EARLIER RECRUITMENT OR EARLIER DEATH? ON THE ASSUMPTION OF EQUAL SURVIVAL IN RECRUITMENT STUDIES

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Abstract. In species with deferred breeding, the population can be viewed as composed of phenotypes with different underlying age of first breeding defined at birth. The distribution of underlying age of first breeding within cohorts and the realized distribution of age of recruitment in individuals that survived from birth to first breeding (assessed in the breeding segment of the population) may differ. Realized age of recruitment is governed by the product of two demographic components: [local survival probability from birth to age $i - 1$] $\times$ [transition probability from the ''prebreeder'' state to the ''breeder'' state between age $i - 1$ and i]. The usual approach to gain insight into selective pressures shaping age of recruitment is to address covariation of realized age of first breeding with population size or social and environmental factors. Ideally, one should also conduct comparisons among groups of individuals encountering different conditions at a given age as prebreeders. However, in many species with deferred breeding, individuals are not encountered between birth and first breeding. Consequently, approaches to estimating recruitment probability in the absence of data from prebreeders have been developed. Some of these measures of recruitment ignore variation in the size of the pool of prebreeders among groups (as opposed to transition probability). Unless survival before full recruitment is known to be identical in the groups, inferences about the causes of variation in realized age of first breeding among groups are difficult: such differences may result from differences in survival probability before all the individuals make the transition between states.

We assessed the consequences of differences in prebreeding survival among groups on realized age-specific recruitment probability using numerical simulations. Depending on the specific scenario, realized age-specific breeding proportions were delayed or advanced compared to those expected according to the true underlying age-specific transition probabilities. We consider an example of this problem using data from a population of a seabird species, the kittiwake (*Rissa tridactyla*), where data from prebreeders and breeders were available. Consistent with results from our numerical simulations, we show that transition probabilities directly estimated (the underlying local recruitment probabilities) and those derived from analysis of data from the breeding segment of the population are different.

Key words: age of first breeding; breeder or prebreeder state; capture–mark–recapture; estimation; long-lived seabird; numerical simulations; multistate model; recruitment; reverse-time model; Rissa trydactyla; *Schwarz and Arnason model; unobservable state.*

INTRODUCTION

In species with deferred breeding, individuals may recruit after the individual has reached sexual (physical) maturity. In such species individuals recruit into the breeding segment of the population at different ages (e.g., Clobert et al. 1993, Viallefont et al. 1995*a, b*, Pradel et al. 1997, Cooch et al. 1999, Oro and Pradel 2000, Schwarz and Arnason 2000, Cam et al. 2002*a*, Spendelow et al. 2002, Lebreton et al. 2003). The covariation of age of maturity, and age of first breeding, with other population-level vital rates has been of long-

standing interest. For example, the growth and viability of a population is potentially strongly influenced by variation in age of first breeding (e.g., Caswell 2001, Morris and Doak 2002). In addition, the evolution of age-specific variation in fitness components (fertility, survival) may be linked with variation in age of first breeding in many taxa (Roff 1992, Stearns 1992, Charlesworth 1994, S. Tuljapurkar and C. Boe, *unpublished manuscript*). In both cases, characterization of the distribution and sources of variation in age of first breeding, and covariation with other life-history traits is needed (Cooch et al. 1999, Oro and Pradel 2000, Frederiksen and Bregnballe 2001).

Many studies focusing on the evolution of age of first breeding have attempted to investigate empirically the variation in age of recruitment among ''groups''

defined on the basis of hypotheses relevant to theories of evolution in age-structured populations. For example, they have considered groups of individuals living in habitats with or without predators (e.g., Reznick et al. 1990), or groups of individuals born in the same year (i.e., birth cohorts) and experiencing different environmental conditions during development or after independence (e.g., Albon et al. 1992, Spendelow et al. 2002). In the framework of life-history theory, the classical view is that populations are composed of phenotypic variants for age at maturity (e.g., Charlesworth 1994). Clearly, for structured populations, each grouping will consist of a number of different birth cohorts. For each cohort it is theoretically possible to define a distribution of ''underlying'' (or ''latent'') age of first breeding that exists at birth (sensu Link et al. 2002b), regardless of whether the individuals will survive to age of first breeding. We distinguish this latent probability distribution from the ''realized'' pattern (distribution) of recruitment assessed in the breeding segment of the population. This distinction is necessary because some individuals die before breeding, and the two distributions may differ.

Recruitment is a probabilistic event conditional on three different, potentially independent components (Clobert et al. 1993): (1) survival probability from birth to age $i - 1$, (2) fidelity to the natal area, and (3) the probability that an individual alive and in the ''prebreeder'' state at age $i - 1$ and that survives to age i is in the ''breeder'' state at age i. As emphasized by Clobert et al. (1993), unless relevant data from the locations within the plausible range of distance for natal dispersal are available, the two first components cannot be separated and their product is ''local survival.'' The third component is the ''transition probability'' at age $i - 1$ (a permanent transition between breeding states, sensu Pradel and Lebreton 1999). Hereafter we will refer to ''recruitment probability'' as the transition probability (Pradel and Lebreton 1999). Variation in realized age of first breeding among groups (e.g., cohorts) might result either from (1) group-specific variation in survival before the recruitment process is completed (i.e., ''full breeding''), or (2) variation in recruitment probability—or both. Unless the survival component is known to be identical in all the groups, robust inference about the ''cause'' of variation in realized patterns of age of first breeding among groups is problematic. This is analogous to the problem of comparing return rates (proportions of individuals marked and released alive at time i that are subsequently encountered at some later time j) among groups of individuals as a means of testing for differences in survival among groups of individuals. Return rate is the product of at least two components: the probability of survival from time i to time j, and the probability of encounter of the individual at time j (conditional on survival). Thus, differences in return rate could be due

to differences in survival, encounter rate, or both (Martin et al. 1995).

In a large number of species with deferred breeding (e.g., mammals or birds), individuals are marked and released as young, but they may not be resighted in the year(s) between age of independence (e.g., fledging in seabirds, Spendelow et al. 2002; weaning in marine mammals, Schwarz and Stobo 2000) and the earliest age (k) at which breeding might occur. That is, only limited data from prebreeders are available (i.e., data from 0-year-old individuals). For this reason, many studies have used approaches to estimation of age-specific recruitment probability based (1) on data from the breeding segment of the population exclusively (e.g., Frederiksen and Pradel 2001, Schwarz and Arnason 2001), or (2) on data from marked individuals released at independence (i.e., at age 0) and data from the breeding segment of the population (i.e., after age k; Clobert et al. 1993, Pradel and Lebreton 1999). In the latter case, models for estimating age-specific breeding proportions incorporate the product of yearly survival probability from birth to recruitment (cumulative survival from age 0 to first breeding; Clobert et al. 1993). In this setting, it is theoretically possible to account for group-specific variation in the size of the pool of prebreeders from birth to recruitment by using group-specific cumulative survival (i.e., Clobert et al. 1993, Spendelow et al. 2002). However, this is impossible with approaches based exclusively on data from the breeding segment of the population.

While methods that do not require data from prebreeders in every age class are clearly necessary for the common situations (Spendelow et al. 2002), estimates based on data from the breeding segment of the population exclusively may not always be appropriate for inferences about age-specific probability of ascension to breeding status. Failure to acknowledge that realized patterns of age of first breeding in the breeding segment of the population depend on the product of local survival and transition probability can have significant consequences on interpretations of analyses of variation in age of first breeding in problems whose nature requires distinction between processes affecting survival and transition between prebreeder and breeder states (e.g., evolutionary ecology problems; Mertz 1975). And yet, despite the broad interest in analysis of variation in age of first reproduction, it is perhaps surprising that relatively little attention has been focused on the consequences of potential violations of the assumptions underlying various estimation methods (reviewed in Williams [2002]), particularly those conditioned on analysis of data from the breeding segment of the population. In these approaches, parameters are conditional on the set of individuals ever observed as breeders. From an evolutionary viewpoint, this means that only phenotypes that survived to age of first breeding can be considered. This may be reasonable if there is no covariation between survival and age of first

breeding, but this ignores selective processes based on differential mortality shaping relationships of age to reproduction (e.g., Mertz 1975).

