

Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes

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Summary

1. Many studies have provided evidence that first-time breeders have a lower survival, a lower probability of success, or of breeding, in the following year. Hypotheses based on reproductive costs have often been proposed to explain this. However, because of the intrinsic relationship between age and experience, the apparent inferiority of first-time breeders at the population level may result from selection, and experience may not influence performance within each individual. In this paper we address the question of phenotypic correlations between fitness components. This addresses differences in individual quality, a prerequisite for a selection process to occur. We also test the hypothesis of an influence of experience on these components while taking age and reproductive success into account: two factors likely to play a key role in a selection process.

2. Using data from a long-term study on the kittiwake, we found that first-time breeders have a lower probability of success, a lower survival and a lower probability of breeding in the next year than experienced breeders. However, neither experienced nor inexperienced breeders have a lower survival or a lower probability of breeding in the following year than birds that skipped a breeding opportunity. This suggests heterogeneity in quality among individuals.

3. Failed birds have a lower survival and a lower probability of breeding in the following year regardless of experience. This can be interpreted in the light of the selection hypothesis. The inferiority of inexperienced breeders may be linked to a higher proportion of lower-quality individuals in younger age classes. When age and breeding success are controlled for, there is no evidence of an influence of experience on survival or future breeding probability.

4. Using data from individuals whose reproductive life lasted the same number of years, we investigated the influence of experience on reproductive performance within individuals. There is no strong evidence that a process operating within individuals explains the improvement in performance observed at the population level.

Key-words: age, capture–recapture, experience, fitness components, selection hypothesis.

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Introduction

Data collected in long-term studies have been widely used to investigate variations of demographic parameters throughout life, and several patterns have been described for reproductive success, survival

and breeding probability (among individuals that bred at least once). Several studies on birds and mammals have found evidence of an increase in the probability of breeding at the beginning of reproductive life (i.e. after the first reproduction; Wooller & Coulson 1977; Mougin, Jouanin & Roux 1987; Newton 1989; Wooller *et al.* 1990; Weimerskirch 1992; Boyd *et al.* 1995; Cézilly *et al.* 1996). The same pattern has been observed for breeding success (Ryder 1980; Nelson 1988; Gaillard *et al.* 1994; Lunn, Boyd & Croxall 1994; Forslund & Pärt 1995;

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Clutton-Brock *et al.* 1996; Marrow *et al.* 1996). In this context, some studies have focused on the specific influence of first reproduction (Bradley *et al.* 1989; Wooller *et al.* 1989; Weimerskirch 1990; Weimerskirch 1992; Chastel, Weimerskirch & Jouventin 1995; Viallefont 1995; Viallefont, Cooch & Cooke 1995a). First-time breeders have a lower probability of breeding successfully (Newton 1986), a higher probability of nonbreeding in the following year (Coulson & Thomas 1985; Weimerskirch 1990; Wooller *et al.* 1990; Viallefont *et al.* 1995a; Viallefont, Cooke & Lebreton 1995b), and a lower survival or return rate than experienced individuals (Wooller *et al.* 1989; Promislow 1991; Chastel *et al.* 1995; Clutton-Brock *et al.* 1996). Here we address the question of this specific 'inferiority' of first-time breeders.

Several hypotheses combining the concepts of experience and reproductive costs have been proposed to explain lower performance in inexperienced individuals. First, experience would lead to increased success probability (Nur 1984; Bradley & Wooller 1991) and survival (Newton 1986). Second, first-time breeders may have to invest more to achieve the same reproductive performance as experienced individuals, which could result in higher costs (Ainley & DeMaster 1980; Weimerskirch 1990; Promislow 1991; Viallefont 1995). Lower performance among first-time breeders may also reflect long-term optimization of reproductive effort throughout life (i.e. the *restraint hypothesis sensu* Curio 1983) (Williams 1966; Pianka & Parker 1975; Charlesworth 1980; Pugesek 1981, 1984; Pugesek & Diem 1983, 1990; Pärt 1995). The notion of experience is not involved here, but the intrinsic correlation between age and experience can translate into lower performance in inexperienced individuals.

Third, several hypotheses are based on the possibility of differences in individual quality (Coulson & Porter 1985; Coulson & Thomas 1985; Coulson 1988; Mills 1989; Aebischer & Coulson 1990; Forslund & Pärt 1995; Harris & Wanless 1995; Marrow *et al.* 1996; Cobley, Croxall & Prince 1998), and positive correlations between components of fitness (Reznick 1985; Van Noordwijk & de Jong 1986; Nur 1988; Reznick 1992; Stearns 1992; Viallefont 1995). Heterogeneity in individual quality can lead to a selection process (Curio 1983), that is an age-related decrease in the proportion of lower-quality individuals in cohorts (Thomas & Coulson 1988; Wooller *et al.* 1990; Sydeman *et al.* 1991b; Rexstad & Anderson 1992; Burnham & Rexstad 1993; Forslund & Pärt 1995). Earlier death of lower-quality individuals leads to increased survival at the population level (Vaupel & Yashin 1985). If higher survival is associated with better breeding performance, selection can also explain age-related increased performance at the same level. Lastly, age-specific optimal reproductive strategies may be quality-specific

(reviewed by Forslund & Pärt 1995; Pyle, Nur & Sydeman 1997). As above, those hypotheses do not involve the concept of experience, but the intrinsic correlation between age and experience can lead to poorer performance in first-time breeders.

The processes underlying these hypotheses are clearly different. The selection process operates at the population level: it is based on a progressive change in proportions of individuals with different survival rates. Such a process can be invoked when comparing demographic parameters at different ages using data from individuals, some of which die earlier than others. We will refer to that level as the 'population level'. In contrast, an optimization process or a process based on cumulative experience operates at the 'individual level'. This can be observed within each individual, or formally tested by comparing performance at different ages of individuals with the same longevity. From a methodological viewpoint, a major difference between these processes is the level at which they can be addressed. The optimization/cumulative experience hypotheses permit making predictions at the individual level, whereas the selection hypothesis does not.

