The general patterns of change in population-level and latent breeding probabilities were more similar (fig. 1*B*). Each exhibited an initial increase, a plateau, and a decrease for older individuals. However, the population-level rate progressively departs from the curve corresponding to the mean latent value: the individual-specific rate drops off more steeply at advanced ages.

Latent factors governing individual-specific survival and conditional reproduction are not independent. The interval [0.33, 0.98] contains the central 95% of the mass of the posterior distribution (this is sometimes called a "95% Bayesian confidence interval" or "credible interval"), which indicates that this correlation is unambiguously positive. The estimated joint distribution of survival and breeding probabilities shows that high values of one parameter are associated with high values of the other; birds that are more likely to survive are also more likely to breed, given that they survive (fig. 2). To assess whether our results depended on the use of a specific prior distribution (the possibility that results of a Bayesian analysis are con-

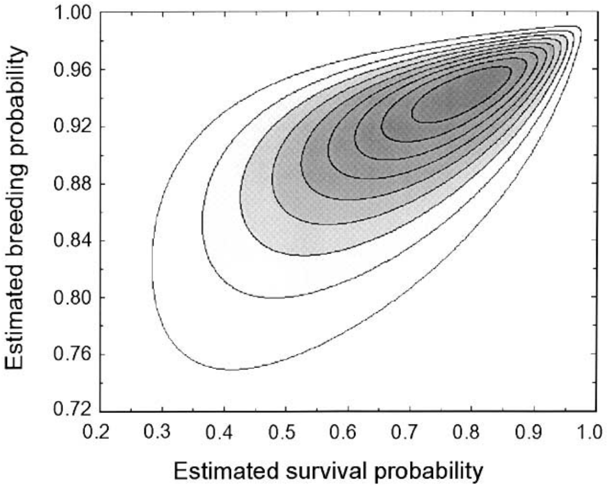

Figure 2: Probability contours of the estimated joint distribution of survival and breeding probabilities. Estimates are scaled to median year effect and age-class 6. These contours delimit regions of size 0.90, 0.80, 0.70, …, 0.10 (90% of the individual values will be in the largest oval, and 10% will be in the smallest oval). There is evidence of a positive correlation between survival and breeding probability at the individual level (individuals with higher latent survival probability also have higher probability of breeding in the following year, given that they survive).

ditional on the choice of priors is a common concern), we reran the analysis using a strongly informative prior for the correlation term between latent rates (ρ). This prior (triangular distribution at top) placed 3 : 1 odds on $\rho < 0$ and 15 : 1 odds on $\rho < 0.50$ and, hence, is clearly not objective. It corresponds to a negative correlation between survival and reproduction and therefore is opposite to the results obtained in the previous step. Yet, under this prior, the 95% credible interval [0.28, 0.90] was only slightly changed from those obtained using the uniform prior [0.33, 0.98]. This sort of result is often described as the data overwhelming the prior; in other words, the strength of the relationship is sufficiently strong that it is robust to the structure of the prior. Results of these analyses provide overwhelming evidence that the correlation between individual-specific survival and conditional reproduction is >0.

Discussion

Our approach revealed substantial variation in individual-specific latent factors governing survival and breeding rates. This heterogeneity is detected after accounting for the influence of age and time on these parameters. The ability to investigate individual variation in fitness components permits important progress in the study of age-related variation in survival and reproduction. Using an approach based on random effects, we were able to characterize the influence of age on these parameters at the individual level, which does not necessarily correspond to the pattern perceptible at the population level (Vaupel and Yashin 1985*a*, 1985*b*; fig. 1). Our results provide confirmation of what has been suggested by other investigators (i.e., within-cohort phenotypic selection can mask senescence; Vaupel and Yashin 1985*a*, 1985*b*; Johnson et al. 1986; Burnham and Rexstad 1993; McDonald et al. 1996; Nichols et al. 1997; Service 2000) and is likely typical. Modeling individual heterogeneity explicitly permits detection of a senescent decline in survival within individuals, which is undetectable in aggregate (survival is constant at the population level; fig. 1*A*). While evidence of senescence has been found in short-lived captive animals (the most famous biological model is certainly *Drosophila melanogaster*), conclusive evidence of senescent decline in fitness components in vertebrates studied in the wild is rare (as discussed in Gaillard et al. 1994; Nichols et al. 1997; Loison et al. 1999). Our results demonstrate senescent changes within individual in a wild population.

McDonald et al. (1996) and Service (2000) extensively discussed the implications of this phenomenon for evolutionary studies of senescent decline in survival. It is legitimate to ask whether lack of evidence for senescent declines in survival in many studies reflects use of inadequate modeling approaches rather than a true absence of senescence (McDonald et al. 1996; Service 2000). Similarly, one may ask whether differences in the influence of age on survival among groups in populations do not reflect differences in the degree of heterogeneity among groups (e.g., sexes; Andersson 1994; Lindström 1999). Indeed, the magnitude of the discrepancy between individual-specific and population-level rates may depend on the degree of heterogeneity in populations.

