

# Habitat Selection, Age-Specific Recruitment and Reproductive Success in a Long-Lived Seabird

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**Abstract** Delayed recruitment (i.e. first reproduction) is a key feature of the demography of long-lived species such as seabirds. If physiological, behavioral, and environmental factors are thought to influence age at first breeding, knowledge of the fitness prospects corresponding to different recruitment tactics is needed to get insight into the evolution of delayed recruitment.

Because the age at which an individual recruits may depend on the location chosen to breed, we first investigated the relationship between habitat quality and age of first breeding in a long-lived seabird, the black-legged Kittiwake (*Rissa tridactyla*). We used multi-state mark-recapture approaches to model the transition from non-breeding to breeding status as a function of age and habitat quality. We also investigated whether there was a relationship between age at recruitment and reproductive success in the year of recruitment. We assessed several non-exclusive hypotheses. (i) If experience plays a part in reproductive success *per se* (e.g. in the quality of parental care), or in acquisition of higher-quality breeding sites (i.e. increased competitive ability), then reproductive success should be lower for early recruits (i.e. age 3) than others. (ii) In the same vein, if delayed recruitment corresponds to a queuing tactic allowing access to higher-quality sites, then late recruits (age 6 or 7) should exhibit higher breeding success than others. Alternatively, delayed recruitment may reflect behavioral inability to access to higher-quality sites; in this case, late recruits should exhibit poorer breeding success than younger ones. (iii) Experience combined with social constraints may lead to an initial increase in breeding success with recruitment age, and a decrease in older recruits.

We found that recruitment probability was highest at intermediate ages (i.e. 5–6 years old), and that recruitment probability was maximal in habitat patches (i.e. ‘cliffs’) of medium quality. This may reflect harsh competition in the most productive cliffs, and avoidance of the least productive ones (i.e. where predation on eggs is high). In accordance with our predictions (i and iii), we found that the youngest

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recruits experienced poor breeding success at the beginning of their reproductive life, and that breeding success was higher for birds recruiting at intermediate age. In addition, recruitment probability was best predicted by apparent habitat quality the year preceding recruitment. The latter result suggests either that habitat selection takes place the year preceding settlement and first reproduction, or that the information available to individuals at the beginning of a season is temporally auto-correlated to past productivity.

Reproductive choices and/or the constraints met during the pre-reproductive stage of life may influence age at recruitment. Our results show that there is a relationship between age of first breeding and breeding success probability. However, age of first breeding may also have substantial effects on breeding success over life. Future study should examine if reproductive success improves, shows senescent decline, or remains the same over the life course of individuals recruiting at various ages.

**Keywords** Age-specific recruitment · Black-legged the Kittiwake · Capture-Mark-Recapture · Habitat selection · Habitat quality · Multi-state modeling · Breeding success

## 1 Introduction

Age of first breeding (i.e. recruitment) in vertebrates is determined in part by age at sexual maturity, a constraint limiting flexibility in the minimum age at recruitment. However, even within the same population, a wide range of ages at first breeding is observed in many vertebrates, and many seabirds delay first reproduction well beyond physiological maturity. Accordingly, the pre-breeding segment of the population constitutes a significant part of the population. It is important to understand factors influencing the timing of recruitment to the breeding population, as the age of first breeding may have a significant impact on population dynamics and fitness (Caswell and Hastings 1980; Stearns 1992; Charlesworth 1994).

A consistent prediction from models based on life history trade-offs is that early reproduction should be favoured by natural selection (Stearns 1992; Charlesworth 1994), except under specific circumstances (i.e. population decline or fluctuating juvenile survival, Charlesworth 1994). Thus, unless one underestimates the importance and evolutionary consequences of temporal variation in juvenile survival, one might expect delayed reproduction to be rare in the wild. Interestingly, empirical observations do not always support this prediction (e.g. in birds: Viallefont et al. 1995; Pradel et al. 1997; Cooch et al. 1999; Lebreton et al. 2003). In a habitat selection framework, delaying recruitment has been suggested to allow individuals to gather information about potential breeding patches before recruitment (Boulinier and Danchin 1997). Reproductive delay might also be beneficial in terms of fitness if reproductive success increases with age, experience (i.e. skill enhancement through learning), or both (Charlesworth 1994), as long as the survival costs associated to such a delay do not exceed its benefits. Furthermore, delayed reproduction can be

adaptive (i.e. 'bet-hedging strategy') in environments where reproduction is uncertain (Tuljapurkar 1990).

In the black-legged Kittiwake (*Rissa tridactyla*), a cliff-nesting seabird, reproduction can begin at age two (Cam et al. 2002b, 2003), but the bulk of recruitment takes place between 3 and 6 years of age (Danchin et al. 1991; Cam et al. 2005), and some individuals delay recruitment even longer (e.g., 15 years; Cadiou 1993). In addition to physiological constraints, a certain level of behavioural maturity is required to complete reproduction successfully (Danchin 1987a; Porter 1988). Behavioral maturity is part of the general complex of 'increasing reproductive ability with age and experience' proposed by Charlesworth (1994), and may explain delayed age of first breeding. A certain level of maturity (e.g. competitive abilities in males to gain ownership on a nest-site), that may require a relatively long learning process, is therefore mandatory before reproduction can begin (Nur 1984; Pickering 1989; Monnat et al. 1990; Danchin et al. 1998).

Environmental conditions may interact with an individual's intrinsic quality and result in a variety of recruitment tactics. Energetic constraints on reproduction are likely to depend on resource acquisition, which is determined by both resource availability (i.e. a feature of the environment) and the individual's ability to harvest them (i.e. intrinsic quality). Only individuals of high quality may be able to recruit early if resource limitation occurs (e.g. in the lesser snow goose, Viallefont et al. 1995; in the blue petrel, Barbraud and Weimerskirch 2005).

Within this framework of constraints setting limits to variation in the age at first reproduction, individuals still have 'a decision to make'. For instance, age at first reproduction may directly depend on habitat selection tactics based on optimization of expected fitness (Fretwell and Lucas 1970). Potential recruits may decide either to breed or to wait until the next breeding season based on the quality of potential breeding locations in a given year (Boulinier and Danchin 1997). For example, severe predation events on eggs or chicks in the colonies attended by pre-breeders in a given year (Cam et al. 2004a) may lead some of them to postpone recruitment until the following breeding season. In this view, habitat selection may be one of the main components of the 'selective environment' of the age at recruitment. The decisions of where and when to start breeding may actually be 'two sides of the same coin' as Ens et al. emphasized (1995), and delayed recruitment might be the outcome of a specific habitat selection strategy involving:

- (1) Information gathering, in order to identify potential habitats and assess habitat quality (e.g., assessment of conspecific reproductive success and predation pressure in different colonies over time, Cadiou 1993; Boulinier and Lemel 1996; Boulinier and Danchin 1997; Danchin et al. 1998);
- (2) Gaining 'ownership' on a new site via competition or by queuing for an already occupied site to become available (see Wiley and Rabenold 1984; Ens et al. 1995; Cam et al. 2002b).

Obviously, constraints related to the acquisition of a nest-site may influence the timing of recruitment, especially in colonial cliff-nesting seabirds where competition amongst individuals to acquire a nest-site is strong, and may in turn delay

accession to the breeding population. In the study-population, nest-site density is stronger in higher-quality patches (i.e. cliffs) than in low-quality ones. Density is part of the environmental features that may influence individual age at recruitment. However, long-term observations (1979–2007) have shown that individuals can always ‘create’ new nest-sites in higher-quality patches if they have the competitive abilities to do so; thus, none of the patches are saturated in the study area. The common observation of individuals competing for specific nest-sites that are already occupied (Cadiou 1993) in higher-quality patches contradicts the idea that density dependence is the main factor influencing settlement decisions. Indeed, these individuals might be more interested in queuing for already occupied nest-sites, or in evicting previous owners of occupied sites, as in both cases they can directly observe how much this site is ‘worth’ (i.e. based on their conspecific’s reproductive success on this particular site). The pays-offs of such behaviour might overtake the benefits associated with the creation of a new nest-site, in which case individuals have no information on its potential. Our assumption is that social constraints and competitive abilities, rather than density dependence *per se*, are the main determinants of the age at first reproduction.

The optimal age at first reproduction, if any, is likely to depend on an individual’s phenotype, the environment, and their interaction. It is probably not achievable to fully understand why an individual recruits at a given age without identifying habitat characteristics (nest-site, territory, colony or breeding location) where recruitment takes place. Regrettably, these tend to be treated independently in the literature (but see Ens et al. 1995; Boulinier and Lemel 1996). To circumvent this shortfall, our main objective was to address the relationship between age at first reproduction and habitat selection. Several behavioural tactics of habitat selection characterized by different ages at first reproduction may coexist in populations. For example, age *per se* may be associated with increased behavioural maturity and competitive ability, which may in turn translate into a higher probability of acquiring a good nest-site in older, more experienced individuals. A non-exclusive hypothesis may explain a similar relationship between age and habitat quality: the queuing hypothesis (Ens et al. 1995). Higher quality individuals may acquire higher quality nest-sites if they wait for a productive site (i.e. site where the current and past reproductive success is high) to become available. Alternatively, individuals with poor competitive abilities may recruit in lower-quality sites, regardless of age, which may lead to a situation where the oldest recruits breed on low-quality sites.