Practically, investigating processes potentially operating at the individual level can raise difficulties: it is possible to address reproductive performance (individuals attempt to breed several times in their reproductive life), but obviously not survival (mortality occurs only once). In contrast, when addressing variation in demographic parameters throughout reproductive life at the population level, processes operating at the population and the individual level are both relevant. The purpose of this paper is to present analysis of factors rarely examined simultaneously: not only the influence of experience (first reproduction vs. subsequent breeding attempts) on survival and future breeding probability, but also phenotypic correlations between fitness components. The sign of these correlations will indicate whether a selection process is likely to occur. We also address variation in breeding performance at the individual level and compare the patterns observed within individuals to that observed at the population level. A given pattern of variation in demographic parameters within individuals does not necessarily translate into the same pattern at the population level (Vaupel & Yashin 1985).

Our first objective is to test the hypothesis of an effect of experience on breeding success, survival and the probability of breeding in the following occasion in the Kittiwake [*Rissa tridactyla* (L.)], a long-lived seabird. This step will provide results that can be compared to previous studies of the influence of the first breeding attempt on demographic parameters. The second objective is to address phenotypic correlations between components of fitness while taking experience into account. Investigation of reproductive success and lifetime production in the

Kittiwake led Coulson (1968), Coulson & Porter (1985), Coulson (1988) and Fairweather (1994) to put forward the hypothesis of differences in individual quality. Similarly, in a previous study on the same species, Cam *et al.* (1998) showed that there are positive phenotypic correlations between current reproduction and survival, as well as between current and future reproduction. In this framework, our first prediction is that breeders (regardless of experience) exhibit a higher survival and probability of breeding in the following year than birds that skipped a breeding opportunity (i.e. nonbreeders). We compare the demographic features of birds that do not breed to those of experienced breeders on the one hand, and of first-time breeders on the other hand. This addresses the sign of the phenotypic correlation between reproduction and survival. We also expect lower survival and breeding probabilities in inexperienced compared to experienced breeders.

Our third objective is to examine in more detail the question of experience by controlling for age (i.e. using a multivariate approach). This analysis addresses whether experience still influences demographic parameters after accounting for the influence of age, which forms the basis of the selection hypothesis. We also control for reproductive success. Assuming that individual quality influences success, successful individuals should exhibit the highest survival and lowest probability of nonbreeding in the following year. A higher proportion of those individuals in older age classes (as assumed by the selection hypothesis) could explain an apparent inferiority of first-time breeders. Controlling simultaneously for age and success permits testing for the influence of experience after accounting for two potential confounding factors linked to selection. These analyses were performed using data from a decreasing number of individuals as they age, which is required to draw inference about the selection hypothesis.

We also address whether a process other than selection could account for the influence of experience on demographic parameters observed at the population level. This requires investigation of variation in performance in individuals with similar reproductive longevity. As we suspect that individuals that die earlier have different features from birds that survive longer, pooling data from birds whose reproductive life lasted *at least* n years is likely to lead to heterogeneous subsets. This could mask the phenomenon of interest if variations in performances throughout life differ according to quality. Consequently, we performed analyses using data from birds whose reproductive life lasted *exactly* 2, 3, ..., n years. In other words, we used reproductive longevity as a surrogate of quality. We tested for an effect of the number of years elapsed since the start of reproductive life on success probability, and the probability of breeding in the fol-

lowing year. We also address the question of the influence of first-reproduction on reproductive success and future breeding activity using the same approach. Improvement of breeding performance within individuals would support the hypothesis of a positive effect of cumulative experience on reproduction, including reduced reproductive costs, or of a long-term optimization of reproductive investment throughout reproductive life.

Methods

DATA COLLECTION AND SELECTION

Data were collected in Brittany (France) from 1979 to 1994. Individuals were marked using a unique colour combination of plastic bands. Only data from individuals marked as chicks and that recruited in one of the study colonies were retained. The data used here were mostly collected between April and August. Each year, individuals were classified as follows: (i) nonbreeders that never previously bred (prebreeders); (ii) first-time (inexperienced) breeders; (iii) experienced breeders; and (iv) nonbreeders that previously bred (nonbreeders). Data from prebreeders were excluded. Individuals were considered as breeders if they built a nest that reached the completion criterion (Maunder & Threlfall 1972). As our objective was to investigate the specific influence of first reproduction on fitness components, we defined a variable *experience* with two modalities: first-time breeder and experienced breeder. Birds were considered as nonbreeders only if they were resighted in a given year and were known to have skipped the breeding occasion.

Individuals were categorized as successful if at least one of the young fledged. Only data collected from 1985 onwards were retained for analyses requiring knowledge of reproductive success (improvement of field methods led to higher precision in determination of breeding state). Reproductive activity (i.e. breeding/nonbreeding) and reproductive success (i.e. in breeders: fledged at least one chick/fledged no chick), were used as measures of components of fitness. The two components used are: (i) adult survival; and (ii) production of at least one chick (i.e. raised to independence) vs. failure to produce any young. We believe that variation in these components reflects differences in fitness.

STATISTICAL METHODS

Analyses were carried out using two methods, in two steps. Proportions based on counts of individuals observed in year t and returning in year $t + 1$ depend on both survival and recapture probability. Unless the latter is equal to one, return rates provide biased estimates of survival probability (Lebreton *et al.* 1992; Clobert 1995). Proportions based on counts

of individuals that return and breed also provide biased estimates of future breeding probability. Differences in return rates among individuals belonging to different categories can reflect variation in recapture probability (Nichols *et al.* 1994). Breeding activity and success can influence individual behaviour, and thus recapture probability (e.g. individuals that fail may leave breeding places earlier than others, which may influence the probability of observing them). To account for variation in recapture probability we used multistate capture–recapture models (Nichols & Kendall 1995), which incorporate state-specific detection probabilities. They permit estimation of parameters—survival or breeding probability—specific to yearly reproductive state (Nichols *et al.* 1994; Nichols & Kendall 1995).

Multistate capture–recapture models (Brownie *et al.* 1993; program MSSURVIV, Hines 1994) were primarily used to test the hypothesis of an effect of state on recapture probability. They also permitted addressing the influence of experience on survival and the probability of breeding in the following year, and exploration of correlations between components of fitness while taking experience into account. The variable *state* had three modalities: (i) experienced breeder; (ii) nonbreeder; and (iii) first-time breeder. This method permits estimation of time- and state-specific recapture and survival probabilities and time-specific transition probabilities between states (Nichols *et al.* 1994; Nichols & Kendall 1995). Some 794 individual histories have been analysed using this approach. The most general model included time- and state-specific recapture and survival probability, and time-specific transition probability between states (Hestbeck *et al.* 1991). Model notation has been defined in Nichols *et al.* (1994). P_r^r (recapture probability) is the probability that a bird is resighted at time t in state r , given that it is alive and present at time t . S_r^r (survival probability) is the probability that a bird in state r at time t survives until occasion $t + 1$. ψ_r^{rs} (transition probability) is the probability that a bird in state r in occasion t is in state s at occasion $t + 1$ given that the individual survived from occasion t to occasion $t + 1$. We used the following notation for states: 1 = experienced breeder; 2 = nonbreeder; and 3 = inexperienced breeder.