Our main objective in this study was to assess the consequences of violations of the assumption of equal survival probability among groups before full breeding on our perception of age-specific realized recruitment rates obtained using methods based exclusively on data from the breeding segment of the population. We used numerical simulations and considered several scenarios corresponding to plausible a priori biological hypotheses. More precisely, we compared cohort- and age-specific breeding proportions estimated using data from the breeding segment of the population (age $\geq k$) with transition probability estimated using data from prebreeders between age 0 and full breeding. In the first class of scenarios, some cohorts had lower prebreeder survival than others (e.g., Albon et al. 1992), which resulted in differences in survival in prebreeders and breeders of the same age in the cohorts in question. In the second class of scenarios we addressed situations where costs of first breeding (e.g., Viallefont et al. 1995*a*, *b*) resulted in lower survival in breeders than in prebreeders of the same age in some cohorts. In the third class of scenarios there was a positive relationship between breeder initial survival and realized age of first breeding in some cohorts, which may correspond to age-specific costs of first breeding.

We next considered recruitment using empirical data from a long-lived seabird species, the kittiwake (*Rissa tridactyla*), from which data were collected in Brittany (France). In this study, data from all age classes of prebreeders and breeders were available, allowing us to compare results using methods making full use of both sources of information (multistate modeling; e.g., Nichols et al. 1994) with those conditioned only on data from breeders (e.g., Pradel and Lebreton 1999, Schwarz and Stobo 2000, Schwarz and Arnason 2000; reviewed in Williams et al. [2002]).

ESTIMATION OF RECRUITMENT PROBABILITY: CAPTURE–RECAPTURE METHODS

Many early studies of recruitment in wild animal populations have used ad hoc approaches to characterize the distribution of age of first breeding, such as age-specific return rates (e.g., Ollason and Dunnet 1988). Inferences based on such approaches are likely to be erroneous (Cooch et al. 1999). An individual observed breeding at age i could have bred at an earlier age, and not have been detected (Ollason and Dunnet 1988). It has long been known that in studies of survival it is necessary to take into account the probability of detecting an individual alive and present in the study area (e.g., Pollock et al. 1990, Lebreton et al. 1992, Clobert 1995); a completely analogous problem arises in recruitment studies (e.g., Lebreton et al. 1990, Clobert et al. 1994, Pradel 1996, Schwarz and Arnason 2000, Williams et al. 2002). Many efforts in the area

of capture–recapture modeling have been devoted to development of recruitment models; they explicitly incorporate "detection" probability (also called "recapture," "resighting," or "encounter probability"; Clobert et al. 1990, Pradel et al. 1997, Pradel and Lebreton 1999, Schwarz and Stobo 2000, Schwarz and Arnason 2001, Williams et al. 2002). In all study designs, successive cohorts of animals are individually marked as young at age 0. Individuals can be resighted or recaptured later, and a capture–recapture history can be recorded for each animal marked as young. For example, in a 16-year study of a long-lived species, a typical history would be "1001011011001100." The individual was marked at age 0 and released. It was observed (resighted or recaptured) at ages 3, 5, 6, 8, 9, 12, and 13.

When data from prebreeders are available in all age classes, multistate models (e.g., Arnason 1973, Brownie et al. 1993, Nichols et al. 1994, Nichols and Kendall 1995) can be used to address recruitment while accounting for age- and state-specific recapture probability (e.g., Cam et al. 2002*a*, 2003). In this case information from the entire individual history is used and there is no "unobservable" state (Pradel and Lebreton 1999, Spendelow et al. 2002). For multistate models, codes are used in longitudinal individual histories to distinguish the sampling occasions (years) when animals were resighted as prebreeders and years animals were resighted as breeders. In other words, observations from the same individual are classified according to its breeding activity or "state" (prebreeder or breeder). In a 16-year study, an individual capture–recapture history could be "1001012022002200". That individual was marked at age 0 and released. It was observed at ages 3 and 5 as a prebreeder ("1"), and then as a breeder ("2") at ages 6, 8, 9, 12, and 13. Multistate models allow estimation of age- and state-specific survival probability S_i^r (the probability that an individual in state r survives between age i and age $i + 1$), and age-specific transition probability from prebreeder state to breeder state (Nichols et al. 1994). Ψ_i^{rs} is the probability that an individual in state r (prebreeder) at age i and that survives to age $i + 1$ is in state s (breeder) at that age; that is, Ψ_i^{rs} corresponds to recruitment probability.

Several capture–recapture approaches to estimating age-specific breeding probability have been designed to handle the absence of data from prebreeders between independence and first breeding (e.g., Lebreton et al. 1990, Pradel and Lebreton 1999, Spendelow et al. 2002, reviewed in Williams et al. [2002]). An approach based on changes in detection probability in age classes including both prebreeders and first-time breeders (Clobert et al. 1993, 1994), the "reverse-time" approach (Pradel 1996), the multistate approach with unobservable states (e.g., Arnason 1973, Brownie et al. 1993, Nichols and Kendall 1995, Pradel and Lebreton 1999, Lebreton et al. 2003), and an approach based on

the Jolly-Seber (J-S) model (Schwarz and Arnason 2000), are all directed at age-specific recruitment. None of these measures of recruitment are based on data from the prebreeding segment of the population except for 0-year-old individuals (i.e., individuals marked and released as newborns). In the corresponding study designs, "successive cohorts of animals are marked as young at a known age. Prior to age k at which the youngest individual breeds, animals cannot be observed. Once an animal starts to breed, it may be recaptured or resighted. After age k and before full breeding, the sample of individuals in a cohort consists of two groups: nonbreeders, which cannot be observed, and breeders, which can be observed" (Schwarz and Arnason 2000:59; see also Lebreton et al. 2003).

Here we will focus on two commonly used approaches to inferences about recruitment: the "reverse-time" approach (Pradel 1996) and the approach developed by Schwarz and Arnason (2000). Both approaches ignore data from prebreeders, including 0-year-old individuals. They use single-state capture–recapture histories where prebreeders cannot be observed after age 0 (e.g., after the animal is released at age 0, it is recaptured several years later as a breeder; a typical history corresponding to the above situation would be: 1000001011001100). Importantly, data from 0-year-old individuals are not used; only data from the breeding segment of the population are.

The most general models for capture–recapture data for open populations account for the processes leading to changes in population size over time; they consider gains (e.g., recruitment) and losses (e.g., deaths) of individuals between sampling occasions (Jolly 1965, Williams et al. 2002). The original Jolly-Seber (J-S) model for open populations accounts for recruitment in situations where every individual can be considered to be of a single age class. Schwarz and Arnason (1996, 2000) proposed a new parameterization where the proportion of new entrants to the breeding population (i.e., direct representation of age-specific breeding proportions) are incorporated in the model. In the Schwarz and Arnason (2000) model, hereafter referred to as "S-A model," the relevant parameter is:

b_{cj} = probability that an animal in cohort c that
        survives until it starts to breed will start
        breeding at age $j + 1$

$$c = 1, \ldots, G \quad j = 0, \ldots, m - 1 \quad \sum_{j=0}^{m-1} b_{cj} = 1.$$

In the "reverse-time" approach (Pradel 1996), single-state individual capture–recapture histories are read backwards, starting from the most recent point in time. As above, initial captures of young animals are ignored. The parameterization of the "recruitment only" model is based on the "seniority probability": γ_i = the probability that an individual alive and breeding in the pop-

ulation at time (age) i was alive and breeding in the population at time (age) $i - 1$. There is a duality between the seniority probability and the survival probability corresponding to encounter histories read in a normal manner (i.e., starting from the most remote point in time; Pradel 1996). Using a reverse-time encounter history an individual of age i (which is equivalent to time i since age and time are collinear within an individual encounter history) "survives" if it already was in the breeding segment of the population at age $i - 1$. That individual was therefore "experienced" at age i, because the individual already bred (i.e., was in the breeding segment of the population and subject to the encounter process) at age $i - 1$. If the individual "dies" between age i and age $i - 1$ (i.e., leaves the breeding segment of the population), this means that the animal was a first-time breeder at age i (it was not in the breeding segment of the population at age $i - 1$).