We used capture-mark-recapture (i.e. CMR) multi-state models (Nichols and Kendall 1995; Nichols 1996; Cam et al. 2005) to estimate recruitment probabilities as a function of age, cohort, as well as covariates used as surrogates for habitat quality. We first examined the age at which birds recruit (whether this choice reflects an individual decision or results from constraints), and where they settle at recruitment (in terms of habitat quality) as a function of age, in order to determine whether delayed recruitment results in the acquisition of higher-quality sites within productive cliffs.

Our second objective was to determine how well individuals recruiting at various ages and in habitat patches of different qualities perform in terms of breeding

success probability in the year of recruitment. This aims at assessing whether delayed recruitment is associated with higher breeding success than early breeding; more generally, we aim at assessing the importance of habitat selection on fitness prospects in the very first breeding event.

## 2 Methods

### *2.1 Estimation of Recruitment Probabilities as a Function of Habitat Quality Using CMR Multi-State Models*

In 1979, a black-legged Kittiwake monitoring program was initiated in Brittany, France, and is continuing today (five colonies located in Cap Sizun a few kilometers apart from each other, 48°5'N, 4°36'W; Monnat et al. 1990). Here, we examine the capture–recapture histories of twelve birth cohorts (1986–1997) over 18 years (1986–2003), that is a total of 4030 individuals. The fieldwork covers each breeding season entirely such that observers do not miss a single reproductive event in the study area (Cam et al. 1998). It is therefore possible to identify the very first reproductive event of each individual returning to the study area (Cam et al. 2002b, 2003, 2005). We acknowledge that some pre-breeding individuals may have recruited into another population (e.g. the British Isles or Spain; Cam et al. 2002b) before breeding in Brittany, that is, we may have missed the very first breeding event. However, we believe that such cases are rare as most individuals resighted as recruits attend Brittany colonies in the years preceding recruitment, and the majority of the recruits are sexed through behaviour before first breeding. Thus, attending Brittany colonies while breeding in the British Isles is likely to be rare.

#### **2.1.1 Habitat Quality**

To address the relationship between habitat selection and recruitment probability, we first defined habitat patches as sections of a cliff delimited by topographical discontinuities (e.g. Danchin et al. 1998). In the following, we will use ‘cliff’ and ‘habitat patch’ interchangeably. Only patches hosting at least ten nest-sites were included in our study. Following the approach developed by Danchin et al. (1998), we calculated yearly ‘habitat quality’ (i.e. local productivity) as the percentage of nests in a success situation within each cliff (0–33% for poor quality cliffs, 33–66% for medium quality cliffs, and 66–100% for highly productive cliffs). A ‘success’ was defined as a nest fledging at least 1 offspring. Similar to Danchin et al. (1998), and Cam and Monnat (2000a), the performance of the focal individual was excluded from the calculation of habitat quality in order to maintain independence between measures of individual breeding success and habitat quality. Our measure of habitat (cliff) quality will be referred to as ‘Cliff’ in the statistical analyses.

## 2.1.2 Approach to Modeling

### Recruitment Probability

We used the definition of recruitment given by Pradel and Lebreton (1999): the probability that a pre-breeder in year  $t$ , which survived up to year  $t+1$ , reproduces in year  $t+1$  (i.e. transition probability from pre-breeding to a breeding state; Brownie et al., 1993). Transition probabilities from breeding to non-breeding states were fixed to zero (i.e. impossible transitions). The recapture probability of breeders is  $\approx 1$  in the study population (Cam et al. 1998, 2005), but previous studies have shown that recapture probabilities for pre-breeders are lower than 1 (Cam et al. 2005). Hence, estimation of transition probabilities conditional on survival (i.e. recruitment probability) requires probabilistic models incorporating recapture probability.

Multi-state (MS) models (Arnason 1973; Nichols et al. 1992, 1993; Nichols and Kendall 1995; Schwarz et al. 1993; Lebreton and Pradel 2002) are designed in such a manner that individuals can move among states (e.g., states can be geographical states, or biological states such as size classes, breeding states, etc.).  $\psi_t$  is the probability of moving among states between time  $t$  and  $t+1$  (in our case, transition from non-breeding to breeding state) conditional on surviving up to time  $t+1$ . We used the multi-state models implemented in Program MARK (White and Burnham, 1999) to estimate recapture, survival, and transition probabilities denoted as:

$P_t^r$ : Recapture probability at time  $t$  for an individual in state  $r$  at time  $t$  ( $t = 2, 3, \dots, k$ )

$S_t^r$ : Probability of being alive at time  $t+1$ , for an individual alive and of state  $r$  at time  $t$  ( $t = 1, 2, 3, \dots, k-1$ )

$\Psi_t^{rs}$ : Transition probability from state  $r$  (non-breeder) at time  $t$  ( $t = 1, 2, 3, \dots, k-1$ ) to state  $s$  (breeder) at time  $t+1$ , for an individual surviving between  $t$  and  $t+1$ .

Here, age is accounted for by inclusion of both cohort and year (for additional details see Cam et al. 2005)

### Influence of Habitat Quality on Recruitment Probability

We modeled the effect of habitat quality on transition probabilities  $\Psi_t^{rs}$  (from a non-breeding state  $r$  to a breeding state  $s$ ) using two different approaches. First, we assigned a covariate corresponding to the quality of the recruitment habitat to each individual. Because previous studies have provided evidence that patch quality the year preceding recruitment ( $t-1$ ) influences settlement decisions in year  $t$  in both dispersers and recruits (Cadiou et al. 1994; Danchin et al. 1998; Cadiou 1999), we considered models with a covariate accounting for habitat quality the year preceding recruitment (covariate  $q_{t-1}$ ), or the year of recruitment (covariate  $q_t$ ). The biological hypotheses underlying a model including habitat quality in the year preceding recruitment is that recruits might be prospecting for a high-quality patch. They might make the decision of where they are going to settle and breed for the first time at least a year in advance. We also considered quadratic

models including  $q_{t-1}$  squared ( $q_{t-1}^2$ ), and  $q_t$  squared ( $q_t^2$ ), to evaluate possible non-monotonic relationships between recruitment probabilities and habitat quality. Testing for a positive linear relationship between recruitment probability and cliff quality is testing whether recruitment probability increases as cliff quality increases. A quadratic relationship term may account for higher recruitment probabilities in habitat of medium quality and lower recruitment probabilities in habitats of poor and high quality, or conversely if the sign is switched. We also considered a model without any covariate accounting for habitat quality to address the 'null' biological hypothesis that is a lack of influence of habitat quality on recruitment probability.

Since one must assign a covariate value to each individual, we had to dispense a value to individuals that did not recruit and for which recruitment-habitat characteristics did not exist (i.e. individuals that have never reproduced, died before recruitment, or emigrated out of the study area before recruitment). Following Cooch and White's (2006) two-step solution to the 'missing-value' issue, we assigned average covariate values to individuals that did not recruit (i.e.  $q_t = 0.464$ ,  $q_t^2 = 0.215$ ,  $q_{t-1} = 0.456$ ,  $q_{t-1}^2 = 0.208$ ). This may artificially skew the estimate of transition probability towards these values (i.e. habitat patches of intermediate quality). To assess the importance of the bias, we compared our results (i.e. models receiving large support) to recruitment estimates obtained in a second set of analyses, where no covariates were involved, but where states were defined differently and accounted for the quality of the recruitment habitat.

The second approach assesses the effect of habitat quality on transition probabilities  $\Psi_i^{rs}$  (from non-breeding state  $r$  to breeding state  $s$ ) by specifying four states. We considered (1) pre-breeders; (2) breeders recruiting in high-quality cliffs (i.e. cliffs where local productivity is between 66 and 100%); (3) breeders recruiting in cliffs of intermediate quality (i.e. local productivity between 33 and 66%); and (4) breeders recruiting in poor quality cliffs (i.e. local productivity between 0 and 33%). Because the previous approach indicated that models including habitat quality the year preceding recruitment performed better than others (according to information criteria, Burnham and Anderson, 1998, see also results), the categorical index of habitat quality used in the second approach to define the states is based on habitat quality the year preceding recruitment.

Our models included covariates (i.e. various measures of habitat quality) or breeding states accounting for habitat quality, as well as age and cohort effects on transition probabilities. We never used interaction terms between age and cohort as it would be equivalent to considering a time effect. However, additive models allowed disentangling age effects on recruitment probabilities from cohort-related effects. The latter may reflect long lasting birth-year effects on age-specific recruitment probabilities (e.g. climatic effects). We also used such additive models (cohort + age) for purely technical reasons, that is to fix some parameters to zero according to the specificity of the distribution of ages at recruitment in the different cohorts (e.g. if in the birth cohort 1992, the minimum transition from a non-breeding to a breeding state occurred between ages 3 and 4, the 'cohort + age' format allowed us to fix the parameters representing the probability of recruitment in younger age classes to zero, such as recruitment probabilities in between age 0 and 1, 1 and 2, or 2 and 3).