Preliminary analysis using this approach indicated that the estimated recapture probability of experienced breeders and nonbreeders was extremely close to one ($0.982 \pm 0.128 \times 10^{-1}$ for these strata; there is no ‘recapture probability’ for first-time breeders). This high resighting probability permitted us to use return rates to estimate survival probabilities. An individual was considered as dead (or permanently emigrated) if it was not resighted in a given occasion. Similarly we estimated transition probabilities between breeding states r and s using the proportion of individuals released in year t in state r and

resighted in year $t + 1$ in state s . Survival and transition probabilities were modelled as linear combinations of explanatory variables using a logit link function (Agresti 1990). The same approach was used to address the question of the effect of age and experience on the probability of success in a given year. In addition, as the probability of observing breeders and birds skipping reproduction is very close to one, it is very unlikely that investigators missed first-time breeders established in the study area. Consequently, the age at which birds were observed as recruits can be considered as a reliable measure of age of first local reproduction.

Software and model notation. Logit models were built using PROC GENMOD, PROC LOGISTIC and the macro GLIMMIX of SAS (logistic regression: SAS Institute Inc. 1995; Stokes, Davis & Koch 1995; Littell *et al.* 1996). Model notation is defined in the STAT User’s Guide (SAS Institute Inc. 1988) for generalized linear models. Main effects are represented using capital letters (E for experience, A for age and S for reproductive success), and interactions using an asterisk (E*A for example). Only pairwise interactions between explanatory variables were included in initial models.

Accounting for extradispersion and nonindependence between observations. We estimated an extradispersion parameter and used QAIC for model selection when that parameter indicated over- or underdispersion (see also Model selection). As there is no objective criterion to interpret the extradispersion parameter (Littell *et al.* 1996), we chose the arbitrary range of values of 0.90–1.10. We used scaled deviance if the value was lower than 0.90 or higher than 1.10 (or very close to these thresholds). In addition, as we used several records from the same individual, nonindependence between observations could bias the analyses. According to Allison (1995), this is not relevant in analyses of survival as a function of the time elapsed since the individual entered the sample (i.e. the first reproduction in our case). We used the repeated statement of the macro GLIMMIX (Littell *et al.* 1996) in analyses of the probability of breeding, and the probability of success. We used two correlation structures corresponding to two possible scenarios. In all cases we used a compound symmetric structure, which corresponds to the idea that individuals differ in success probability for example, and that they keep that individual value for their entire reproductive life. We also used an autoregressive structure of order 1 in models that did not include previous reproductive state. This structure corresponds to a situation where observations from the same individual spaced at long time intervals are not correlated in the same way as observations close in time. Models including previous reproductive state already accounted for a possible relationship between consecutive breeding attempts.

Choice of initial logit models. Our objective was primarily to test a priori hypotheses on the effect of experience, age and reproductive success. We did not include all possible factors known to influence reproductive performance, survival or transition probability. In particular, when models contained the variable *age*, sample sizes corresponding to some modalities of the response variables were sometimes small. This occurred when data were stratified according to the independent variables *age*, *experience*, *reproductive success* and *time* in models requiring data from two consecutive years (for breeding state transition probabilities). Consequently, we limited the number of explanatory variables: we excluded the effect of time when too many parameters could not be estimated.

Effect of age. In initial models including the variables *age*, *experience* and *reproductive success*, age classes were defined a priori so that experienced, inexperienced, successful and failed birds are represented in each class: [2-, 3-, 4-year olds], [5-year olds] and [6-, 7-year olds]. Only one individual bred for the first time at age two during the study and 12 at age seven, with known breeding success. Data from birds older than seven were excluded from analyses.

Model selection. Model selection was based on Akaike's information criterion (AIC or QAIC; Akaike 1973; Burnham & Anderson 1992; Lebreton *et al.* 1992; Burnham & Anderson 1998), likelihood ratio (LR) tests and *F*-tests (Littell *et al.* 1996). NP corresponds to the number of estimated parameters. Model selection based on these criteria requires that the most general models fit the data adequately, which was assessed using a G-statistic (White 1983) for capture–recapture models and a Hosmer and Lemeshow statistic (Glanz & Slinker 1990) for logit models. For logit models, we systematically built every possible model corresponding to simplifications of the most general model, which always included main effects and pairwise interactions. We only present the general model and candidate constrained models from that initial step. The lowest-AIC model was selected. When the AIC values of two nested models differed by less than two with a higher value for the constrained model we used a LR test or *F*-test (Lebreton *et al.* 1992). After selecting a model new constraints were used to test specific a posteriori hypotheses.

Results

EFFECT OF EXPERIENCE AND BREEDING ACTIVITY

Recapture probabilities. Recapture probability varied with state, but not time (Table 1).

Survival probability. Survival probability varied with time and state (Table 1). There was no significant difference between the survival probabilities of first-time breeders and nonbreeders (Table 2). Experienced breeders had a higher mean survival probability ($\hat{S}_t^1 = 0.82 \pm 14 \cdot 10^{-2}$) than first-time breeders and nonbreeders ($\hat{S}_t^2 = \hat{S}_t^3 = 0.76 \pm 16 \cdot 10^{-2}$).

State transition probability. Transition probabilities were time-specific (Table 1). We found no evidence of a difference between breeding transition probabilities of first-time breeders and nonbreeders. Inexperienced birds and nonbreeders had a lower probability of breeding in the following year ($\hat{\Psi}_t^{32} = \hat{\Psi}_t^{22} = 0.21 \pm 1.5 \cdot 10^{-2}$) than experienced breeders ($\hat{\Psi}_t^{12} = 0.08 \pm 1.2 \cdot 10^{-2}$).