Pradel and Lebreton (1999) and Frederiksen and Pradel (2001) introduced two related recruitment parameters, a_i, and α_i. Here a_i is the probability that an as-yet-inexperienced individual of age i starts to breed at that age:

$$a_i = (1 - \gamma_i) \frac{\prod_{j>i} \gamma_j}{1 - \prod_{j \geq i} \gamma_j} \qquad k \leq i \leq f \qquad (1)$$

where k is the youngest age of first breeding and f is the assumed age of full breeding; and α_i is the probability that an animal of age i is a first-time breeder,

$$\alpha_i = a_i \prod_{k \leq j < i} (1 - a_j) \qquad i \leq f. \qquad (2)$$

This corresponds to α_i as the relative proportion of first-time breeders among all individuals alive at age i (Pradel and Lebreton 1999). Frederiksen and Pradel (2001:975) noted that the two probabilities, α_i and the S-A model's b_{cj}, are "related through survival between the earliest age of breeding (k) and age i ($j + 1$ in Schwarz and Arnason 2000)" (see also Schwarz and Stobo 2000). For the sake of clarity, we will subsequently use the notation defined in Schwarz and Stobo (2000): b_{ci} = probability that an individual from cohort c will give birth for the first time at age i.

Under some assumptions (Pradel and Lebreton 1999, Frederiksen and Bregnballe 2001), a_i is strictly equivalent to the Ψ_i^{rs} parameter of multi-state approaches. a_i is the relative proportion of first-time breeders to the sum of first-time breeders and prebreeders at age i (Pradel and Lebreton 1999). One of the necessary assumptions for equivalence of the various measures of age-specific recruitment derived from the reverse-time approach (a_i), or directly estimated using multistate models (Ψ_i^{rs}) is equal survival in individuals in different states before full breeding. Frederiksen and Pradel (2001:275) explained that "information about survival

is necessary to estimate the α_i, and if prebreeders are not observable, the α_i can only be estimated under the assumption of equal (possible age-specific) survival of prebreeders and breeders'' (see also Pradel and Lebreton 1999, Williams et al. 2002). It is always possible to get estimates of α_i and a_i even if prebreeders are unobservable, but if the above condition is not met in one cohort, there will be no relationship between a_i and Ψ_i^{rs} in this cohort. Comparisons among realized age of first breeding in different cohorts are likely to lead to apparent differences in age-specific recruitment probability among cohorts, whereas only survival differs among cohorts.

Neither the reverse-time approach nor the S-A approach relies on the assumption that prebeeders of the same age have equal survival probability in all the groups (e.g., cohorts). But if there are differences in prebreeder survival among groups before full breeding, unless the same differences among groups hold in breeder survival, this necessarily implies differences between breeder and prebreeder survival within some groups. This explicitly violates the conditions that have to be met to derive transition probability from seniority probability (Frederiksen and Bregnballe 2001). Unlike the reverse-time approach, the S-A approach does not rely on the assumption of equal survival probability in prebreeders and breeders of the same age. However, with equal age-specific transition probability in all the groups, differences in prebreeder survival before full recruitment among cohorts is likely to lead to variation in the size of the group of prebreeders available for recruitment among cohorts, and thus variation in realized age of first breeding estimated with the S-A method. Our primary objective in this study was to assess consequences of differences in survival among cohorts on estimates of realized age-specific breeding proportions, when data from prebreeders were unavailable or ignored, obtained using reverse-time capture–recapture models (Pradel 1996) and the approach developed by Schwarz and Arnason (2000).

Numerical Simulations

Approach to inferences

To assess the consequences of violations of the assumption of equal survival in breeders and prebreeders of the same age before full recruitment, we simulated data sets under three types of scenarios (see below, see also the *Introduction*). The data sets included (1) four cohorts that met the assumption that prebreeders and breeders of the same age have equal survival probability (Type I cohorts), and (2) two cohorts where this assumption was violated in some specified way (Type II cohorts). It is important to note that in most scenarios the age-specific transition probabilities (''latent'' or ''underlying'' recruitment probabilities; Ψ_i^{rs}) used to create the data sets did not vary among cohorts. Logically, when the simulated data sets are used to estimate

recruitment probability using the reverse-time model or the S-A (Schwartz and Arnason 1996, 2000) model, if the measures of recruitment provided by these methods correctly reflect the underlying recruitment probabilities, then we should not detect any cohort effect on the resulting measures of recruitment. In contrast, detection of an influence of cohort on seniority probability or breeding probabilities from the S-A method would provide evidence that these measures of recruitment do not reflect underlying recruitment probability. We used this type of possible ''artifact'' to draw inferences about the consequences of violations of the assumption of equal survival in prebreeders and breeders of the same age.

We fitted recruitment reverse-time models including an influence of age and a ''cohort'' effect on seniority probability (two cohort types; the most general model included an interaction between ''age'' and ''cohort''), and compared them to models without the cohort effect. Comparison was carried out using AIC or AICc (i.e., information criteria; Burnham and Anderson 1998). We proceeded in the same manner for the S-A models, except that we considered fewer models (the parameterization currently available in the relevant software program [POPAN-7; Arnason et al. 1998] constrains breeding probabilities to add up to 1 across all time points within each cohort, which precludes consideration of some models; C. Schwarz, *personal communication*). We reported estimates of b_{ci} and γ_i and derived values of a_i and α_i. With strictly identical age-specific latent transition probability in all the cohorts, we anticipated that differences in survival before full recruitment would lead to differences in age of first breeding with both approaches. We derived estimates of transition probability from seniority rates (a_i's) for Type I cohorts and cohorts with state-specific differences in survival before full breeding (Type II). We compared estimates of a_i's among the two cohort types. We might expect to obtain a_i values close to transition probabilities (Ψ_i^{rs}) in these cohorts where the above assumption was met, but markedly different in others (Type II). The corollary is that we might expect estimates of a_i's to differ among cohort types.

As the expected pattern of realized age of first breeding depended on combinations of latent transition probabilities and survival probabilities, it was difficult to be specific about whether ''age'' (and thus the interaction between ''age'' and ''cohort'') should be retained. In all situations considered but one (see scenarios below), latent transition probabilities were age specific, but this pattern could be masked by differences in survival among cohorts. In contrast, even in the absence of a cohort effect on latent transition probabilities, we set up the problem so that an artificial ''cohort'' effect should be detected in the realized pattern of recruitment. Consequently, in all the situations addressed we expected the cohort effect to be retained, and models with a cohort effect on recruitment param-

TABLE 1. Parameter values for Type I and Type II cohorts for scenario 1A: lower survival in prebreeders than in breeders of the same age.

Prebreeder survival		Types I and II		
Type I	Type II	Transition probability	Breeder survival	Age i
0.60	0.60	0.20	...	0
0.70	0.30	0.40	0.70	1
0.80	0.30	0.60	0.80	2
0.80	0.30	1.00	0.80	≥ 3

Notes: Type I, no violation of the assumption of equal survival in breeders and prebreeders of the same age; Type II, violation of the assumption of equal survival in breeders and prebreeders of the same age. Recruitment starts at age 1 (the survival probability of 0-year-old breeders is not defined).

eters to obtain the largest support according to the information criterion.

Apart from the classical notation for states ''r'' (prebreeder) and ''s'' (breeder) in multistate models, notation for the different classes of models was as follows. Model parameters (e.g., γ, Ψ, or b) had subscripts indicating the factors according to which they varied. The subscript ''i'' stood for ''age'', ''t'' for ''time'' (year), ''c'' for cohort, and ''$2c$'' for ''two cohort types'' (i.e., parameters were identical for all the cohorts of the same type). The subscript ''•'' stood for ''constant.'' For parameters varying according to age, in numerical simulations the number of age classes was always the same (full breeding at age 4). In the empirical example, the number of age classes was specified using a figure in parentheses (e.g., ''$i(7)$''). Lastly, ''$\times$'' stood for interactions between two main effects (e.g., ''$i \times c$''), and ''+'' corresponded to models where the influence of the two covariates on the parameter in question was additive (e.g., ''$i + c$'').

Scenarios, biological hypotheses and predictions

Given the quasi-complete absence of estimates of age-specific demographic parameters from prebreeders in wild-animal populations, it was not possible to seek ''biological realism'' for values used in simulations. Our main objective was rather to assess the effect of violation of assumptions on the parameter estimates within the framework of conceptually biologically realistic scenarios. Thus, we intentionally chose sets of parameters designed to violate the assumptions in specified ways.