## Model Selection

Based on prior studies of recruitment probability (Cam and Monnat 2000a; Cam et al. 2002b, 2003, 2005), and movement among colonies of black-legged kittiwakes in Brittany (Danchin and Monnat 1992; Danchin et al. 1998), we were primarily interested in hypotheses pertaining to the relationship between age-specific recruitment probability and habitat selection, conditional on age- and state-specific survival. Accordingly, we designed a general model reflecting all biological processes of interest. Because recapture probability of the youngest pre-breeders is known to be low, sample sizes within age-by-state combinations were assessed to design the most general model (e.g. Cam et al. 2002b, 2003, 2005).

Previous studies indicated that adult recapture probabilities have always been  $\approx 1$  in the study area (Danchin and Monnat 1992; Cam et al. 1998, 2005), hence we assumed that adult recapture probabilities were independent of time and cohort in all models:  $p2(\cdot)$  (state '2' corresponds to adults i.e., after recruitment). On the contrary, we expected recapture probabilities to vary with age amongst pre-breeders:  $p1(\cdot)$  (state '1' corresponds to pre-breeders). As the majority of pre-breeders recruit before 7 years old, we pooled data from pre-breeders of age 7 or more (i.e., recapture at age 1, 2, 3, 4, 5, 6, 7 or greater).

Previous work also indicated that apparent survival probability is lower for pre-breeders than for breeders (Cam et al. 2005), as they might be subjected to greater extrinsic causes of death than adults, or have a higher probability of permanent emigration. Therefore, we considered a 7 age-class effect on pre-breeders' survival as well. Climatic conditions experienced during early development or during the first winter at sea may affect differently each birth cohort justifying why we considered cohort variations in pre-breeders' survival (i.e.  $S1(c12, a7)$ , where 'c12' stands for the cohort effect and 'a7' for the seven age-class effect). We did not consider cohort variation in adult survival, as we were trying to limit model size (i.e. number of estimated parameters). We focussed preferentially on the parameters of interest (i.e. parameters representative of the 'pre-breeding' stage, and of 'first-time breeding' events). We then considered an age effect on adult survival (denoted as  $S2(a5)$ ). In the case of adults, we defined only 5 age classes (i.e.  $a5$  defines age classes 2, 3, 4, 5, 6, 7+, where 7+ stands for individuals aged 7 years old and more), as the minimum age to become a breeder is 2 years old.

The last set of assumptions concerns the probability of transition from a non-breeding to breeding state,  $\Psi$ . As previous studies have provided evidence of an increase in recruitment probability with age, and in a limited sense, with experience as well (Cam et al. 2002b, 2003, 2005), we considered age effects on transition probabilities. Also, we included an additive cohort effect to account for the influence of annual environmental change (climatic conditions or predation events affecting the proportion of high-quality breeding habitats available to recruits), when individuals belonging to different cohorts reach the age at which transition to the breeding state is theoretically possible. Such environmental factors may influence age-specific recruitment differently from one cohort to another. As our primary objective was to examine the influence of habitat quality on age at first reproduction, we also

included the effect of habitat quality, either by using individual covariates (approach 1), or by stratifying the data set into different states, reflecting different combinations of habitat quality and age (approach 2). The initial model accounted for an age effect on recruitment probabilities characterized by 6 age-specific transition probabilities (transition in between 1 and 2 years old, 2 and 3, 3 and 4, 4 and 5, 5 and 6, 6 and 7). Transition probabilities were denoted  $\Psi_{12}(c_{12} + a_6 + q_t + q_t^2 + (a_6 \times q_t))$  in the first approach and  $\Psi_{12}(c_{12} + a_6)$   $\Psi_{13}(c_{12} + a_6)$   $\Psi_{14}(c_{12} + a_6)$  in the second, where 2, 3 and 4 corresponded to the three different habitat qualities (i.e. poor, medium, high) in which a bird can recruit. As transitions cannot biologically occur in the opposite direction,  $\Psi_{21}(\cdot)$   $\Psi_{31}(\cdot)$   $\Psi_{41}(\cdot)$  were fixed to zero.

For each approach, our starting model was defined as follows:

Approach 1 (with individual covariates):

$$S1(c_{12} + a_7) S2(a_5) p1(a_7) p2(\cdot) \Psi_{12}(c_{12} + a_6 + q_t + q_t^2 + (a_6 \times q_t)) \Psi_{21}(\cdot)$$

Approach 2 (discrete states):

$$S1(c_{12} + a_7) S2(a_5) S3(a_5) p1(a_7) p2(\cdot) p3(\cdot) p4(\cdot) \Psi_{12}(c_{12} + a_6) \Psi_{13}(c_{12} + a_6) \Psi_{14}(c_{12} + a_6)$$

We acknowledge that both global (starting) models are not saturated, even though it would be desirable to compare the performance of saturated models and less parameterized ones. A saturated model is defined as the model where the number of parameters equals the number of data points. Such a model is needed to compute the baseline deviance, which is in turn used to estimate the amount of over-dispersion in the data (Cooch and White 2006). However, we had to limit the degree of stratification of the data to make parameter estimation feasible. Furthermore, the large number of biological parameters of interest made it difficult to define a small set of alternative models defined ‘a priori’ (Burnham and Anderson 1998). We sequentially specified models by simplifying the starting model to test for specific biological hypotheses. Nevertheless, we acknowledge that sequential development of models might lead to different conclusions compared to considering a set of models defined *a priori*.

Unfortunately, formal goodness-of-fit tests for MS models do not allow for treatment of situations with permanent transitions (Pradel 2006). As an alternative approach to a formal goodness-of-fit test, we estimated an overdispersion parameter (i.e.  $\hat{c}$ ) for the global model without individual covariates (approach 2 described above) using bootstrap simulations in MSSURVIV (Hines 1994).

We used Akaike’s Information Criterion modified for small sample size, AICc, in the first approach (where no overdispersion parameter  $\hat{c}$  can be calculated), and the qAICc modified for overdispersion in the second approach (where q stands for quasi-likelihood; Akaike 1973, see also Sakamoto et al. 1986; Lebreton et al. 1992; Burnham and Anderson 1998). We also used Akaike’s weights,  $w_i$ , to select the best models from our set of candidate MS models in both approaches 1 and 2. Only models with an Akaike weight exceeding 0.95 were systematically retained. If the weight was shared among 2 or more models, we discussed the interpretation of each of them.

## 2.2 *Estimation of Breeding Success in the Year of Recruitment*

### 2.2.1 **Sample Specifications**

Only individuals that survived until recruitment and recruited were considered in analyses of breeding success (1450 individuals, 5054 observations). More specifically, we addressed breeding success probability in the year of recruitment and in subsequent breeding occasions. As emphasized above, for birds recruiting in the Cap Sizun, the probability of recapture is virtually 1 after recruitment (Cam et al. 1998, 2005). Working on the sample of individuals that has recruited allows us to use simple statistical models that do not account for recapture probabilities, such as generalized linear models and mixed models. Individuals whose breeding success in the year of recruitment was unknown or uncertain were excluded from the analyses. Only individuals that fledged at least one chick up to independence were considered ‘successful’, others were considered to have ‘failed’.

### 2.2.2 **Generalized Linear Models (glm) and Mixed Models (glmmM)**

We used generalized linear models (Agresti 1990) to address the influence of two covariates (i.e. age at first reproduction and habitat quality) on breeding success probability, a binary response variable (i.e. success *versus* failure). Sample sizes incited us to minimize the number of states in the analysis, thus we did not include different levels of failure (e.g. early failure when the chick dies at the nest or late failure when the chick died at fledging) or success (e.g. kittiwakes generally produce 1 or 2 eggs, and occasionally produce up to 3 eggs, and may fledge several chicks).

We built a series of glms (use of the logit link) accounting for cliff quality the year preceding recruitment (found to be a better predictor of the recruitment process than cliff quality the year of recruitment, see Results) and age at recruitment. Age at recruitment was treated either as a continuous or as a categorical covariate. We tested several transformations of cliff quality (i.e. proportions of successful nests within a cliff in a given year):

- the arcsine transformation, suitable for binary data summarized as proportions.
- the square root transformation, suitable for Poisson-distributed covariates where sample means are proportional to the variances of the respective samples; replacing each measure by its square root will often result in homogeneous variances (Neter et al. 1996).

We also built models including a quadratic effect and a cubic effect of age and habitat quality on breeding success probability. A quadratic effect of cliff quality on success probability would mean that maximum (or minimum) success probability is reached in cliffs of intermediate quality. Similarly, a quadratic effect of age on success probability would account for a minimum, or maximum breeding success at intermediate ages. A cubic relationship would account for a bimodal pattern in success probability as a function of covariates.

We accounted for temporal variation in breeding success (possibly resulting from environmental fluctuations; e.g. climatic conditions, predation events, food shortage, etc.) by incorporating a random effect of time (year) only to the best performing model. We modeled year as a random effect for two reasons. First, we had no motive to suspect any specific shape for the influence of year on breeding success probability (e.g. a systematic trend). Second, using a random effect to account for temporal variation in breeding success leads to fewer parameters than a fixed effect model. We viewed this as an advantage (i.e. larger sample sizes) to address the influence of covariates more relevant to hypotheses pertaining to habitat selection (e.g. habitat quality). We used the package ‘glmmML’ (i.e. package ‘MASS’, R version 2.3.1) to implement mixed models.