Interaction between state and time. We built a model where temporal variations of survival probabilities of experienced breeders on the one hand and of a category composed of first-time breeders and nonbreeders on the other hand, were parallel on a logit scale. This model was not selected (AIC = 377.7 vs. M3, Table 1). However, estimates made under model M3 (i.e. with the interaction) indicated that the survival probability of experienced breeders was higher or equal to that of inexperienced birds and nonbreeders, in all years (Fig. 1). We also built a model with an additive effect of state and time for breeding transition probabilities. This model had a higher AIC (664.0) than model M3 (AIC = 344.6, Table 1). Estimates of the probability of skipping the next breeding opportunity made under the model with interaction (M3) showed that experienced birds had a lower probability of nonbreeding than first-time breeders and nonbreeders, in all years (Fig. 2).

Success probability. The general model included the effect of experience, time and the interaction between them. We used models with a correlation term between observations from the same individual. We first used an exchangeable correlation structure. The extradisersion parameter estimated using this model indicated underdispersion (0.89). Consequently, we used QAIC for model selection. General model (E T E*T), QAIC = 3289.30, NP = 20, Hosmer and Lemeshow statistic = 1.85, d.f. = 8, *P* = 0.98. We found no evidence of an effect of the interaction (additive model: QAIC = 3277.34, NP = 11). Models with main effects only were not retained ('experience': QAIC = 3346.59, NP = 2; 'time': QAIC = 3424.78, NP = 10). The model with no effect of time or experience on success probability was not retained either (QAIC = 3424.43, NP = 1). Experienced breeders had a higher probability of success than first-time breeders, in all years (Fig. 3). Results were similar using a first-order autoregressive correlation structure.

Table 1. Likelihood ratio tests for an effect of time and state on recapture, survival and transition probability. AIC values for corresponding models

Model names	H0 vs. Ha	LR tests χ^2	d.f.	P	AIC H0	Ha	Biological hypothesis (H0)
P1 vs. A	(P^r, S^r, ψ^r) vs. (P^r, S^r, ψ^r)	0.00	15	1.00	362.5	418.6	No effect of time on P
P2 vs. P1	(P^r, S^r, ψ^r) vs. (P^r, S^r, ψ^r)	4.60	1	0.03	365.13	362.5	No effect of state on P
S1 vs. P1	(P^r, S^r, ψ^r) vs. (P^r, S^r, ψ^r)	71.84	27	0.00	380.4	362.5	No effect of time on S
S2 vs. P1	(P^r, S^r, ψ^r) vs. (P^r, S^r, ψ^r)	38.67	20	0.00	361.20	362.5	No effect of state on S
S3 vs. P1	$\ddagger(P^r, S^r, \psi^r) = S^2, \psi^r$ vs. (P^r, S^r, ψ^r)	19.96	10	0.03	362.5	362.5	Equal survival in experienced breeders and nonbreeders
S4 vs. P1	$(P^r, S^r) = S^2, \psi^r$ vs. (P^r, S^r, ψ^r)	16.05	10	0.10	358.6	362.5	Equal survival in inexperienced breeders and nonbreeders
S5 vs. P1	$(P^r, S^r) = S^3, \psi^r$ vs. (P^r, S^r, ψ^r)	19.83	10	0.03	362.3	362.5	No effect of experience on survival in breeders
M1 vs. S4	$(P^r, S^r) = S^2, \psi^r$ vs. $(P^r, S^r) = S^2, \psi^r$	118.15	27	0.00	422.7	358.6	No effect of time on transition probability
M2 vs. S4	$(P^r, S^r) = S^2, \psi^r = \psi^{12}$ vs. $(P^r, S^r) = S^2, \psi^r$	59.49	10	0.00	398.1	358.6	Experienced and inexperienced breeders have equal probabilities of nonbreeding in the following year
M3 vs. S4	$(P^r, S^r) = S^2, \psi^r = \psi^{22}$ vs. $(P^r, S^r) = S^2, \psi^r$	5.98	10	0.82	344.6	358.6	Nonbreeders and inexperienced breeders have equal probabilities of nonbreeding in the following year
M4 vs. S4	$(P^r, S^r) = S^2, \psi^r = \psi^{22}$ vs. $(P^r, S^r) = S^2, \psi^r$	33.64	10	0.00	372.2	358.6	Nonbreeders and experienced breeders have equal probabilities of nonbreeding in the following year

Goodness-of-fit P-value > 0.10 for the initial model (A).

†When survival or transition probabilities are constrained, only constrained parameters are specified in the model's description.

‡State notation: 1 = experienced breeder; 2 = nonbreeder; 3 = inexperienced breeder.

Selected model: M3

EFFECT OF AGE, EXPERIENCE AND BREEDING SUCCESS

Survival probability. Survival probability was modelled as a function of experience, age, reproductive success and the three corresponding pairwise interactions (Table 2). The extradispersion parameter was very close to 1.00 ($\hat{c} = 1.0054$). The lowest-AIC model (M1) included the effect of age and breeding success. We tested several a posteriori hypotheses using the model M1 (Table 2). The model with a linear trend in age was not selected (M3). The model with equal survival in 5-year-old birds and younger individuals (M4) was not retained either. We pooled 5-year-old birds with older individuals (M5). The AIC value of this model was slightly higher than the lowest value (1497.26 vs. 1496.59), but the LR test between these models was not significant ($\chi^2 = 4.67$, d.f. = 2, $P = 0.10$). Consequently, we selected the most parsimonious model (with only two age classes: M5). Successful breeders had a higher survival probability than failed ones when age was controlled for (Fig. 4a). In addition, the youngest successful breeders had the highest survival probability (Fig. 4a).

Probability of breeding in the following occasion. As above, the initial model comprised the effect of experience, age, breeding success and pairwise interactions (Table 3). The extradispersion parameter was very close to 1.00 ($\hat{c} = 1.0306$). Consequently, we used AIC for model selection. Three models had very close AIC values (M1, M2 and M3). These models were considered as candidate models to test a posteriori hypotheses (Table 3).