Scenario 1A: lower survival in prebreeders than in breeders of the same age.—Here we considered situations where prebreeder survival differed among cohorts. All the cohorts had equal age-specific transition probabilities, that is, all the individuals surviving to age i had the same a priori probability of breeding at age $i + 1$ if they survived (Table 1). Two cohorts had an a priori probability of surviving at age i in prebreeders lower than the survival probability of breeders

of the same age (Type II cohorts; Table 1). This may correspond to a situation where prebreeders and breeders use different wintering areas and environmental conditions influencing survival probability vary over space. Prebreeders of some cohorts may experience particularly unfavorable environmental conditions. Differential mortality in prebreeders and breeders of the same age may also reflect differences in individual quality. Birds not able to breed at a given age may be lower-quality individuals than those that breed at that age; the former may have lower survival probability (Nur 1988). State-specific differences in survival at a given age may also correspond to a higher probability of dispersing in prebreeders experiencing poorer environmental conditions (e.g., natal vs. breeding dispersal; Greenwood and Harvey 1982). Indeed, survival estimates based on data from a subset of monitored locations corresponds to local survival and incorporate [1 − (probability of dispersing)] (Spendelow et al. 1995).

Here we might expect earlier realized age of first breeding in cohorts with lower survival in prebreeders (Type II cohorts), regardless of the approach (Reverse-time model or S-A model [Schwartz and Arnason 2000]). Once the individuals of the Type II cohorts start recruiting progressively, lower survival in prebreeders (compared to Type I cohorts) should result in a more rapid decrease in the size of pool of prebreeders remaining available for recruitment. In older age classes there should be fewer first-time breeders in those cohorts, and the proportion of experienced breeders should be larger than in Type I cohorts.

Scenario 1B: lower survival in prebreeders than in breeders of the same age, delayed recruitment.—This is a variant of the above scenario: patterns of variation in survival were identical to those of scenario 1A, but we assumed delayed recruitment (i.e., lower probability of recruiting in younger age classes) in Type II cohorts (Appendix A). In this case the lower survival probability and its influence on realized age of first breeding (see scenario 1A) should be partly or completely compensated for. Depending on the strength of the compensatory phenomenon, several patterns may be expected. We might expect either no detectable cohort effect on measures of recruitment, or a cohort effect with either a slightly earlier apparent recruitment, or a delayed recruitment in Type II cohorts compared to Type I cohorts. Here a cohort effect on seniority probability would not be an artifact because the values of transition probability used to simulate data were cohort specific. However, the estimated age-specific breeding proportions may not reflect the underlying parameter values used to create the data for Type II cohorts: delayed recruitment.

Scenario 2A: higher survival in prebreeders than in breeders of the same age.—Two cohorts had an a priori prebreeder survival probability larger than the survival probability of breeders of the same age (Type II co-

TABLE 2. Parameter values for Type I and Type 2 cohorts for scenario 2A: lower survival in breeders than in prebreeders of the same age.

Prebreeder survival		Types I and II		
Type I	Type II	Transition probability	Breeder survival	Age i
0.60	0.60	0.20	…	0
0.70	0.85	0.40	0.70	1
0.80	0.93	0.60	0.80	2
0.80	0.93	1.00	0.80	≥3

Notes: Type I, no violation of the assumption of equal survival in breeders and prebreeders of the same age; Type II, violation of the assumption of equal survival in breeders and prebreeders of the same age. Recruitment starts at age 1 (the survival probability of 0-year-old breeders is not defined).

horts; Table 2). This may correspond to a situation with a high cost of reproduction for example. We assumed that the decrease in breeder survival is not age specific. All the cohorts had the same age-specific transition probabilities (Table 2). As breeders had a lower survival probability than prebreeders of the same age in Type II cohorts, this should result in a more rapid decrease in the size of the pool of experienced individuals in these two cohorts compared to the Type I cohorts. In the Type II cohorts, the pool of prebreeders should remain large compared to the pool of experienced breeders as the recruitment process progresses. Consequently, we might expect the mean realized age of first breeding to be older in Type II cohorts than in Type I ones.

Scenario 2B: higher survival in prebreeders than in first-time breeders of the same age.—This is a special case of scenario 1B: only first-time breeders had lower survival probability than prebreeders of the same age in Type II cohorts (Appendix B). This may correspond to a situation where first-time breeders incur a specific reproductive cost for example (e.g., Viallefont et al. 1995*a*, *b*). However, after first breeding all the experienced breeders had the same survival probability. With the reverse-time approach, as in scenario 2A we might expect a delayed realized age of first breeding

in Type II cohorts compared to Type I cohorts. In contrast, as the differences in survival among cohorts concern animals only after recruitment, estimates of breeding proportions from the S-A approach should not vary with cohort type.

Scenario 3: positive relationship between breeder initial survival and realized age of first breeding.— Here we assumed that all the individuals had equal probability of recruiting at any age before full breeding (4 yr of age), but depending on the age of realization of recruitment, subsequent survival differed in Type II cohorts. More specifically, in these cohorts individuals recruiting earlier had lower initial survival probability after recruitment than individuals recruiting at older ages. Survival then increased with age in breeders; the rate of increase was independent of age of first breeding (Table 3). As above, as the differences among cohorts concern the breeding segment of the population, we might expect to detect a cohort effect on seniority probability, but no artifact in breeding probability from the S-A model. With the reverse-time approach, the consequences of violations of the hypothesis of equal survival in prebreeders and breeders of the same age strongly depend on the set of parameter values chosen. Here individuals had a high probability of recruiting at age 1 (0.75), and if they delayed breeding and survived, they still had a high probability of recruiting in the following age class (0.75). Consequently, on average, recruitment should take place early. As earlier breeders had lower survival probability in Type II than in Type I cohorts, the present scenario was very likely to lead to similar consequences as those of scenarios 2A and 2B.

Simulated data and analytical approach

We created five sets of 60 000 multistate capture–recapture histories (e.g., Arnason 1973, Brownie et al. 1993, Nichols et al. 1994) according to specific sets of demographic parameters (age- and state-specific survival probability, and age-specific transition probability from ''prebreeder'' state to ''breeder'' state) that corresponded to several different scenarios. Individual

TABLE 3. Parameter values for Type I and Type II cohorts for scenario 3: positive relationship between breeder initial survival and realized age of first breeding.

Types I and II		Breeder survival					
Prebreeder survival	Transition probability	Type I	Type II Realized age of first breeding				Age i
			1	2	3	4	
0.60	0.75	…	…	…	…	…	0
0.75	0.75	0.75	0.60	0.70	0.75	0.80	1
0.85	0.75	0.85	0.70	0.70	0.85	0.90	2
0.85	1.00	0.85	0.70	0.70	0.85	0.90	≥3

Notes: Type I, no violation of the assumption of equal survival in breeders and prebreeders of the same age; Type II, violation of the assumption of equal survival in breeders and prebreeders of the same age. Recruitment starts at age 1 (the survival probability of 0-year-old breeders is not defined).

encounter histories were encoded with two states: "prebreeder" and "breeder," with a distinction between "first-time breeder" and "experienced breeder" in some cases (see above). They included 13 occasions and corresponded to six cohorts of 10 000 individuals released in years 1 to 6. These encounter histories (including information from both prebreeders and breeders) were first analyzed using multistate models; this was done to provide estimates from the simulated data using the "true" underlying model(s). The large number of simulated histories was sufficient to lead to high precision of our estimates; the latter were very close to underlying parameters (results not presented here).

In the next step, data were recoded so that only the "breeder" state was retained, and analyzed using the reverse-time approach (Pradel 1996) or the model developed by Schwarz and Arnason (2000). Analyses were performed using the "recruitment only" model (i.e., where the death process is not modeled; Pradel 1996) implemented in the software program MARK (White and Burnham 1999). We used the software program POPAN-7 (Arnason et al. 1998) to conduct analyses with the approach developed by Schwarz and Arnason (2000). In this case we treated the first recapture as an initial mark (Schwarz and Arnason 2000). Model selection was based on AIC in analyses with POPAN-7, and on AICc in analyses with program MARK. AIC and AICc are provided by the two respective pieces of software as default criteria and have similar properties in the situations addressed here (very large sample size and small number of parameters; Burnham and Anderson 1998).

For all simulations we assumed there was an age of full breeding: 4 years of age. We used 13 occasions to allow all the individuals from the sixth cohort to recruit before the end of the study (Schwarz and Arnason 2000). Recapture probability was always set equal to 0.70 in prebreeders and 0.80 in breeders and was not age specific (estimates are not presented). All the models had constant recapture probability ($p_.$) in the reverse-time and the S-A setting (only data from breeders were retained for these analyses). For analyses conducted using the S-A model, breeder survival probability was age specific in the first three scenarios (because the parameter values used to simulate data depended on age), and age- and cohort-specific in the last two scenarios. It is important to note that we created only one data set for each scenario. Running multiple simulations per scenario will require development of appropriate simulation routines in new or existing software programs (each simulation currently requires use of several pieces of software in a sequential manner); this is beyond the scope of this paper.