### 2.2.3 Model Selection

First, we compared pairs of models containing the same covariate but parameterized in different ways (e.g. a model containing the age at first reproduction AFR, treated as a continuous covariate, was tested against a model containing AFR treated as a factor). After retaining the best parameterization, we compared models with an additive effect or an interaction term. Each model was created to discriminate between various underlying biological hypotheses. The models selected will be discussed in the manuscript. For model comparison, we only reported model selection based on Akaike’s Information Criterion AIC (Akaike 1973; Burnham and Anderson 1998), as results based on AICc were consistent with results based on AIC.

## 3 Results

### 3.1 *Estimation of Recruitment Probabilities as a Function of Habitat Quality: A CMR Approach Using Multi-State Models*

The estimated overdispersion parameter (i.e. variance inflation factor) for the global model was 1.94 (bootstrap procedure in MSSURVIV, 1000 simulations).

#### 3.1.1 Analysis with Individual Covariates

The best model, ‘2-state-model-19’, is structured as follow (see Appendix 1; Table 1):

$$S1(c12 + a6) S2(.) p1(a4) p2(.) \Psi12(c12 + a6 + q_{t-1} + q_{t-1}^2) \Psi21(.)$$

This model includes a cohort effect on survival probability of pre-breeders, and survival probability at a given age varied according to birth year. Pre-breeder

**Table 1** Modelling the influence of habitat quality on the recruitment process I: model selection results based on the first approach (approach with covariates, see Methods)

Model selection	AICc	$\Delta_i$	$W_i$	Likelihood	NP	Deviance
M19	21374	0.00	0.77	1.00	42	21290
M24	21377	2.69	0.20	0.26	43	21290
M13	21382	7.98	0.01	0.02	43	21296
M18	21838	8.87	0.01	0.01	44	21294
M11	21384	9.93	0.00	0.01	33	21318
M7	21384	10.44	0.00	0.00	33	21318
M12	21395	20.50	0.00	0.00	50	21294
M5	21396	21.98	0.00	0.00	49	21297
M4	21397	22.51	0.00	0.00	51	21294
M3	21401	26.75	0.00	0.00	40	21320
M14	21404	30.35	0.00	0.00	57	21290
M20	21406	32.16	0.00	0.00	58	21289
M6	21408	34.17	0.00	0.00	59	21289
M10	21409	35.22	0.00	0.00	56	21297
M16	21418	44.06	0.00	0.00	43	21332
M22	21420	45.78	0.00	0.00	43	21333
M15	21428	53.50	0.00	0.00	43	21341
M21	21430	55.55	0.00	0.00	43	21343
M9	21449	75.11	0.00	0.00	45	21359
M8	21457	83.04	0.00	0.00	34	21389
M17	21643	268.88	0.00	0.00	38	21567
M23	21643	269.12	0.00	0.00	38	21567
M1	21826	452.40	0.00	0.00	60	21706
M1bis	21861	934.67	0.00	0.00	47	21766
M2	22666	1291.50	0.00	0.00	54	22557

Note: NP: number of estimated parameters; AIC: Akaike's Information Criterion =  $-2 \cdot \log\text{-likelihood} + 2 \cdot \text{NP}$ ;  $W_i = \exp(-0.5 \cdot \Delta \text{AIC}) / \text{NP}$ .

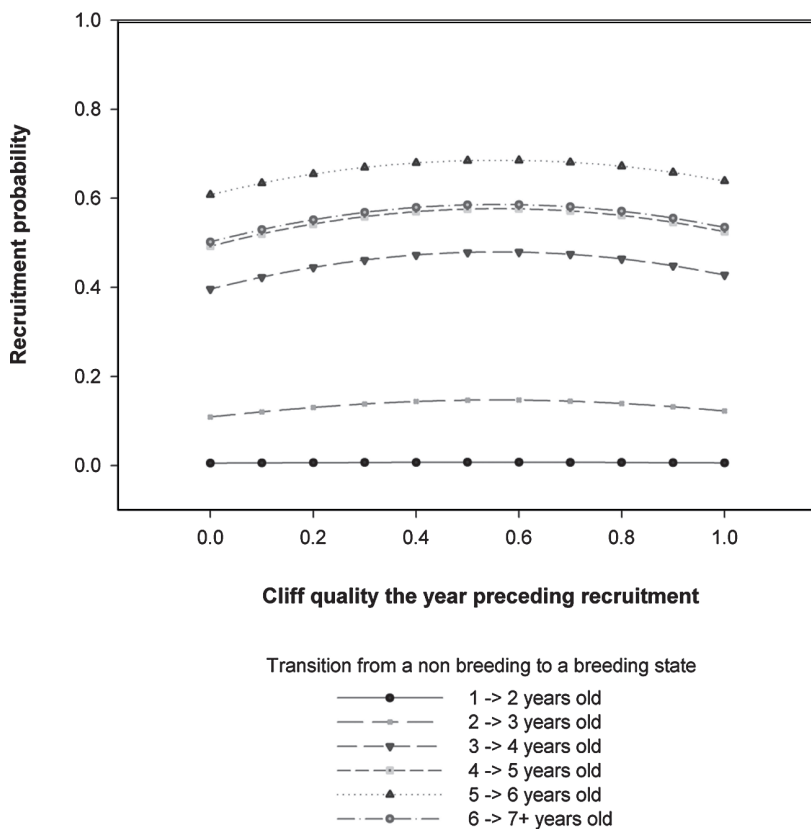
survival also varied across ages (i.e. survival probabilities between ages 0-1, 1-2, 2-3, 3-4, and 4-5 years old were significantly different).

Adult survival probability was best accounted for by a model with constant survival across ages and cohorts ( $S2(\cdot)$ ).

The recapture probability of pre-breeders did not vary across cohorts, but varied across ages ' $p1(a4)$ '. The best model retained had a 4 age-class structure (0-1, 1-2, 2-3, and 3-4 years old and more) showing a non-negligible difference in recapture probabilities across age groups.

Recapture probability of adults was  $\approx 1$ , regardless of cohort and age class ( $p2(\cdot)$ ) and confirms previous findings (Danchin and Monnat 1992; Cam et al. 1998; 2005).

The probability of transition from the 'pre-breeding' to the 'breeding' state varied across cohorts and ages ( $\Psi12(c12 + a6 + q_{t-1} + q_{t-1}^2)$ ). The model selected included six age classes (transition from 1 to 2, 2 to 3, 3 to 4, 4 to 5, 5 to 6 and 6 to 7+ years old and more). Averaged across cohorts, the recruitment probability between ages 1 and 2 was close to zero (only a handful of individuals recruited at such an early age). Model selection provided support for a model where recruitment probability increased with age at first breeding up to 5 and 6 years of age, after which it declined (i.e. recruitment probability peaks for the transition occurring in between



**Fig. 1** Recruitment probabilities as a function of habitat quality and age at first reproduction Cliff quality (i.e. continuous covariate) was calculated the year preceding recruitment. Recruitment probabilities were estimated from the best performing multi-state model. The recruitment probabilities were averaged across cohorts (birth cohorts 1986 to 1997, followed from 1986 to 2003).

age 5 and 6; Fig. 1). The model selected also included an effect of cliff quality the year preceding recruitment (i.e.  $q_{t-1}$ ), largely preferred (according to AICc) over a model with an effect of cliff quality in the recruitment year (i.e.  $q_t$ ), and over a model without a covariate accounting for cliff quality. Moreover, a quadratic effect of cliff quality in the year preceding recruitment (i.e.  $q_{t-1} + q_{t-1}^2$ ) received more support than a linear effect (Table 1). Thus, for each recruitment tactic, maximum recruitment probability occurred in cliffs of intermediate quality the year preceding recruitment (Fig. 1).

One may argue that this result does not reflect any active individual choice, but rather that the availability of habitat patches of intermediate quality exceeds that of patches of other qualities (i.e. poor and highly productive cliffs). Individuals may simply distribute themselves randomly according to habitat availability. That is true

**Table 2** Time series of the proportion of poor, medium, and high quality cliffs from 1986 to 2003

Year	Cliffs of good quality (%)*	Cliffs of intermediate quality (%)**	Cliffs of poor quality (%)***
1986	29	45	26
1987	32	39	30
1988	16	35	49
1989	6	34	59
1990	11	39	50
1991	35	40	26
1992	33	35	33
1993	23	28	49
1994	10	23	67
1995	26	21	53
1996	19	19	62
1997	24	34	41
1998	7	22	7
1999	15	54	31
2000	21	62	17
2001	41	32	27
2002	20	44	36
2003	62	35	4

*Note:* Cliff quality was calculated the year preceding recruitment as model selection results indicated that this quantity best predicts recruitment probability.

\* Proportion of cliffs in a given year containing 66–100% nests in a success situation.

\*\* Proportion of cliffs in a given year containing 33–66% nests in a success situation.

\*\*\* Proportion of cliffs in a given year containing 0–33% nests in a success situation.

in less than half of the cases (see Table 2, years 1986, 1987, 1991, 1992, 1999, 2000 and 2002). Consequently, a higher recruitment probability in cliffs of intermediate quality cannot be interpreted as resulting exclusively from a spatially random recruitment process. In more than half of the years included in this study, individual choice and/or constraints led recruits to select habitat features different from those that would be obtained by random settlement.