We first built models with a linear trend in age, but they were not selected [M'1 (1), M'2 (1) and M'3 (1)]. Neither was the model where 5-year-old and younger birds have equal probability of breeding in the following occasion [M'1 (2), M'2 (2) and M'3 (2)]. We also built models where 5-year-old and older birds had equal probabilities of breeding in the following year [M'1 (3), M'2 (3) and M'3 (3)]. The constrained model with an additive effect of age and reproductive success [M'3 (3)] was the lowest-AIC model (857.19). We estimated breeding probabilities using this model: failed breeders had a higher probability of nonbreeding in the following year when age was controlled for (Fig. 4b). In addition, the youngest breeders had a higher probability of nonbreeding in the following occasion when reproductive success was controlled for (Fig. 4b). Another model with only two age classes could also be considered as a candidate model [M'2 (3)]. However, the LR tests between this model and the lowest-AIC model [M'3 (3)] was not significant (Table 3) ($\chi^2 = 0.47$, d.f. = 1, $P = 0.49$). Consequently, we conclude that there is no strong evidence that incor-

Table 2. Influence of age (A), breeding success (S) and experience (E) on survival probability

Model name	Description of the models	NP	AIC
<i>Initial model selection procedure</i>			
M0	E A S E*A E*S A*S	10	1501.10
M1	A S A*S	6	1496.59
M2	S	2	1499.34
<i>A posteriori hypotheses</i>			
M3	A _(continuous) S A _(continuous) *S	4	1501.49
M4	A _[(2-3-4-5) (6-7)] S A _[(2-3-4-5) (6-7)] *S	4	1502.53
M5	A _[(2-3-4) (5-6-7)] S A _[(2-3-4) (5-6-7)] *S	4	1497.26

Goodness-of-fit test for M0: Hosmer and Lemeshow statistic = 3.09, d.f. = 8; *P* = 0.93.

1597 observations from 656 individuals.

Selected model in the initial selection procedure: M1.

Selected model: M5.

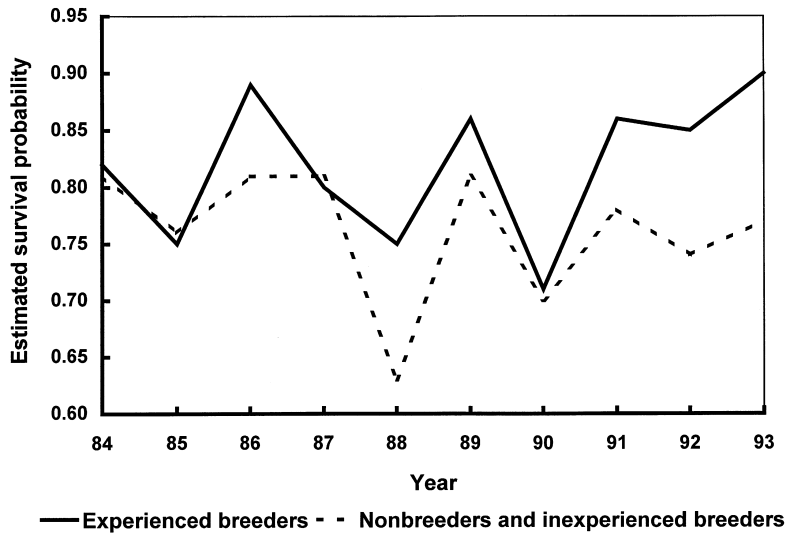


Fig. 1. Influence of experience and reproductive activity on survival probability.

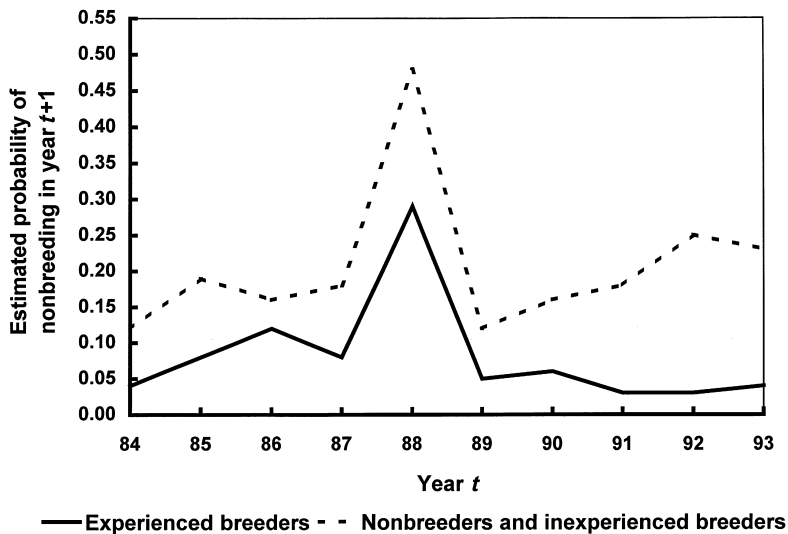


Fig. 2. Influence of experience and reproductive activity on the probability of nonbreeding in the following occasion.

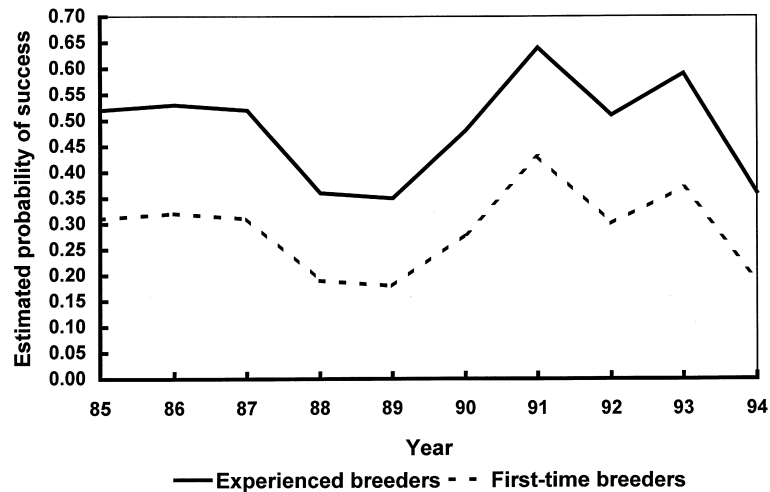


Fig. 3. Influence of experience on success probability.

poration of the variable *experience* improves the fit of the models.