RESULTS

Reverse-time approach

In all cases, the reverse-time models with the lowest AICc value included a cohort effect on seniority probability (Appendix C), and an interaction between "cohort" and "age" for scenarios 1A, 1B, 2B, and 3 (see *Numerical Simulations: Scenarios* . . . , above). For scenarios 1A and 1B, we expected apparent earlier recruitment in the two cohorts with lower survival in prebreeders than in breeders of the same age (Type II), compared to Type I cohort. For scenario 1A, results supported this hypothesis: γ_2 estimates from the model with larger support indicated earlier realized age of first breeding in cohorts with lower survival in prebreeders, i.e., $\hat{\gamma}_i$'s were larger for Type II than for Type I cohorts after age 1 (Table 4). Derived values of a_1 showed that a larger proportion of individuals surviving to age 1 recruited at that age in Type II cohorts compared to Type I ones (Table 4). All the a_i's corresponding to Type II cohorts were larger than those of Type I cohorts in the youngest age classes. For scenario 1B, estimates of a_i corresponding to the lowest-AICc model also showed earlier realized age of first breeding in Type II cohorts than in Type I ones, except in the youngest age class. The difference among cohorts was in the opposite direction in the youngest age class, which reflects the underlying delayed recruitment probabilities compared to Type I cohorts. As expected, the difference between a_i's corresponding to Type I and Type II cohorts was smaller than for scenario 1 (i.e., delayed recruitment in Type II cohorts was partly compensated for by lower survival in prebreeders than in breeders of the same age).

For scenarios 2A, 2B, and 3 we expected an apparent delayed recruitment. This hypothesis was supported: estimates corresponding to the lowest-AICc models showed that $\hat{\gamma}_i$'s and a_i's from Type II cohorts were smaller than those of Type I cohorts before full breeding (Table 4). This held only in the oldest age classes in scenario 3. This difference between scenarios 2 and 3 results from the large initial underlying transition probability at age 0 in scenario 3, which led to a larger number of recruits at age 1. After age 1, estimates of a_i's were smaller for Type II than for Type I cohorts, which is consistent with scenarios 2A and 2B.

Schwarz and Arnason approach

With the Schwarz and Arnason (S-A) approach (Schwartz and Arnason 2000) we also found evidence of an influence of cohort on breeding probability in all cases but scenarios 2B and 3. This was consistent with our predictions for scenario 3. For scenario 2B, two models had close, low AIC values: the model with cohort- and age-specific breeding probability, and the reduced model with an influence on age on b_{cj} (Appendix C). It was not possible to draw definitive conclusions here (Burnham and Anderson 1998).

For scenario 1A, as expected, a larger proportion of individuals bred for the first time at age 1 in cohorts with lower prebreeder survival (Type II) than in others, i.e., $\hat{b}_1$ was larger in Type II cohorts than in Type I ones (Table 4). For scenario 1B, we expected partial

TABLE 4. Parameter estimates.

| | Cohorts | | | | | | | |
| | Type I† | | | | Type II‡ | | | |
Age i	$\hat{\gamma}_i$	$\hat{\alpha}_i$	$\hat{a}_i$	$\hat{b}_{ci}$	$\hat{\gamma}_i$	$\hat{\alpha}_i$	$\hat{a}_i$	$\hat{b}_{ci}$
Scenario 1A								
1	0.000	0.196	0.197	0.292 (0.004)	0.000	0.507	0.507	0.606 (0.010)
2	0.383 (0.079)	0.316	0.393	0.331 (0.005)	0.581 (0.027)	0.365	0.742	0.309 (0.016)
3	0.634 (0.089)	0.295	0.605	0.248 (0.003)	0.892 (0.028)	0.105	0.829	0.072 (0.007)
4	0.817 (0.087)	0.192	1.000	0.129 (0.003)	0.978 (0.021)	0.022	1.000	0.012 (0.003)
5	1.000	⋯	⋯	⋯	1.000	⋯	⋯	⋯
Scenario 1B								
1	0.000	0.199	0.2199	0.299 (0.004)	0.000	0.190	0.190	0.275 (0.011)
2	0.388 (0.002)	0.314	0.392	0.328 (0.005)	0.273 (0.006)	0.506	0.625	0.498 (0.014)
3	0.643 (0.001)	0.284	0.583	0.239 (0.004)	0.761 (0.017)	0.219	0.722	0.172 (0.012)
4	0.797 (0.002)	0.203	1.000	0.135 (0.003)	0.916 (0.004)	0.084	1.000	0.056 (0.007)
5	1.000	⋯	⋯	⋯	1.00	⋯	⋯	⋯
Scenario 2A								
1	0.000	0.198	0.2199	0.294 (0.004)	0.000	0.147	0.147	0.233 (0.005)
2	0.381 (0.007)	0.322	0.402	0.340 (0.005)	0.327 (0.008)	0.304	0.357	0.332 (0.006)
3	0.647 (0.007)	0.284	0.593	0.239 (0.005)	0.591 (0.010)	0.313	0.571	0.270 (0.006)
4	0.805 (0.134)	0.195	1.000	0.127 (0.003)	0.765 (0.153)	0.235	1.000	0.165 (0.005)
5	1.000	⋯	⋯	⋯	1.00	⋯	⋯	⋯
Scenario 2B								
1	0.000	0.203	0.203	0.297 (0.004)	0.000	0.105	0.105	0.304 (0.006)
2	0.388 (0.007)	0.320	0.402	0.337 (0.005)	0.256 (0.015)	0.304	0.339	0.356 (0.007)
3	0.642 (0.009)	0.291	0.602	0.241 (0.005)	0.547 (0.023)	0.338	0.572	0.226 (0.007)
4	0.815 (0.046)	0.815	1.000	0.125 (0.003)	0.747 (0.183)	0.253	1.000	0.114 (0.005)
5	1.000	⋯	⋯	⋯	1.00	⋯	⋯	⋯
Scenario 3								
1	0.000	0.747	0.747	0.804 (0.003)	0.000	0.677	0.804	0.804 (0.003)
2	0.799 (0.006)	0.192	0.757	0.154 (0.003)	0.759 (0.026)	0.215	0.665	0.154 (0.003)
3	0.952 (0.004)	0.047	0.763	0.033 (0.002)	0.928 (0.023)	0.069	0.640	0.033 (0.002)
4	0.985 (0.001)	0.015	1.000	0.009 (0.001)	0.961 (0.010)	0.039	1.000	0.009 (0.001)
5	1.000	⋯	⋯	⋯	1.00	⋯	⋯	⋯

Notes: Numbers in parentheses are estimated standard errors, only for the estimated parameters (not derived parameters $\hat{\alpha}_i$ and $\hat{a}_i$); ellipses (⋯) indicate undefined parameters. Parameters are as follows: γ_i is the probability that an individual alive and breeding in the population at age i was also alive and in the population at age $i - 1$; α_i is the probability that an animal of age i is a first-time breeder; a_i is the probability that an as-yet-inexperienced individual of age i starts to breed at that age; Ψ_i^{rs} is the probability that an individual in state r (prebreeder) at age i and that survives to age $i + 1$, is in state s (breeder for $r \neq s$) at age $i + 1$; and b_{ci} is the probability that an individual from cohort c that survives to first breeding gives birth for the first time at age i.

† Type I, no violation of the assumption of equal survival in breeders and prebreeders of the same age.

‡ Type II, violation of the assumption of equal survival in breeders and prebreeders of the same age.

compensation of lower prebreeder survival in Type II cohorts by delayed recruitment. Our results confirmed that this compensatory process operated in age class 1 ($\hat{b}_1$ is smaller in scenario 1B than in scenario 1A). This process did not operate after age 1: the realized probability of recruiting was larger in Type II cohorts at age 2 than Type I ones, whereas the values used to create the data set corresponded to delayed recruitment (Appendix A).