### 3.1.2 Analysis Without Individual Covariates

The above results provided evidence that models including an effect of cliff quality in the year preceding recruitment on transition probability best fit the data. In the second approach (i.e. without individual covariates), we therefore defined three states for breeders ('2', '3', and '4', settling in poor, medium, and high quality habitat patch, respectively) according to cliff quality in the year preceding recruitment, as the model including a quadratic form of this covariate was found to perform better than models including cliff quality the year of recruitment (Appendix 2; Table 3).

**Table 3** Modeling the influence of habitat quality on the recruitment process II: model selection results for the second approach (approach without covariates, see Methods)

Model selection	qAICc*	$\Delta_i$	$W_i$	Model likelihood	NP	Deviance
Md21	32218	0.00	1.00	1.00	76	16355
Md12	32238	20.35	0.00	0.00	86	16355
Md8	32238	20.37	0.00	0.00	86	16355
Md7	32239	21.32	0.00	0.00	87	16354
Md9	32240	22.39	0.00	0.00	85	16360
Md15	32241	22.82	0.00	0.00	84	16362
Md6	32241	23.15	0.00	0.00	88	16354
Md14	32242	24.53	0.00	0.00	85	16362
Md20	32244	26.36	0.00	0.00	83	16368
Md4	32241	33.25	0.00	0.00	102	16336
Md3	32252	34.08	0.00	0.00	103	16335
Md1	32254	36.12	0.00	0.00	104	16335
Md5	32255	37.05	0.00	0.00	101	16342
Md11	32284	66.32	0.00	0.00	76	16422
Md19	32291	73.34	0.00	0.00	53	16475
Md16	32348	130.43	0.00	0.00	50	16539
Md13	32481	263.59	0.00	0.00	81	16609
Md18	32513	295.45	0.00	0.00	68	16667
Md10	32550	331.86	0.00	0.00	69	16702
Md17	32561	342.85	0.00	0.00	35	16781
Md2	34003	1785.50	0.00	0.00	98	18096

Note: NP: number of estimated parameters.

\* We used Akaike’s Information Criterion modified for sample size qAICc (where q stands for quasi-likelihood) and for an estimated overdispersion parameter  $\hat{c}$  of 1.93 using bootstrap simulations (see Methods).

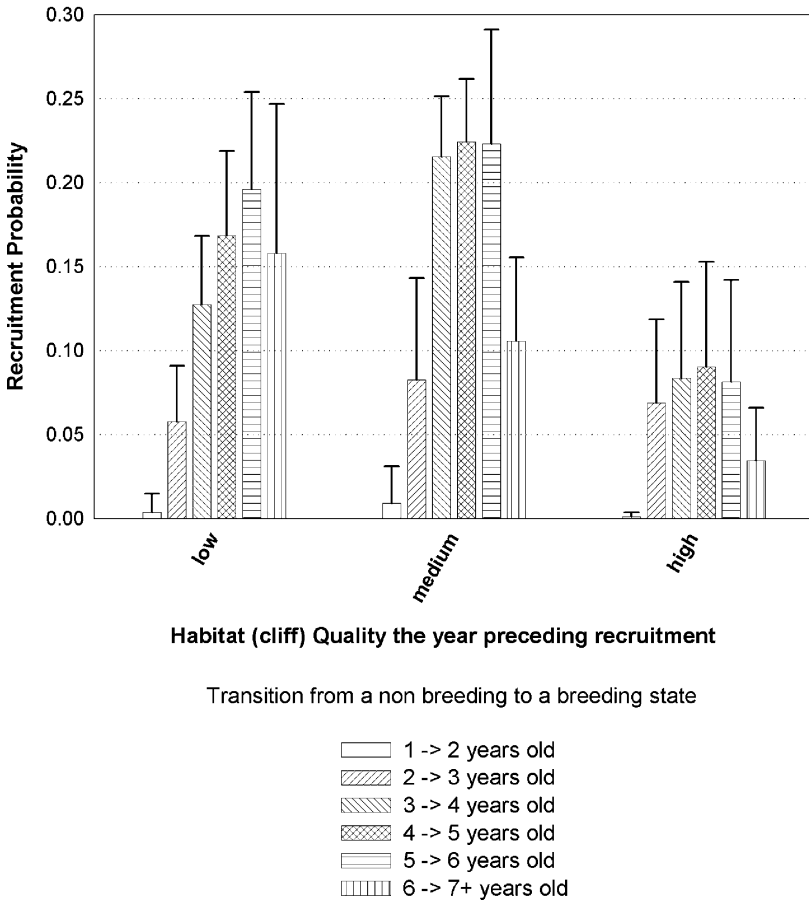
The best approximating model, ‘4-states-model-21’, had the following structure:

$$S1(c12 + a6)S2,3,4(a3)p1(a5)p2,3,4(.)\Psi12(c12 + a6)\Psi13(c12 + a6)\Psi14(c12 + a6)$$

This model included a cohort effect on pre-breeder survival, ‘ $\Phi1(c12)$ ’, showing that birth year influences survival. In addition, pre-breeder survival probabilities changed with age,  $S1(a6)$  (i.e. survival probabilities from age 0 to 1, 1 to 2, 2 to 3, 3 to 4, 4 to 5, and from 5 years old to any higher age were significantly different). Adult survival probability did not vary across cohorts or across cliff qualities in the year preceding recruitment. We did however detect an age effect on adult survival (where individuals aged 3, 4, 5 years old and more had different survival probabilities: ‘ $S2,3,4(a3)$ ’).

Recapture probability of pre-breeders was constant across cohorts, but varied across five age classes: 0, 1, 2, 3, 4 years and more; ‘ $p1(a5)$ ’. For adults, neither cliff quality, cohort, nor age influenced recapture probabilities.

Recruitment probabilities varied according to birth cohort and age (transition probabilities from 1 to 2, 2 to 3, 3 to 4, 4 to 5, 5 to 6, 6 to 7 years old and more were significantly different). Consistent with the results obtained using the previous approach, transition probabilities were highest at intermediate ages (i.e. 5 and 6 years old; quadratic age effect on recruitment probability). In addition, age-specific



**Fig. 2** Recruitment probability as a function of habitat quality and age at first reproduction. Cliff quality was calculated the year preceding recruitment. Three states accounted for the quality of the recruitment habitat the year preceding recruitment: poor, medium and high quality cliffs. A fourth state accounted for the pre-breeding segment of the population. Recruitment probabilities were estimated from the multi-state model that received the most support, and were averaged across cohorts (birth cohorts 1986–1997, followed from 1986 to 2003).

recruitment probabilities varied according to cliff quality in the year preceding recruitment, and were higher in habitat patches of intermediate quality (Fig. 2).

### 3.2 Breeding Success the Year of Recruitment

The best model contained both an effect of age at first reproduction (treated as a factor: AFR = 3, 4, 5, 6, 7 years old and more) and a quadratic effect of cliff quality, on breeding success (Table 4; Fig. 3). Breeding success probability was maximal

**Table 4** Model selection results: generalized linear models and mixed model testing the effects of age at recruitment and habitat quality on breeding success in the year of recruitment

Model	NP	AIC	$\Delta_i$	$\exp(-(1/2)*\Delta_i)$	$W_i$
<b>AFR.cat + (Cliff)<sup>2</sup> + <math>\epsilon</math> (time)*</b>	<b>7</b>	<b>1613.0</b>	<b>0.0</b>	<b>1.000</b>	<b>0.609</b>
<i>AFR.cat * (Cliff)<sup>2</sup></i>	10	1619.6	6.6	0.037	0.022
<i>AFR.cat + (Cliff)<sup>2</sup></i>	6	1614.0	1.0	0.606	0.369
.....					
Cliff + (Cliff) <sup>2</sup>	3	1658.4	45.4	0.0	0.0
Sqrt (Cliff)	2	1668.5	55.5	0.0	0.0
(Cliff) <sup>2</sup>	2	1656.9	43.9	0.0	0.0
Arcsin (Cliff)	2	1661.1	48.1	0.0	0.0
Cliff	2	1659.6	137.3	0.0	0.0
AFR + (AFR) <sup>2</sup> + (AFR) <sup>3</sup>	4	1733.0	120.0	0.0	0.0
AFR + (AFR) <sup>3</sup>	3	1735.8	122.8	0.0	0.0
AFR + (AFR) <sup>2</sup>	3	1734.5	121.5	0.0	0.0
AFR.cat	5	1733.3	120.3	0.0	0.0
AFR	2	1750.3	137.3	0.0	0.0

*Note.* Model selected in bold characters; Models contained above in italic character(s) are models that were not retained but that have some weight in explaining the biological process that gave rise to the data; we used a mixed model to add a random time effect ‘ $\epsilon$  (time)’ to the best performing glm; ‘+’ additive effect; ‘\*’ interaction; NP = number of estimated parameters; AIC: Akaike’s Information Criterion =  $-2*\log\text{-likelihood} + 2*NP$ ;  $W_i = \exp(-0.5*\Delta AIC) / \sum \exp(-0.5*\Delta AIC)$ . Covariates: Age at first reproduction (AFR if continuous, AFR.cat if categorical, AFR<sup>2</sup> for a quadratic effect, AFR<sup>3</sup> for a cubic effect); cliff quality (Cliff if continuous, Arcsin(Cliff) if arcsinus transformed, Sqrt(Cliff) if square root transformed, and Cliff<sup>2</sup> for a quadratic effect).