Success probability. The initial model included age, experience and the interaction (Table 4). The extra-dispersion parameter estimated using an exchangeable correlation structure indicated slight underdispersion ($\hat{\epsilon} = 0.9140$). The lowest QAIC model in the initial selection step was the general model (M0): we used this model to test a posteriori hypotheses. The model with a linear trend in age was not retained (M1). We found evidence that the

probability of success of 5-year-old birds differs from that of younger individuals (M2 was not retained). We tried to pool 5-year-old birds with older birds: that model was selected (M3). We built a model where there was no effect of age in experienced breeders (M4) or in first-time breeders (M5), successively. The former was selected (M4). Similar results were obtained using a first-order, autoregressive correlation structure. The youngest inexperienced birds have the lowest probability of success. Estimated probability of success: experienced breeders $\hat{\phi} = 0.46$ (95% C.I.: 0.42–0.49); 5-, 6- and 7-

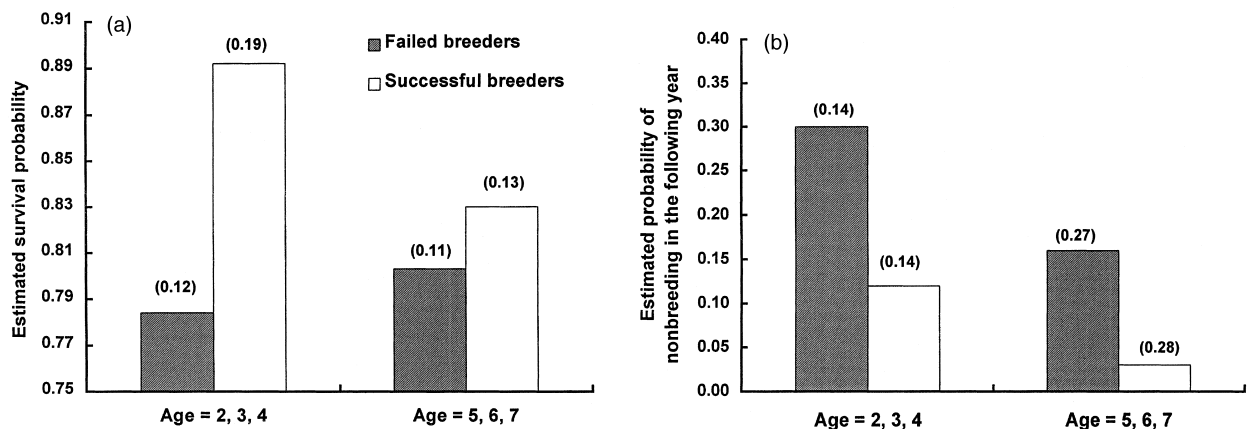


Fig. 4. (a) Influence of age and reproductive performance on survival probability; subset of data from birds belonging to age classes where experienced and inexperienced individuals are represented. In brackets: estimated standard errors. (b) Influence of age and reproductive performance on the probability of nonbreeding in the following occasion; subset of data from birds belonging to age-classes where experienced and inexperienced individuals are represented. In brackets: estimated standard errors.

Table 3. Influence of age (A), reproductive success (S) and experience (E) on the probability of nonbreeding in the following occasion

Model name	Description of the models	NP	AIC
<i>Initial model selection procedure</i>			
M0	E A S S*E S*A E*A	10	861.80
M1	E A S E*A	7	858.70
M2	E A S	5	859.85
M3	A S	4	858.64
<i>A posteriori hypotheses</i>			
M'1 (1)	E A _(continuous) S E*A _(continuous)	5	860.27
M'1 (2)	E A _[(2-3-4-5) (6-7)] S E* A _[(2-3-4-5) (6-7)]	5	863.93
M'1 (3)	E A _[(2-3-4) (5-6-7)] S E* A _[(2-3-4) (5-6-7)]	5	860.20
M'2 (1)	E A _(continuous) S	4	868.29
M'2 (2)	E A _[(2-3-4-5) (6-7)] S	4	870.40
M'2 (3)	E A _[(2-3-4) (5-6-7)] S	4	858.72
M'3 (1)	A _(continuous) S	3	869.82
M'3 (2)	A _[(2-3-4-5) (6-7)] S	3	876.27
M'3 (3)	A _[(2-3-4) (5-6-7)] S	3	857.19

Goodness-of-fit test for M0: Hosmer and Lemeshow statistic = 11.76, d.f. = 8, $P = 0.16$.

1130 observations from 521 individuals.

M1, M2 and M3: lowest-AIC models from the initial selection procedure.

M'1, M'2 and M'3: constrained models corresponding to M1, M2 and M3, respectively.

M'1 (3), M'2 (3) and M'3 (3): candidate models.

Selected model: M'3 (3).

year-old inexperienced breeders $\hat{\phi} = 0.39$ (95% C.I.: 0.32–0.47); 2-, 3- and 4-year-old inexperienced breeders $\hat{\phi} = 0.26$ (95% C.I.: 0.22–0.30).

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Success probability. . We first modelled the probability of success as a function of the number of years Y elapsed since first reproduction (included) (Table 5). This variable was retained in one case: birds with a reproductive life of 4 years. There is an important initial increase in success probability (between the first reproduction and the following attempts), but this is not observed in birds with a longer reproductive life (Table 5). We then compared the first repro-

duction to subsequent attempts (Table 5): this contrast was significant in birds with a reproductive life of 4 and 5 years. Estimates were consistent with those previously obtained: success probability was lower in the first breeding attempt. When Y was considered as a continuous variable (i.e. a linear trend in breeding probability with Y), none of the analyses provided evidence of an influence of that variable (these analyses are not presented here). Results were consistent when using an autoregressive correlation structure of order 1.

Breeding transition probability. . The probability of nonbreeding in the following year was modelled as a function of Y (Table 6). We did not find evidence of such an effect. The contrast between the first breed-

Table 4. Test for an effect of age (A) and experience (E) on success probability

Model name	Description of the models	NP	QAIC
<i>Initial model selection procedure</i>			
M0	A E A*E	6	2299.61
<i>A posteriori hypotheses</i>			
M1	A _(continuous) E A _(continuous) *E	4	2305.42
M2	A _[(2-3-4-5) (6-7)] E A _[(2-3-4-5) (6-7)] *E	4	2310.58
M3	A _[(2-3-4) (5-6-7)] E A _[(2-3-4) (5-6-7)] *E	4	2299.63
M4	No effect of age in experienced breeders	3	2295.68
M5	No effect of age in inexperienced breeders	3	2310.60

Goodness-of-fit test for M0: Hosmer and Lemeshow statistic = 9.91, d.f. = 8, $P = 0.27$.

Correlation structure: compound symmetry.

Selected model: M4.