Concerning scenario 2A, we expected delayed apparent age of first breeding in cohorts with lower survival in breeders than in prebreeders of the same age (Type II), compared to Type I cohorts. Results supported this hypothesis: the proportion of animals recruiting at age 1 ($\hat{b}_1$) was smaller in Type II cohorts than in Type I ones (Table 4), and larger at age 3 and 4 ($\hat{b}_3$ and $\hat{b}_4$). For scenario 2B it was not possible to draw definitive conclusions concerning the influence of

cohort on breeding probability (see above), whereas we expected not to detect any cohort effect. However, breeding proportion estimates made under the most general model showed that the cohort effect was very slight (Table 4). Lastly, for scenario 3, as expected (see ''*Predictions*'' above), the model with the lowest AIC included only the influence of age on breeding probability (Appendix C). Results from the reverse-time and the S-A approaches were consistent for the scenarios where a cohort effect was expected (1A, 1B, and 2A).

APPLIED EXAMPLE: ANALYSIS OF DATA FROM KITTIWAKES

We used data from individually marked Black-legged Kittiwakes (*Rissa tridactyla*) collected from 1984 to 2001 in Brittany (France; e.g., Danchin and Monnat 1992, Cam et al. 1998, Cam et al. 2002*a*, *b*, 2003). Birds were marked as chicks (3370 birds released at

age 0 from 1984 to 1994; only birds that fledged were considered as released; Cam et al. 2002*a*, *b*, 2003) and the breeding activity of individuals that recruited in the study area was recorded every year (Nichols et al. 1994, Cam et al. 1998). Data were analyzed using reverse-time models because this approach allows consideration of a larger set of models (i.e., biological hypotheses) than the currently available parameterizations of the S-A model (C. Schwarz, *personal communication*). Cohorts released after 1994 were excluded from analyses so that all individuals from the latest cohorts released had time to recruit before the end of the study (seniority estimates are conditional on the pool of individuals that recruited, which is why the data set considered must include the oldest age of recruitment for every cohort). In this population the bulk of recruitment takes place between ages 2 and 7 years; 2-yr-old first-time breeders are rare, and data from first-time breeders older than 6 yr are too sparse to estimate separate age-specific recruitment probabilities with reasonable precision (Cam et al. 2002*a*, 2003).

The distinctive feature of this study is that some prebreeders are resighted in the study area in every age class where they are represented. However, their recapture probability is <1 in younger age classes (Cam et al. 2002*a*, 2003), which makes capture–recapture methods necessary to estimate demographic parameters specific to prebreeders. It is possible to use multistate models and estimate survival and transition probabilities (''prebreeder − breeder'') for all age classes where prebreeders are represented (Cam et al. 2002*a*, 2003). In this study, a typical multistate capture–recapture history includes ''0's'' only in the prebreeding stage of life (1010122222222, where ''1'' stands for ''prebreeder'' and ''2'' for ''breeder'').

We were able to assess age of first breeding directly because the recapture probability of individuals is virtually equal to 1 from recruitment onwards in this population regardless of breeding activity (Cam et al. 1998, Cam and Monnat 2000). As no breeding attempt in the study area is missed, the first observed breeding event can be considered as the first local breeding attempt (i.e., the first ''2'' in the individual history is the genuine first breeding event). The vast majority of prebreeders are resighted several times in the study area before recruitment, and the rate of attendance in colonies is usually high in the 1 or 2 years preceding recruitment (Danchin et al. 1991, Cadiou 1993, 1999, Cadiou et al. 1994, Cadiou and Monnat 1996). We believe that this breeding attempt is the actual first breeding attempt in the majority of cases (see Cam et al. [2002*a*] for a discussion of this assumption). After recruitment, we did not draw any distinction between breeders and nonbreeders (Cam et al. 1998): as individuals are resighted anyway, only the state ''has recruited into the breeding segment of the population'' was considered.

In the first step we analyzed data using a multistate model (Nichols and Kendall 1995). We used results obtained in earlier analyses to specify a starting model with constant recapture probability in breeders (Cam et al. 2002*a*, 2003; $p_i^1 p_{\bullet}^2 S_{i(7) \times c}^1 S_t^2 \Psi_{i(7) \times c}^{12}$, Appendix D). As with any live capture–recapture model, the fit of the most general model has to be assessed (Burnham et al. 1987). For multistate models, one possible approach is to assess formally the assumptions underlying the Arnason-Schwarz model (Pradel et al. 2003). However, this method cannot be used here because the tests currently available cannot handle permanent transitions (R. Pradel, *personal communication*). Consequently, we used a bootstrap approach available in program MSSURVIV (Hines 1994) to estimate an overdispersion parameter to take into account to perform model selection ($\hat{c} = 1.42$, 1000 simulations). In this case model selection was subsequently based on QAICc (Akaike's information criterion based on quasi-likelihood; Burnham and Anderson 1998) with program MARK (White and Burnham 1999).

Another analysis was conducted using the ''recruitment only'' model (Appendix E; starting model: $p_{\bullet} \gamma_{i \times c}$). Pradel's approach (1996) and the multistate approach (Nichols and Kendall 1995) permit assessment of a large number of hypotheses concerning combinations of an influence of time (year), age, or cohort on seniority probability, transition probability, and survival probability before recruitment. Our objective was to address a set of specific questions. (1) Are there cohort and age effects on survival before recruitment and on transition probability (i.e., the parameters of the multistate approach)? (2) Are there cohort and age effects on seniority probability (the parameter of Pradel's approach)? (3) Do breeders and prebreeders have equal survival probability? (4) Are estimates of transition probability from the multistate model and estimates of transition probability derived from seniority estimates equal?

We obtained estimates of age-specific seniority probability for a subset of 650 philopatric individuals from the above data set (i.e., individuals that returned to the study area to breed; Schwarz and Arnason 2000). Analyses were conducted using MARK (White and Burnham 1999). We compared estimates of age-specific transition probability obtained using multistate models and values of a_i, derived from estimates of seniority probability. In addition, we compared estimates of age-specific survival probabilities of prebreeders and breeders to assess whether the assumption under which a_i and Ψ_i^{rs} are equivalent is met.

The analysis conducted using the multistate approach provided evidence of an influence of cohort and age on prebreeder survival (Appendix D). Similarly, the analysis based on the reverse-time approach provided evidence of an influence of cohort and age on seniority probability (Appendix E). There was an influence of cohort and age on transition probability (Appendix D). In some cohorts estimates of transition probability from multistate models differed from the values

TABLE 5. Estimates of recruitment probability in kittiwakes: reverse-time and multistate approach.