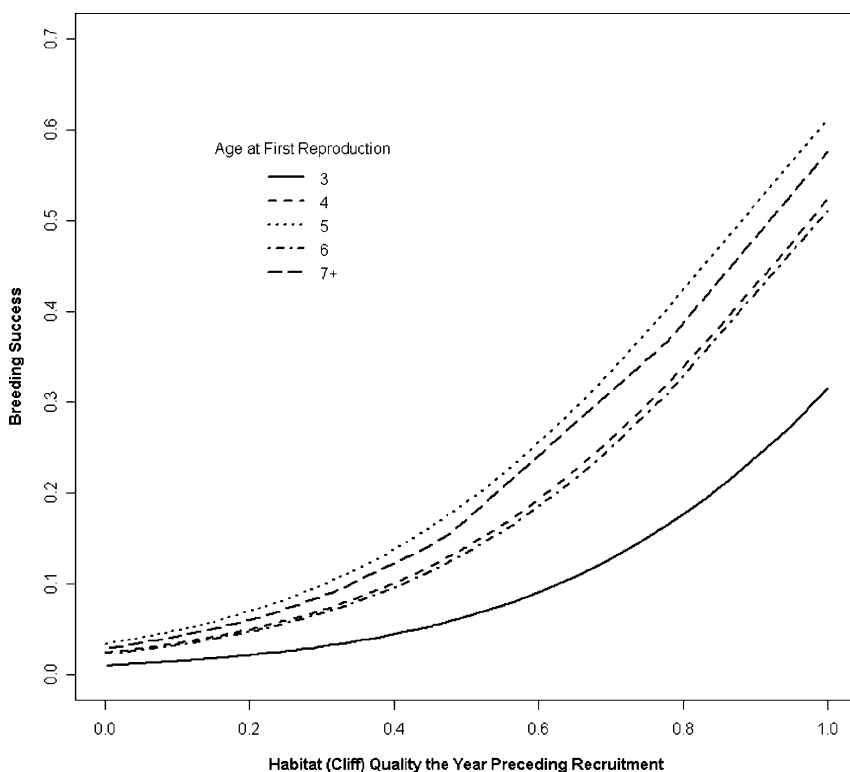
for individuals recruiting at an intermediate age of 5 years old (Fig. 3). By including a random effect of time in this model, the AIC dropped by 1 unit, down to the value of 1613, providing slight evidence of yearly variation in breeding success over time.

## 4 Discussion

In this paper, we first aimed at examining whether habitat selection and age at recruitment were linked, and if so, which recruits gained the best breeding habitats: early recruits or individuals delaying recruitment. We also examined which recruitment tactic led to the highest breeding success in the year of recruitment. Overall, this paper studies (1) recruitment-habitat selection, (2) when and where recruits breed for the first time, and (3) breeding success as a function of the location and the age at which individuals recruit.

### 4.1 The Timing of Habitat Selection, Habitat Quality and Age-Specific Recruitment

A number of investigators (Danchin 1988b; Danchin et al. 1991, 1998; Cadiou et al. 1994) have suggested that dispersers actively select their recruitment habitat the year preceding settlement (e.g. the number of prospectors in habitat patches



**Fig. 3** Breeding success the year of recruitment as a function of cliff quality the year preceding recruitment and age at first reproduction

depends on their current productivity; Cadiou 1993). Corroborating their hypothesis, we also observed that models including cliff quality the year preceding recruitment performed better in explaining the recruitment process than models including cliff quality the year of recruitment (Appendix 1; Table 1). Two *scenarii* can be proposed. Habitat selection may take place in the year of recruitment based on information available at the beginning of a breeding season on habitat quality (i.e. information based on social activity and attendance of individuals that bred in that patch the previous year and returned to the same breeding patch). Such information may be strongly autocorrelated to local productivity in the preceding year (Boulinier et al. 1996). However, young recruits (i.e. recruiting at 3 years old) might only benefit from an imperfect knowledge of cliff quality, as they arrive on average 2 months later than individuals delaying recruitment (based on direct observations). Alternatively, settlement decisions may be made the year preceding recruitment. This implies that pre-breeders prospect for a breeding ground at least a year in advance (Danchin et al. 1991). Both *scenarii* rely on the assumption that habitat quality in a given year  $t$  is a reliable indicator of its quality in year  $t+1$  (Boulinier and Lemel 1996).

If so, temporal autocorrelation in breeding success over 2 consecutive years in a given patch should allow pre-breeders to locate a higher-quality breeding location a breeding season in advance. Although we only considered habitat quality in the year of recruitment and the year preceding recruitment, recruitment probability may depend on past productivity over several consecutive years (with temporal autocorrelation of cliff quality being superior to a year).

In most age classes, recruitment probability in a given year (from 1986 to 2003) was highest in cliffs of intermediate quality the year preceding recruitment (with the exception of individuals recruiting at age 2, for which transition probabilities are not reliable as sample size is very small). According to habitat selection theory, if no constraints are operating (i.e., no competition, no dominance in social hierarchy, and if individuals have information on the range of habitats available), we might expect natural selection to favour habitat selection tactics that maximize fitness (Holt and Barfield 2001). That is, recruitment probability should be highest in the most productive cliffs, where the fitness prospects are maximal. Our results do not support this prediction, and therefore suggests the existence of constraints. High-quality cliffs may not be accessible to most recruits (i.e. the youngest). They may be constrained to breed in habitats where competition for nest-sites is lower. Our results also provided evidence that older first-time breeders recruit in habitats of lower quality than intermediate age individuals; therefore, the queuing hypothesis is unlikely to explain the pattern observed in these recruits. Features of individual quality relevant to habitat selection may involve differences in behavioural maturity, social and territorial dominance. These differences could be expressed in terms of the age at recruitment, whereby old recruits (i.e. of low intrinsic quality) can only afford to breed in low-quality patches because of competitive inferiority. However, in the case of young recruits, if they are sometimes assumed to be of high intrinsic quality (Nur 1988), we did not find evidence that this translates into access to higher-quality habitat, as they do have the advantage of an early breeding start, but still do not recruit on the best breeding-sites. These individuals may not be of lower intrinsic quality, they may simply lack competitive skills. Behavioral maturation may explain why individuals recruiting at intermediate age have access to higher-quality sites.

These results are valuable only if one assumes that recruits make an active selection of the habitat in which they will breed for the first time. One could imagine that individuals breed preferentially in intermediate quality cliffs because these are more abundant than other cliffs type (i.e. cliffs of low or high quality). However, our results suggest that we are observing the outcome of an individual choice involving active habitat selection rather than random settlement. Indeed, over all the years studied, the proportion of cliffs of intermediate quality was not larger than the proportion of cliffs of high or poor quality, as cliffs of low, high, and intermediate quality were equally available in the study area. In addition, we acknowledge that density dependant processes may influence settlement decisions. However, we believe that density dependance alone cannot explain the observed distribution of recruits according to habitat quality. Indeed, behavioural studies have provided evidence that creation of new nest-sites by pre-breeders is possible even in highly

productive patches, but that this option is not usually preferred by pre-breeders: they mostly compete for occupied sites (Cadiou 1993; Cadiou et al. 1994).

Both multi-state modeling approaches showed age-related variation in recruitment probability, with highest recruitment probabilities reached at intermediate ages (transition probability in between 5 and 6 years old). Yet, a non-negligible proportion of individuals recruited earlier (i.e. recruitment probability of 0.15 at age 3, and approximately 0.40 at age 4). Age-specific variation in recruitment probability, more specifically the initial increase in recruitment probability, may partly reflect the progressive acquisition of behavioural and physiological maturity of individuals in the population. Whether individuals delaying reproduction do so because they are not sexually mature, or because of a lack of behavioural maturity (in sexually mature individuals), is beyond the scope of this paper: physiological and behavioural data are required to address this question. However, within the framework of physiological and social constraints (e.g. competition), it is possible to address whether there is scope for natural selection processes to operate on age of first breeding by evaluating and comparing fitness components associated with each age-specific recruitment tactic. We addressed whether there was a relationship between each tactic and age-specific reproductive success in the recruitment year to determine which one(s) might yield highest breeding success levels.

## ***4.2 Breeding Success***

We found evidence that birds recruiting at intermediate ages (i.e. recruiting at age 5) experienced the highest reproductive success in the year of recruitment. These results complete our findings regarding age-specific recruitment probability, where again, the highest probability of recruitment was observed at that age. Based on these results, it is tempting to suggest that the age at first reproduction has been shaped by an optimization process. Under this view, recruiting around age 5 (i.e. delaying recruitment up to intermediate ages) would be associated with fitness advantages that offset the direct costs of delayed recruitment (i.e. costs such as 'missed' breeding opportunities in comparison with individuals recruiting earlier).