Our analyses also provided evidence of a strong positive correlation between latent survival and breeding probabilities in the kittiwake. This correlation explains the progressive departure of the breeding rate observed at the population level from the mean individual-specific rate (fig. 1*B*). Phenotypic selection within birth cohorts leads to a decrease in the proportion of individuals with lower survival and correspondingly lower breeding probability, thus raising the apparent average breeding probability in older individuals. This result confirms that differential mortality can also lead to discrepancies between age-specific variation in measures of reproductive effort expressed at the individual level and the population level. Until now, the main question regarding this discrepancy was whether increases in reproductive rate in younger individuals observed in previous studies resulted from within-cohort phenotypic selection or reflected a phenomenon valid at the individual level (e.g., Curio 1983; Forslund and Pärt 1995). Our results show that this initial increase is detected in individual-specific rates as well as in population-level rates. However, we found evidence that the latter underestimate the senescent decline in reproduction in older individuals.

In addition to the question of the evolution of senescence, assessing the influence of age on reproduction and survival at the individual level is crucial for understanding the evolution of age-specific reproductive strategies. Hypotheses in the field of life-history theory rest on processes operating at the individual level, such as long-term optimization of reproductive investment and progressive increase in investment at the start of reproductive life (e.g., Stearns 1992; Charlesworth 1994; Forslund and Pärt 1995). Patterns resulting from within-cohort phenotypic selection are not relevant to the study of age-specific reproductive strategies if they differ from patterns at the individual level. Models accounting for individual heterogeneity in reproductive rates have seldom been used with data from wild animal populations, and we are not aware of studies that have accounted for the correlation between survival and reproduction at the individual level. Thus, one may also ask to what extent the patterns described in previous studies actually reflect age-specific variation in reproductive parameters valid at the individual level (e.g., initial improvement in the probability of breeding successfully in younger breeders; Forslund and Pärt 1995) and whether differences among groups do not result from differences in the degree of heterogeneity in both latent survival and reproductive rates in these groups.

Models accounting for individual heterogeneity in studies of survival have seldom been used with data from wild animal populations. One reason for this is that many of the models commonly used in human demography can be applied only in situations where no individual alive and present in the study area is missed by investigators or where no death event is missed (e.g., in captive animals). This situation is very rare when using data collected in the wild (Nichols 1992; Clobert 1995). Accommodating incomplete registration will require development of models for capture-recapture data incorporating the probability of capturing/observing individuals (Lebreton et al. 1992; Gaillard et al. 1994) and random individual effects (Lebreton 1995).

Our approach rests on the assumption that each individual has its own fitness components (as opposed to approaches based on group-specific components). These components are analogous to the concept of frailty used in survival studies based on hazard functions (e.g., Service 2000), where each individual is assumed to have its own mortality risk. They reflect the underlying individual potential for survival and reproduction. It is very likely that this potential is molded throughout the entire life, including developmental and prebreeding stages (which last several years in the kittiwake). Thus, these components integrate experience during prebreeding stages of life and partly reflect the epigenetic load (Williams 1992). They can be viewed as measures of individual quality, where quality is not restricted to a genetically determined characteristic. Models incorporating individual characteristics changing over time are also possible. Applied to reproduction in animals for example, latent effects would then integrate experience at any stage of life and would better reflect the epigenetic load. It is also possible to include in the modeling covariates that may capture part of the variation assumed to be associated with individual quality (e.g., variables sometimes used to characterize quality; Bjornstad and Hansen 1994; McDonald et al. 1996; McNamara and Houston 1996; Wolf et al. 1997). This may provide means for assessing the ability of quality criteria to capture variation among individuals in the trait under study. Lastly, development of models incorporating individual heterogeneity in fitness components should permit investigation of questions for which empirical evidence is limited, for example, the possible influence of individual quality on age-specific reproductive strategies (Nur 1988).

Assessing differences in fitness among phenotypes is a central objective in evolutionary biology. Until now, lack of appropriate statistical tools constrained biologists to assess selective values using estimates of mean fitness corresponding to classes defined on the basis of factors of interest (e.g., age), trait values, or arbitrary criteria assumed to be associated with individual quality (Coulson 1968; Bjornstad and Hansen 1994; McNamara and Houston 1996; Wolf et al. 1997; Morris 1998; but see McGraw and Caswell 1996). Because of genetic differences or differences in experience during development or prereproductive or reproductive life (Williams 1992; Schlichting and Massimo 1996; Lindström 1999; Sedinger et al. 1999), individuals in such classes are very unlikely to have identical fitness. Models permitting description of the distribution of fitness values in the population, or in subpopulations defined on the basis of some factor of interest, are more realistic. In addition, the use of approaches permitting the description of the genuine influence of age on survival and reproduction (i.e., eliminating the confounding effect of within-cohort phenotypic selection) is critical to robust inference in comparative studies of senescence and of evolution in age-structured populations in general. The current tendency in several fields is to integrate individual characteristics in order to produce more realistic models and testable predictions (e.g., population dynamics, natural, sexual, or kin selection; McNamara and Houston 1992, 1996; Bjornstad and Hansen 1994; Morris 1998; Widemo and Seather 1999). From this perspective, the development of models permitting access to individual variation in fitness is a promising advance for the study of evolutionary processes.

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