Table 5. Test for an effect of the number of years Y elapsed since first reproduction (included) and of experience (first vs. subsequent attempts), on the probability of success (ϕ) in individuals whose reproductive life lasted n years. AIC or QAIC values for corresponding models

Reproductive life span (n)	Influence of the number of years elapsed since first reproduction						Contrast between the first and subsequent breeding attempts					
	Information Criterion	H0	Ha	test χ^2 or F	d.f.	P	Information Criterion	H0	Ha	LR test χ^2 or F	d.f.	P
2	QAIC	273.85	275.06	0.40	1, 56	0.53	QAIC	273.85	275.06	0.40	1, 56	0.53
3	AIC	235.29	234.60	3.98	2	0.14	AIC	235.29	234.61	2.68	1	0.10
4	AIC	163.76	152.87 A	16.89	3	0.00	AIC	163.76	158.01 B	7.76	1	0.00
5	QAIC	201.55	195.72	2.18	4, 85	0.08	QAIC	204.01	198.90 C	4.22	1, 88	0.04
6	AIC	203.82	211.55	2.27	5	0.81	AIC	206.20	207.06	1.13	1	0.29
7	AIC	88.56	97.20	3.36	6	0.76	AIC	88.56	90.53	0.03	1	0.87
8	AIC	115.65	124.63	5.02	7	0.66	AIC	115.65	116.82	0.83	1	0.36

H0 = no influence of experience on ϕ ; Ha: experience influences ϕ .

Information criterion in bold: selected model.

Correlation structure: compound symmetry.

Number of individual histories used: 96, 76, 42, 41, 33, 14 and 13 for $y = 2, 3, 4, 5, 6, 7$ and 8, respectively.

A: estimated probability of success (ϕ) and 95% confidence interval, for birds in the y^{th} year of reproductive life ($\hat{\phi}_y$): $\hat{\phi}_1 = 0.14$ (0.05–0.32); $\hat{\phi}_2 = 0.58$ (0.41–0.73); $\hat{\phi}_3 = 0.23$ (0.12–0.40); $\hat{\phi}_4 = 0.35$ (0.26–0.46).

B: estimated probability of success (ϕ) and 95% confidence interval: $\hat{\phi}_{(\text{first reproduction})} = 0.14$ (0.05–0.32); $\hat{\phi}_{(\text{subsequent attempts})} = 0.38$ (0.28–0.49).

C: estimated probability of success (ϕ) and 95% confidence interval: $\hat{\phi}_{(\text{first reproduction})} = 0.13$ (0.05–0.33); $\hat{\phi}_{(\text{subsequent attempts})} = 0.35$ (0.26–0.46).

ing attempt and subsequent attempts was significant in birds whose reproductive life lasted 5 years: the probability of nonbreeding in the following year was higher in first-time breeders (Table 6). As above, we did not find evidence of an influence of Y on transition probability when Y was considered as a continuous variable (these analyses are not presented

here). In addition, results were similar using a first-order, autoregressive correlation structure.

Discussion

We found evidence of an influence of experience on survival and future breeding probability when age

Table 6. Test for an effect of the number of years Y elapsed since first reproduction (included) and of experience (first vs. subsequent attempts), on the probability of breeding in the following year (ω) in individuals whose reproductive life lasted n years. AIC or QAIC values for corresponding models

Reproductive life span (n)	Influence of the number of years elapsed since first reproduction						Contrast between the first and subsequent breeding attempts					
	Information Criterion	H0	Ha	test χ^2 or F	d.f.	P	Information Criterion	H0	Ha	LR test χ^2 or F	d.f.	P
3	QAIC	217.71	217.22	0.17	1, 37	0.68	QAIC	217.71	217.22	0.17	1, 37	0.68
4	QAIC	61.78	65.05	0.57	2, 50	0.57	QAIC	63.96	65.20	0.41	1, 51	0.52
5	QAIC	130.49	125.10	1.99	3, 55	0.12	QAIC	144.11	139.11 A	4.11	1, 57	0.05
6	QAIC	123.24	130.43	0.73	4, 86	0.58	QAIC	128.18	129.18	0.08	1, 89	0.78
7	QAIC	75.61	80.11	1.07	5, 35	0.39	AIC	53.53	54.66	0.87	1	0.35

H0 = no influence of Y on ω ; Ha: Y influences ω .

Information criterion in bold: selected model.

Correlation structure: compound symmetry.

Number of individual histories used: 68, 40, 40, 33 and 13 for $y = 3, 4, 5, 6$ and 7, respectively.

A: estimated probability of breeding in the following year (ω) and 95% confidence interval: $\hat{\omega}_{(\text{first reproduction})} = 0.66$ (0.46–0.82); $\hat{\omega}_{(\text{subsequent attempts})} = 0.84$ (0.74–0.91).

and reproductive success were not taken into account. Inexperienced breeders systematically performed less well than experienced breeders. These results are consistent with several other studies (Coulson & Thomas 1985; Wooller *et al.* 1989; Weimerskirch 1990; Wooller *et al.* 1990; Promislow 1991; Chastel *et al.* 1995; Viallefont *et al.* 1995a; Viallefont, Cooke & Lebreton 1995b). Although age and experience are highly correlated, they correspond to distinct biological phenomena (Curio 1983; Nelson 1988; Promislow 1991; Forslund & Pärt 1995; Partridge & Barton 1996). Thus, a measure of experience could be needed to describe the data in addition to age. Our results supported that hypothesis only in one case: success probability. Yet the influence of experience on survival and future breeding probability was significant when age was not controlled for. Such a phenomenon has been observed elsewhere (Croxall, Rothery & Crisp 1992; but see Sydeman *et al.* 1991a).

The equivocal effect of experience could be an artefact linked to the multivariate approach: it is most likely that age and experience provide redundant information. Another explanation is that the number of breeding attempts is not an accurate measure of experience. Experienced individuals are supposed to have reproductive and foraging skills increasing the efficiency of their activities (Nur 1984; Bradley & Wooller 1991). Some skills could be acquired before recruitment. In many long-lived seabirds, prebreeders attend colonies, defend breeding sites and form pairs (Nelson 1983; Nelson 1988; Klomp & Furness 1990, 1991; Danchin *et al.* 1991; Zack & Stutchbury 1992). Prebreeders defending territories have a higher probability of success when they recruit (Klomp & Furness 1991; Zack & Stutchbury 1992; Cadiou 1993). In the Kittiwake, recruitment is a progressive social process in which the activities of prebreeders are likely to play a prominent part in the preparation of the first reproduction (Danchin *et al.* 1991; Cadiou 1993; Cadiou, Monnat & Danchin 1994).