One of the predictions of life history theory is that early reproduction should be favoured by natural selection in stable or increasing populations (Stearns 1992; Charlesworth 1994), except in situations where delayed reproduction is beneficial in terms of fitness. A well-known case explicitly addressed by Charlesworth (1994) is when reproductive success increases with age, experience (or both). In this case, theory suggests that younger individuals may balance the potential benefits of recruiting early (e.g. more breeding events accumulated throughout life compared to recruits delaying first reproduction), with the cost of unsuccessful breeding attempts early in life (Charlesworth 1994), as the youngest recruits lack experience and have a higher probability of breeding failure than others. Also, the time spent prospecting for a site may provide benefits in terms of information gathered on a potential breeding site, despite the costs associated with missing breeding opportunities (Boulinier and Danchin 1997). Early recruitment in this population is indeed associated with low reproductive success in the year of recruitment. Behavioural

maturity and competitive abilities gained before breeding may explain why individuals recruiting at intermediate ages exhibit higher breeding success than early recruits (Nol and Smith 1987; Lunn et al. 1994).

Also, it has been suggested that heterogeneity in individual quality contributes to explain the age-specific variation in age at first breeding (Nur 1988; Curio 1983). According to this hypothesis, higher-quality individuals are assumed to be able to invest more into reproduction without incurring as large costs as lower-quality individuals; this may favour early investment into reproduction for higher-quality individuals. At this point, our results concerning breeding success probability are not consistent with this hypothesis. Overall, our results provided evidence that the youngest first-time breeders (the ones that theoretically are assumed to be of highest intrinsic quality: Nur 1988; Pyle et al. 1997), experienced the poorest breeding success probability in the recruitment year, compared to intermediate-age recruits, regardless of the quality of the recruitment habitat. However, it is possible that early recruits improve their breeding success as they age and gain experience; again, they may not be of lower intrinsic quality. Heterogeneity in quality among individuals may explain only partially our results: the decrease in recruitment probability in first-time breeders after age 5 (i.e. individuals delaying recruitment), and the fact that late breeders recruit in lower-quality habitat than birds recruiting at intermediate age. Social inferiority may prevent these individuals from beginning reproduction earlier in life. However, their breeding success probability in the year of recruitment is high: experience gained over a longer pre-breeding period may result in this pattern.

Attempting to explain the evolutionary (dis)advantages of early or delayed recruitment by addressing reproductive success in the first breeding attempt exclusively is too restrictive: first reproduction is only a snapshot of the lifetime profile of reproductive success for individuals recruiting at various ages in each habitat type. However, this first step was crucial in the understanding of the age-specific recruitment process and how it is related to habitat selection theory.

### ***4.3 Prospects***

Regarding habitat selection mechanisms, preliminary analysis conducted in the same study population (Aubry, unpublished; Bled 2006; Bled et al. in prep), suggests that it is critical to work at a much finer spatial scale to address recruitment; that is the nest-site itself, within a given cliff (e.g. it may be disadvantageous to gain ownership on a site of poor quality within the most productive cliff). Using an approach based on the quality of patches, there is no clear hierarchy among age classes in terms of access to habitat of lower, intermediate, or higher quality, but there is a relationship between habitat quality at the patch level and success probability in the year of recruitment. The shape of the relationship between age and success probability (which is highest in birds of intermediate age) cannot be explained by higher recruitment probability in higher-quality habitat: intermediate age first-time breeders do not recruit in higher-quality habitats than others (e.g. the interaction between age and quality was not retained in multi-state models with

individual covariates). Heterogeneity in quality among sites within habitat patches may obscure the relationship between habitat quality, age, and individual success probability. A more detailed study of habitat selection at the site level may help understand the observed influence of age on breeding success probability. In this mobile species exhibiting breeding dispersal (Danchin and Monnat 1992; Danchin et al. 1998), it may not be possible to fully understand age-specific variation in fitness components (e.g. variation over life) without considering features of the habitat where each reproductive event takes place. But the very high degree of stratification required by such analysis of age-specific reproductive success as a function of habitat quality may be a major obstacle, and further work is needed to assess whether it is feasible using this data set.

The study of reproductive success indicates that reproductive choices and/or the constraints met during the pre-reproductive stage of life may influence age at recruitment, which may in turn have substantial effects on breeding success over life. To address the overall fitness of recruitment tactics, one may consider measures of lifetime fitness such as Lifetime Reproductive Success (Clutton-Brock 1988), or individual lambda (McGraw and Caswell 1996). This would be a first step to assess whether different tactics are associated with a different total number of viable offspring, and if there is scope for natural selection to operate on age of first breeding in a different manner than understood on the basis of breeding success in the first breeding attempt exclusively. However, the same lifetime fitness may be achieved in very different ways in terms of longevity, age-specific reproductive investment, and choices in terms of habitat selection. As for further investigations, an interesting step to take would be to look over the life course of individuals recruiting at different ages (i.e., recruitment tactics), and determine whether breeding success improves, shows senescent decline, or remains the same across ages for the different recruitment tactics identified above. Our results provided evidence that early recruits (i.e. 3 years old) start their reproductive life with a handicap, as their initial breeding success probability is the lowest (Fig. 3). It would be worth addressing whether recruits experiencing poor breeding success in the year of recruitment catch up and perform increasingly better throughout life. One may also assess whether individuals recruiting at intermediate ages (i.e. recruits of 5 years old which show the highest reproductive success in the recruitment year), are the ones performing best overall (i.e. highest fitness prospects). Last, one may determine if recruiting beyond this age leads to the lowest fitness prospects or not. Assessing fitness differences among reproductive tactics and determining the selective advantages of adopting one tactic or the other will require additional work (e.g. Evolutionary Stable Strategy modeling; Maynard Smith 1982).

Moreover, our work suggests that there may be a substantial level of individual heterogeneity in the study population (i.e. variation in age-specific recruitment tactics leading to variation in reproductive success), and highlights the need to develop multi-state models for estimating transition probabilities while properly accounting for unobserved heterogeneity in reproduction (and in survival) in cases where recapture probability is lower than 1. Multi-state CMR models allowed us to address the influence of observable covariates on recruitment

probability, but measurable covariates may not account for heterogeneity in a satisfying manner. Heterogeneity in survival (e.g. frailty) has been looked at in human demography starting some 20 years ago (Vaupel and Yashin 1985), and ecologists have long been concerned with heterogeneity as well (e.g. Burnham and Rexstad 1993; Pledger and Schwarz 2002). However, developments regarding heterogeneity in both survival and reproductive success in wild animal population are only fairly recent (Burnham and Rexstad 1993; Cam et al. 2002b; Pledger and Schwarz 2002; Barbraud and Weimerskirch 2005; Crespin et al. 2006; Gordon et al. 2006; Royle 2008), and require additional efforts.

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# Appendix 1

**Table 5** Multi-state model pertaining to various biological hypothesis underlying the recruitment process, while accounting for potential sources of variation in recapture and survival probabilities

Model	Recapture probability	Survival probability	Transition probability
2-state-model-1	$p1(a7), p2(.)$	$S1(c12 + a6), S2(.)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-1-bis	$p1(a7), p2(.)$	$S1(c12 + a6), S2(.)$	$\Psi12(c12 + a6), \Psi21(.)$
2-state-model-2	$p1(c), p2(.)$	$S1(c12 + a7), S2(a5)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-3	$p1(a6), p2(.)$	$S1(c12 + a7), S2(a5)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-4	$p1(a5), p2(.)$	$S1(c12 + a7), S2(a5)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-5	$p1(a4), p2(.)$	$S1(c12 + a7), S2(a5)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-6	$p1(a3), p2(.)$	$S1(c12 + a7), S2(a5)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-7	$p1(a4), p2(.)$	$S1(c12 + a7), S2(.)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-8	$p1(a4), p2(.)$	$S1(c12 + a7), S2(.)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-9	$p1(a4), p2(.)$	$S1(c12), S2(.)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-10	$p1(a4), p2(.)$	$S1(a7), S2(c)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-11	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-12	$p1(a4), p2(.)$	$S1(c12 + a5), S2(c)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-13	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a6 + q1 + q1c), \Psi21(.)$
2-state-model-14	$p1(a4), p2(.)$	$S1(c12 + a7), S2(a5)$	$\Psi12(a6 + q1 + q1c), \Psi21(.)$
2-state-model-15	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a6 + q1), \Psi21(.)$
2-state-model-16	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a6 + q1 + q1c + (a6^*q1)), \Psi21(.)$
2-state-model-17	$p1(a4), p2(.)$	$S1(c), S2(c)$	$\Psi12(c12 + q1 + q1c), \Psi21(.)$
2-state-model-18	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a5 + q1 + q1c), \Psi21(.)$
<b>2-state-model-19*</b>	<b><math>p1(a4), p2(.)</math></b>	<b><math>S1(c12 + a6), S2(c)</math></b>	<b><math>\Psi12(c12 + a6 + q2 + q2c), \Psi21(c)</math></b>
2-state-model-20	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(a6 + q2 + q2c), \Psi21(c)$
2-state-model-21	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a6 + q2), \Psi21(c)$
2-state-model-22	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a6 + q2c), \Psi21(c)$
2-state-model-23	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + q2 + q2c), \Psi21(c)$
2-state-model-24	$p1(a4), p2(.)$	$S1(c12 + a6), S2(c)$	$\Psi12(c12 + a5 + q2 + q2c), \Psi21(c)$

**2-state-model-19\***: Model selected based on AIC weight –  $w_i = 0.99$  (see Table 3).

## Appendix 2

**Table 6** Multi-state models based on biological hypotheses pertaining to the recruitment process (second approach without covariates, see Methods) various while accounting for potential sources of variation in recapture and survival probabilities