		Probability						Probability			
Cohort	Age i	$\hat{\gamma}_i$	$\hat{\alpha}_i$	$\hat{a}_i$	$\hat{\Psi}_i^{rs}$	Cohort	Age i	$\hat{\gamma}_i$	$\hat{\alpha}_i$	$\hat{a}_i$	$\hat{\Psi}_i^{rs}$
84	2				0.268 (0.008)	90	2				0.26 (0.012)
	3	0.00	0.338	0.338	0.570 (0.005)		3	0.000	0.299	0.299	0.570 (0.013)
	4	0.479 (0.061)	0.366	0.553	0.649 (0.001)		4	0.414 (0.085)	0.424	0.606	0.659 (0.018)
	5	0.704 (0.053)	0.295	1.000	0.000		5	0.788 (0.076)	0.194	0.704	0.662 (0.018)
	6	1.000					6	0.918 (0.056)	0.082	1.000	0.684 (0.021)
85	2				0.145 (0.018)		7	1.000			0.000
	3	0.000	0.290	0.290	0.382 (0.034)	91	1				0.014 (0.003)
	4	0.619 (0.085)	0.179	0.252	0.462 (0.037)		2	0.000	0.009	0.006	0.249 (0.014)
	5	0.572 (0.084)	0.351	0.662	0.486 (0.038)		3	0.025 (0.027)	0.300	0.306	0.547 (0.016)
	6	0.923 (0.054)	0.069	0.383	0.502 (0.040)		4	0.407 (0.059)	0.455	0.662	0.628 (0.020)
	7	0.889 (0.074)	0.110	1.000	0.502 (0.040)		5	0.877 (0.039)	0.108	0.464	0.641 (0.021)
	8	1.000			0.000		6	0.954 (0.027)	0.042	0.340	0.664 (0.023)
86	2				0.169 (0.019)		7	0.980 (0.019)	0.018	0.225	0.664 (0.023)
	3	0.000	0.029	0.029	0.417 (0.032)		8	0.936 (0.036)	0.064	1.000	0.000
	4	0.045 (0.031)	0.629	0.648	0.499 (0.035)			1.000			
	5	0.749 (0.065)	0.251	0.735	0.513 (0.034)	92	2				0.186 (0.017)
	6	0.879 (0.047)	0.121	1.000	0.000		3	0.000	0.294	0.294	0.453 (0.027)
	7	1.000					4	0.536 (0.088)	0.255	0.359	0.535 (0.032)
87	2				0.164 (0.018)		5	0.817 (0.074)	0.123	0.271	0.549 (0.032)
	3	0.000	0.056	0.056	0.416 (0.031)		6	0.818 (0.082)	0.148	0.452	0.574 (0.034)
	4	0.089 (0.042)	0.578	0.613	0.497 (0.036)		7	0.819 (0.079)	0.181	1.000	0.000
	5	0.769 (0.061)	0.190	0.521	0.512 (0.038)		8	1.000			
	6	0.885 (0.050)	0.108	0.615	0.537 (0.04)	93	1				0.006 (0.001)
	7	0.933 (0.038)	0.067	1.000	0.000		2	0.00	0.022	0.022	0.135 (0.012)
	8	1.000					3	0.087 (0.055)	0.237	0.243	0.362 (0.022)
88	2				0.235 (0.021)		4	0.541 (0.079)	0.201	0.271	0.441 (0.028)
	3	0.000	0.240	0.240	0.528 (0.028)		5	0.706 (0.069)	0.201	0.386	0.456 (0.030)
	4	0.334 (0.070)	0.478	0.629	0.609 (0.031)		6	0.814 (0.057)	0.156	0.489	0.481 (0.033)
	5	0.784 (0.062)	0.198	0.704	0.622 (0.031)		7	0.871 (0.058)	0.123	0.759	0.000
	6	0.959 (0.029)	0.049	0.592	0.646 (0.033)		8	0.961 (0.038)	0.039	1.000	
	7	0.966 (0.031)	0.034	1.000	0.000		9	1.000			
	8	1.000				94	2				0.119 (0.043)
89	2				0.202 (0.015)		3	0.000	0.137	0.137	0.329 (0.090)
	3	0.000	0.327	0.328	0.478 (0.021)		4	0.365 (0.143)	0.239	0.277	0.406 (0.095)
	4	0.386 (0.096)	0.521	0.770	0.560 (0.025)		5	0.441 (0.098)	0.477	0.766	0.419 (0.094)
	5	0.888 (0.067)	0.107	0.705	0.575 (0.026)		6	0.854 (0.081)	0.146	1.000	0.000
	6	0.953 (0.045)	0.044	1.000	0.000		7	1.00			
	7	1.000									

Notes: Numbers in parentheses are estimated standard errors, SE. Probability definitions: γ_i is the probability that an individual alive and breeding in the population at age i was also alive and in the population at age $i - 1$; α_i is the probability that an animal of age i is a first-time breeder; a_i is the probability that an as-yet-inexperienced individual of age i starts to breed at that age; Ψ_i^{rs} is the probability that an individual in state r (prebreeder) at age i, and that survives to age $i + 1$, is in state s (breeder for $r \neq s$) at age $i + 1$; and i indicates "age."

derived from estimates of seniority probability (Table 5). Furthermore, there was a positive influence of age on resighting probability in prebreeders: Age 1, $\hat{p}_1^1 = 0.082$ ($\widehat{SE} = 0.006$); Age 2, $\hat{p}_2^1 = 0.687$ ($\widehat{SE} = 0.011$); Age 3, $\hat{p}_3^1 = 0.931$ ($\widehat{SE} = 0.002$); Age 4 or more, $p_{\geq 4}^1 = 0.965$ ($\widehat{SE} = 0.001$).

For prebreeder survival, there were differences among cohorts in individuals of the same age (Table 6). We did not find evidence of an influence of age on survival in breeders, but estimates of state-specific survival probability suggest that prebreeders tend to have lower local survival probability than breeders, except in some years the mean breeder survival is particularly low (Table 7). The model with equal survival in prebreeders and breeders of the same age (in the relevant age classes) had the largest QAICc value in the set of models considered (model: $p_i^1 p_{\cdot}^2 S_{i(7) \times c}^{\cdot} \Psi_{a(7) \times c}^{12}$ QAICc $= 19483.40$, number of parameters $= 130$).

We cannot formally compare estimates of transition probabilities obtained with different approaches because the data used are different (one of the data sets is a subset of the other, which precludes comparison of models using information criteria). In addition, the precision on some parameter estimates was poor because of small sample sizes (e.g., only a few individuals of each cohort recruit at older age; Table 5). Consequently, some of the observed differences may not be relevant, especially those corresponding to recruitment at older ages. However, some values estimated with reasonable precision differed by more then 0.10. If those differences do not completely result from uncertainty in the sampling and the estimation process, they are not negligible.

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TABLE 6. Estimates of prebreeder kittiwake survival probability, (S_i^r).

Cohort	S_i^r, by age i (yr)					
	0	1	2	3	4	≥5
84	0.566 (0.001)	0.549 (0.001)	0.647 (0.001)	0.549 (0.001)	0.647 (0.001)	0.591 (0.002)
85	0.582 (0.005)	0.565 (0.005)	0.778 (0.003)	0.687 (0.004)	0.662 (0.004)	0.607 (0.005)
86	0.648 (0.005)	0.632 (0.005)	0.823 (0.003)	0.736 (0.004)	0.721 (0.004)	0.671 (0.005)
87	0.653 (0.004)	0.653 (0.004)	0.825 (0.003)	0.739 (0.004)	0.725 (0.004)	0.675 (0.005)
88	0.633 (0.005)	0.617 (0.005)	0.813 (0.003)	0.723 (0.004)	0.715 (0.004)	0.656 (0.005)
89	0.625 (0.003)	0.608 (0.003)	0.807 (0.002)	0.716 (0.002)	0.700 (0.003)	0.648 (0.003)
90	0.639 (0.003)	0.623 (0.003)	0.812 (0.002)	0.728 (0.003)	0.720 (0.003)	0.662 (0.003)
91	0.654 (0.004)	0.638 (0.004)	0.826 (0.002)	0.740 (0.003)	0.726 (0.003)	0.676 (0.004)
92	0.588 (0.003)	0.571 (0.003)	0.782 (0.002)	0.683 (0.002)	0.667 (0.003)	0.612 (0.003)
93	0.678 (0.004)	0.663 (0.004)	0.842 (0.002)	0.761 (0.003)	0.747 (0.003)	0.700 (0.004)
94	0.605 (0.005)	0.587 (0.005)	0.794 (0.003)	0.698 (0.004)	0.682 (0.004)	0.628 (0.005)

Notes: Numbers in parentheses are estimated standard errors. S_i^r is the probability that an individual in state r survives between age i and age $i + 1$. Here r = ''1'' (prebreeder).

DISCUSSION

Analyses of the kittiwake data set provided evidence that estimates of recruitment probabilities obtained with the multistate approach using data from all the age classes where prebreeders are represented, and the values derived from seniority estimates (which do not use data from prebreeders) differ in some cohorts. In addition, estimates of state-specific (i.e., breeder or prebreeder) local survival probabilities suggested that, in many age classes, prebreeders tend to have lower local survival than breeders in most years. This violates one of the necessary conditions for equivalence of the measures of recruitment from the reverse-time approach (seniority probability) and the probability that an individual makes a transition between prebreeder and breeder states. As shown by our analysis of simulated data, differences in breeder and prebreeder survival may be sufficient to create an apparent influence of cohort on seniority probability, even if such a cohort effect does not exist. We also found that there was an influence of cohort on age-specific recruitment probability when accounting for cohort-specific differences

TABLE 7. Estimates of breeder survival probability in known-age kittiwakes released at age 0 from 1984 to 1994.

Year	S_i^r
1987	0.888 (0.007)
1988	0.777 (0.015)
1989	0.757 (0.011)
1990	0.718 (0.012)
1991	0.859 (0.005)
1992	0.813 (0.005)
1993	0.849 (0.003)
1994	0.768 (0.006)
1995	0.842 (0.004)
1996	0.844 (0.004)
1997	0.730 (0.005)
1998	0.854 (0.003)
1999	0.696 (0.008)
2000	0.801 (0.004)

Notes: Numbers in parentheses are estimated standard errors. For definition of S_i^r, see Table 6 notes; here ''t'' stands for ''time'' (year) and r = ''2'' (breeder).

in prebreeder survival in kittiwakes. That is, the differences in prebreeder survival among cohorts may in part explain the influence of cohort on estimates of recruitment obtained with data from the breeding segment of the population exclusively. However, it is impossible to tell to what extent this influence also reflects genuine cohort-specific variation in transition probability between the states ''prebreeder'' and ''breeder''.