A third hypothesis can be put forward: the apparent influence of experience on survival and future breeding probability, observed when age and success are not controlled for, could reflect an underlying age-related change in the proportions of individuals of different quality in the population. A set of elements suggests that selection is likely to occur in that population. First, we did not find evidence of negative phenotypic relationships between reproduction and survival or between current and future reproduction. This supports the hypothesis of heterogeneity in individual quality, which is a prerequisite for selection to occur. This is consistent with previous studies on the same species (Coulson & Porter 1985; Coulson & Thomas 1985; Coulson 1988; Aebischer & Coulson 1990; Cam *et al.* 1998). Second, failed breeders have a lower survival and a

lower probability of breeding in the following occasion, regardless of experience. Last, we found evidence that first-time breeders have a lower success probability. The higher proportion of failed breeders in first-time breeders might reflect a higher proportion of lower-quality individuals in this category.

Selection is not the only potential process explaining the improvement of performance in experienced breeders compared to first-time breeders. There is an initial increase in performance between the first breeding attempt and the following attempt in some subsets of individuals with similar reproductive longevity. This provides slight evidence that a process operating at the individual level contributes to explain the influence of experience on breeding activity and performance observed at the population level. However, this pattern is not observed in subsequent breeding attempts. In addition, results vary drastically among subsets of individuals with similar reproductive longevity. The majority of our analyses indicated that experience does not influence breeding performance within individuals. This process alone can probably not account for the results obtained at the population level.

Our results are consistent with the scenario described by Vaupel & Yashin (1985): patterns of variation within homogeneous categories can be very different from patterns observed at the population level. An increase in survival (and parameters positively correlated with survival, such as performance) can be observed in populations while there is no variation within homogeneous categories of individuals. This can also be observed when performance varies within categories without any systematic trend, or even deteriorates. The hypothesis of earlier disappearance of individuals with lower survival and performance and the hypothesis of improvement of performance within individuals are not alternative: results supporting one of them do not allow rejection of the other. Forslund & Pärt (1995) suggested that several processes operate simultaneously in populations. In the present case, patterns observed at the individual level cannot explain the pattern at the population level (but see Rockwell *et al.* 1993).

Considering what Vaupel & Yashin (1985) called 'heterogeneity's ruses' can be critical when testing the hypothesis of differential reproductive costs using distinct samples that might include different proportions of individuals of different quality; for example when conducting experiments (e.g. clutch or brood size manipulation) using data from different individuals (inexperienced and experienced individuals or individuals of different age). The selection process should also be considered when addressing variation in survival or reproductive performance at the population level. Heterogeneity in survival among individuals can lead to age- or experience-related patterns of variation in demographic para-

meters at the population level, apparently consistent with the predictions of various hypotheses based on the notion of reproductive costs or cumulative experience. Heterogeneity can also mask a decrease in survival in older individuals (Johnson, Burnham & Nichols 1986; Nichols, Hines & Blums 1997), which is an assumption of the hypothesis of long-term optimization in reproductive effort.

Data from individuals with similar reproductive longevity permit access to processes other than selection. Such an approach should be used in manipulative as well as observational studies to address processes operating within individuals. For fitness components that cannot be addressed that way, such as survival, we recommend investigation of phenotypic correlations between reproductive success and survival using an unmanipulated reference sample (e.g. Rockwell *et al.* 1993; Boyd *et al.* 1995). If results support the hypothesis of heterogeneity in the population, only development of statistical methods accounting for individual differences or use of quality as a covariate (i.e. an individual characteristic determined a priori) would provide means of disentangling the various processes responsible for improvement of fitness throughout reproductive life. Otherwise, several nonexclusive hypotheses have to be considered as possible explanations for observed patterns in demographic parameters. One of the major results of syntheses on long-term studies in birds is the very important disparity among individuals in lifetime reproductive success (Newton 1989). Although environmental stochasticity partly explains this disparity, heterogeneity in individual quality is likely to be a common feature in long-lived species (Newton 1989; McNamara & Houston 1992, 1996; in the kittiwake: Coulson 1968). Thus, selection is a process likely to be operating in most populations of long-lived species.

Many models developed to investigate age-specific reproductive strategies are based on the theory of optimization (Charlesworth 1980; Nur 1988; Stearns 1992; Seger & Stubblefield 1998). Heterogeneity in quality has long been recognized as one of the main obstacles to testing the predictions of these models using data from observational studies (Nur 1988; McNamara & Houston 1996). Incorporation of sources of heterogeneity in models is viewed as a promising means of progressing in the study of the evolution of life histories (McNamara & Houston 1992, 1996). Age-specific reproductive strategies might be optimal within quality groups (Nur 1988; McNamara & Houston 1992, 1996; Cichoń, Oljniczak & Gustafsson 1998; Pettifor, Perrins & McCleery 1998), while they appear suboptimal in heterogeneous groups such as populations. As an illustration, we could speculate that the higher probability of nonbreeding in first-time breeders observed in the present study supports the restraint hypothesis. Indeed, this group probably includes a

higher proportion of lower-quality birds likely to incur higher costs for a given investment. In lower-quality birds, nonbreeding could be associated with higher survival and future breeding probabilities, but at the population level nonbreeding is associated with the lowest values for these parameters. The inference that nonbreeding reflects reproductive costs or is beneficial in terms of fitness would have to be restricted to lower-quality individuals and cannot be drawn at the level of a heterogeneous group.

Understanding age-related variation in life history traits requires access to patterns corresponding to homogeneous groups that can be considered as reliable descriptions of patterns at the individual level. In addition, developing state-dependant life-history models (McNamara & Houston 1992, 1996) and testing corresponding predictions using data collected in the wild requires increased stratification of data according to criteria influencing individual performance. This requires estimation of fitness components specific to quality categories (Cichoń *et al.* 1998). From that perspective, it is necessary to increase the efforts devoted to identification of the variables influencing quality (McNamara & Houston 1992, 1996). The influence of heterogeneity on age-related variation in survival has long been recognized in human populations (e.g. in medical surveys) and has led to important methodological developments (Manton & Stallard 1981; Manton, Stallard & Vaupel 1981; Hougaard 1984; Manton & Stallard 1984). There is an urgent need for development of approaches to estimation of survival and breeding probabilities accounting for heterogeneity among individuals in animal populations (Rexstad & Anderson 1992; Burnham & Rexstad 1993) in situations where not all the individuals are resighted during sampling efforts.

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