While our results suggest differences in survival as a function of breeding state, we note that our analyses considered differences in local survival probability. In every study based on data from only part of the range of a species, in the absence of additional information, analysis of live encounter data cannot differentiate between true mortality and permanent emigration from the study area (e.g., Spendelow et al. 1995). Thus, it might also be possible that the apparent difference in local survival among breeding states partially reflects differences in site fidelity (natal vs. breeding dispersal) among individuals. Recruitment analyses based on data from part of the range of a species address local recruitment, regardless of whether data from prebreeders are available or not. We acknowledge the fact that as natal dispersal is unknown (and ignored), the age-specific transition probability obtained here might not reflect the genuine underlying distribution of latent age of first breeding among phenotypes that existed at birth in this population (Link et al. 2002*b*). Some individuals may have survived, emigrated, and recruited out of the study area.

In addition, within a given age class and cohort, the pool of prebreeders may be composed of a mixture of philopatric individuals and dispersers temporarily present in the natal area (i.e., the prebreeding segment of the population may be heterogeneous and include prospectors; J.-D. Lebreton, *personal communication*). Goodness-of-fit tests are commonly used to detect such heterogeneity in parameters (e.g., Burnham et al. 1987, Choquet et al. 2003, Pradel et al. 2003). Although our estimate of ĉ (overdispersion statistic for the most general model) was close to 1, indicating no substantial

overdispersion, the robustness of bootstrap goodness-of-fit tests for multistate models is not well known (Pradel et al. 2003), and it possible that we have simply committed a Type II error in failing to detect overdispersion. Detection of heterogeneity in survival probability in the prebreeding segment of the population will require development of approaches to assessing goodness of fit of multistate models in situations where there is a permanent transition (such approaches are not yet available; R. Pradel, *personal communication*).

It is important to note that estimates of realized age-specific probability of entering the breeding segment of the population can be useful even if the conditions are not met for equivalence of the measures of realized age of first breeding and the probability that a pre-breeder makes the transition to breeder state. For example, such estimates can be used to assess the population consequences of changes in realized age of entry in the breeding segment of the population (e.g., see Frederiksen and Pradel [2001] for Leslie-type population projection matrices). Depending on the objective of the study, approaches based on data from the breeding segment of the population exclusively may, or may not, allow the desired inferences. In some situations investigators may not be interested in going into the details of the processes potentially involved in variation in realized age of entry in the breeding segment of the population (i.e., survival, philopatry, and transition probability). In addition, several studies have used models that can theoretically account for group-specific variation in the size of the pool of prebreeders from birth to recruitment by using group-specific cumulative survival (i.e., Clobert et al. 1993, Spendelow et al. 2002, Lebreton et al. 2003). These approaches require data from the size of the cohorts of 0-year-old individuals released plus data from the breeding segment of the population; such data are fairly common in studies of wild-animal populations.

Separation of the demographic components underlying realized age of first breeding is particularly relevant in situations where investigators intend to design conservation actions and need to identify the relevant vital rates (e.g., Morris and Doak 2002). If the objective is to draw inferences about the influence of environmental factors (e.g., resource availability, habitat quality), human-induced, or not, or social factors (e.g., density dependence and competition) on individual ''decisions'' regarding age of first breeding (whether individuals actually chose to recruit at a given age, or were constrained to do so; Zack and Stutchbury 1992, Ens et al. 1995, Oro and Pradel 2000), we need to make sure variation in the realized distribution of age of first breeding reflects differences in transition probabilities, not survival probability before recruitment. The issue of separation of the two demographic components underlying realized patterns of age of first breeding is particularly relevant in studies focusing on the evolution of age of first breeding. Hypotheses proposed in

the framework of life-history theory (e.g., Stearns 1992) or behavioral ecology (e.g., Ens et al. 1995) draw a clear distinction between factors influencing survival before recruitment and age of first breeding, and they are sometimes based on the covariation between them. For example, phenotypes with breeding deferred beyond age ''*i*'' may die before ever breeding. The increased cumulative probability of dying before reproducing associated with delayed breeding is often invoked as a major selective pressure favoring earlier breeding (e.g., reviewed in Roff 1992, Stearns 1992, and Charlesworth 1994). Correlations between species-specific mortality rates or population-specific mortality rates and ''characteristic age at maturity'' form the raw material of empirical studies of life-history evolution (e.g., Stearns 1992, Charlesworth 1994, S. Tuljapurkar and C. Boe, *unpublished manuscript*).

In this study we have explicitly considered the problem of estimation of recruitment probability in terms of true (latent) probability of making the transition between prebreeding and breeding states. We simulated our encounter histories using an approach assuming that recruitment is the realization of an underlying stochastic process, where the individual has a given underlying (latent) probability of making the transition between reproductive states at a given age (Link et al. 2002*b*). While numerically convenient, this approach may be difficult to reconcile with the classical view of populations composed of phenotypic variants for age at maturity (e.g., Charlesworth 1994). In that view accession to the status of breeder is not necessarily a probabilistic process; it is often assumed (at least implicitly) that each individual should recruit at a fixed age if it survives to that age. We chose to use an approach where individuals were assigned age-specific recruitment probabilities to account for the distinction between age at maturity and age of effective recruitment. Age at maturity may set the earliest age breeding is possible, but environmental and (in vertebrates) social constraints may partly explain the differences between age at maturity and age of recruitment (Ens et al. 1995, Prévot-Julliard et al. 1998). In addition, reaching behavioral maturity and gaining social dominance may take a different amount of time in different classes of individuals using different behavioral tactics, which may translate into differences between age of maturity and effective age of recruitment (Cadiou 1993, Cadiou et al. 1994, Cam et al. 2002*a*). There are also biological reasons to treat recruitment as a probabilistic process at the individual level.

Empirical studies aiming at evaluating many of the hypotheses about the evolution of age of first breeding need to disentangle factors influencing survival and age-specific breeding probabilities. In studies of wild-animal populations, this may imply increased efforts in the field to collect data from prebreeders. Methodological development of new approaches to modeling longitudinal data may also permit assessment of bio-

logical hypotheses that lack empirical basis. The multistate approach used here with data from kittiwakes allows estimation of the "mean transition probability of prebreeders that survived to age i." The models we used account for the influence of age on prebreeder local survival, but do not account for the possible covariation between prebreeder survival and age of first breeding.

Such covariation forms the basis of several theoretical models of the evolution of age at maturity (e.g., Mertz 1975, Charlesworth 1994). In addition, our estimates of age-specific survival and recruitment probability partly reflect genuine age-specific changes in these parameters and within-cohort mortality selection (Curio 1983, Endler 1986, Cam et al. 2002b). The latter phenomenon may mask genuine age-specific variation in these demographic parameters (Cam et al. 2002b). To address genuine effects of age on parameters, it may be judicious to treat recruitment and survival probability as an individual latent demographic parameter (see Service 2000, Cam et al. 2002b, Link et al. 2002a, b for latent survival and breeding probability), possibly as correlated individual random effects (Yue and Chan 1997, Cam et al. 2002b, Link et al. 2002a, b, Cam et al. 2004) to address the covariation between fitness components. This will require further methodological development.

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APPENDIX A

Parameter values for scenario 1B (lower survival in prebreeders than in breeders of the same age; delayed recruitment) are available in ESA's Electronic Data Archive: *Ecological Archives* M075-016-A1.

APPENDIX B

Parameter values for scenario 2B (lower survival in first-time breeders than in experimental breeders of the same age) are available in ESA's Electronic Data Archive: *Ecological Archives* M075-016-A2.

APPENDIX C

Model selection for the five scenarios is available in ESA's Electronic Data Archive: *Ecological Archives* M075-016-A3.

APPENDIX D

A table reporting the influence of age and cohort on prebreeder survival and transition probability in kittiwakes (multistate models) is available in available in ESA's Electronic Data Archive: *Ecological Archives* M075-016-A4.

APPENDIX E

A table reporting the influence of age and cohort on seniority probability in kittiwakes (reverse-time models) is available in available in ESA's Electronic Data Archive: *Ecological Archives* M075-016-A5.