Model	Recapture probability	Survival probability	Transition probability
4-state-model-1	$p1(a7), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a5), S3(a5), S4(a5)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-2	$p1(c), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a5), S3(a5), S4(a5)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-3	$p1(a6), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a5), S3(a5), S4(a5)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-4	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a5), S3(a5), S4(a5)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-5	$p1(a4), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a5), S3(a5), S4(a5)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-6	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a5), S3(a5), S4(a5)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-7	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a4), S3(a4), S4(a4)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-8	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-9	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a7), S2(a2), S3(a2), S4(a2)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-10	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-11	$p1(a5), p2(c), p3(c), p4(c)$	$S1(a7), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-12	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a6), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-13	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-14	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a5), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-15	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a4), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-16	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a6), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a7), \Psi13(c12+a7), \Psi14(c12+a7)$
4-state-model-17	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a6), S2(a3), S3(a3), S4(a3)$	$[\Psi12(c12+a7), \Psi13(c12+a6), \Psi14(c12+a7)]$
4-state-model-18	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a6), S2(a3), S3(a3), S4(a3)$	$\Psi12(c), \Psi13(c), \Psi14(c)$
4-state-model-19	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a6), S2(a3), S3(a3), S4(a3)$	$\Psi12(a7), \Psi13(a7), \Psi14(a7)$
4-state-model-20	$p1(a5), p2(c), p3(c), p4(c)$	$S1(c12+a6), S2(a3), S3(a3), S4(a3)$	$\Psi12(c12+a6), \Psi13(c12+a6), \Psi14(c12+a6)$
<b>4-state-model-21*</b>	<b><math>p1(a5) [ p2(c), p3(c), p4(c) ]</math></b>	<b><math>S1(c12+a6) [ S2(a3) S3(a3) S4(a3) ]</math></b>	<b><math>\Psi13(c12+a6) \Psi13(c12+a6) \Psi14(c12+a6)</math></b>

**4-state-model-21\***: Model selected based on AIC weight -  $w_i = 0.99$  (see Table 3).

## References

- Agresti A (1990) *Categorical data analysis*. John Wiley and Sons, New York.
- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In Petron BN, Csaki F (eds.) *International Symposium on Information Theory*, 2nd edition, pp 267–281. Akademiai Kiado, Budapest, Hungary.
- Arnason AN (1973) The estimation of population size, migration rates, and survival in stratified populations. *Research on Population Ecology* 15:1–8.
- Barbraud C, Weimerskirch H (2005) Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* 86, 3:682–692.
- Bled F (2006) *Selection de l'habitat de reproduction au sein de la falaise chez un oiseau marin longévif: Rissa tridactyla*. Master 2 Biodiversité Ecologie Evolution. Université Paul Sabatier, Toulouse, France.
- Boulinier T, Lemel JY (1996) Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection. *Acta Oecologica* 17:531–552.
- Boulinier T, Danchin E, Monnat J-Y, Doutrelant C, Cadiou B (1996) Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology* 27:252–256.
- Boulinier T, Danchin E (1997) The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evolutionary Ecology* 11:505–517.
- Brownie C, Hines JE, Nichols JD, Pollock KH, Hestbeck JB (1993) Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- Burnham KP, Rexstad E (1993) Modeling heterogeneity in survival rates of banded waterfowl. *Biometrics* 49:1194–1208.
- Burnham KP, Anderson DR (1998) *Model selection and inference, a practical information-theoretic approach*. Springer-Verlag, New York.
- Cadiou B (1993) *L'accession à la reproduction: un processus social d'ontogenèse. Cas de la mouette tridactyle (Rissa tridactyla)*. Thèse. Université de Rennes I.
- Cadiou B (1999) Attendance of breeders and prospectors reflects the quality of colonies in the kittiwake *Rissa tridactyla*. *IBIS* 141:321–326.
- Cadiou B, Monnat JY, Danchin E (1994) Prospecting in the kittiwake, *Rissa tridactyla*: different behavioural patterns and the role of squatting in recruitment. *Animal Behaviour* 47:847–856.
- Cam E, Monnat JY (2000a) Apparent inferiority in first time breeders in the kittiwake: the role of heterogeneity among age-classes. *Journal of Animal Ecology* 69:380–394.
- Cam E, Hines JE, Monnat JY, Nichols JD, Danchin E (1998) Are adult non breeders prudent parents? The Kittiwake model. *Ecology* 79:2917–2930.
- Cam E, Link WA, Cooch EG, Monnat JY, Danchin E (2002b) Individual covariation between life-history traits: seeing the trees despite the forest. *American Naturalist* 159:96–105.
- Cam E, Monnat JY, Hines JE (2003) Long term fitness consequences of early conditions in the kittiwake. *Journal of Animal Ecology* 72:411–424.
- Cam E, Monnat JY, Royle JA (2004a) Dispersal and individual quality in a long-lived species. *OIKOS* 106:386–398.
- Cam E, Cooch E, Monnat JY (2005) Earlier recruitment or earlier death? On the assumption of homogeneous survival in recruitment studies. *Ecological Monographs* 75:419–434.
- Caswell H, Hastings A (1980) Fecundity, developmental time, and population growth rate: an analytical solution. *Theoretical Population Biology* 17:71–79.
- Charlesworth B (1994) *Evolution in age-structured populations*. 2nd Edition. Cambridge University Press, Cambridge, UK.
- Clutton-Brock TH (1988) *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. The University of Chicago Press, Chicago.
- Cooch EG, White GC (2006) *Mark book*: <http://www.phidot.org/software/mark/docs/book/>.
- Cooch EG, Lank DB, Rockwell RF, Cooke F (1999) Body size and recruitment in snow geese. *Bird Study* 46:112–119.

- Crespin L, Harris MP, Lebreton J-D, Frederiksen M, Wanless S (2006) Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology* 75:228–238.
- Curio E (1983) Why do young birds reproduce less well? *IBIS* 125:400–404.
- Danchin E (1987a) The behaviour associated with the occupation of the breeding site in the kittiwake gull *Rissa tridactyla*: the social status of landing birds. *Animal Behaviour* 35:81–93.
- Danchin E (1988b) Role of behavioural processes in the mechanisms of population regulation in colonial seabirds: Case of the Kittiwake (*Rissa tridactyla*). Thèse d'Etat, Université Paris VI, France.
- Danchin E, Monnat JY (1992) Population dynamic modeling of two neighboring kittiwake *Rissa tridactyla* colonies. *Ardea* 80:171–180.
- Danchin E, Cadiou B, Monnat JY, Rodríguez Estrella R (1991) Recruitment in long lived birds: conceptual framework and behavioral mechanisms. *Proceedings of the International Ornithology Congress* 20:1641–1656.
- Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79:2415–2428.
- Ens JB, Weissing FJ, Drent R (1995) The despotic distribution and deferred maturity: two sides of the same coin. *The American Naturalist* 146:625–650.
- Fretwell S, Lucas HJ (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:1636.
- Gordon AF, Kendall BR, Fitzpatrick JW, Woolfenden GE (2006) Consequences of heterogeneity in survival probability in a population of Florida scrub-jays. *Journal of Animal Ecology* 75: 921–927.
- Hines JE (1994) MSSURVIV User's Manual. National Biological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708 USGS-PWRC. Available at: <http://www.mbr-pwrc.usgs.gov/Software.html>.
- Holt RD, Barfield M (2001) On the relationship between the ideal free distribution and the evolution of dispersal. In Clobert J, Danchin E, Dhondt A and Nichols JD (eds) *Dispersal*, pp 83–95. Oxford University Press, Oxford, UK.
- Lebreton JD, Pradel R (2002) Multistate recapture models: modeling incomplete individual histories. In Morgan BJT and Thomson DL (eds) *Statistical Analysis of Data from Marked Bird Population*. *Journal of Applied Statistics* 29:353–369.
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lebreton JD, Hines JE, Pradel R, Nichols JD, Spendelov JA (2003) Estimation by capture-recapture of recruitment and dispersal over several sites. *OIKOS* 101:253.
- Lunn NJ, Boyd IL, Croxall JP (1994) Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology* 63:827–840.
- Maynard Smith J (1982) *Evolution and the Theory of Games*, 224 pp. Cambridge University Press, Cambridge.
- McGraw JB, Caswell H (1996) Estimation of individual fitness from life-history data. *The American Naturalist* 147(1):47–64.
- Monnat JY, Danchin E, Rogriguez Estrella R (1990) Evaluation de la qualité du milieu dans le cadre de la prospection et du recrutement : le squattérisme chez la mouette tridactyle. *Comptes rendus de l'Académie des sciences, Paris, Série* 311:391–396.
- Neter M, Kutner H, Nachtsheim C, Wasserman W (1996) *Applied Linear Statistical Models*, 4th edition, 1408 pp. Irwin, Chicago.
- Nichols JD (1996) Sources of variation in migratory movements of animal populations: statistical inference and selective review of empirical results for birds. In Rhodes OE, Chesser RK, Smith MH (eds) *Population Dynamics in Ecological Space and Time*, pp 147–149. University of Chicago Press, Chicago.

- Nichols JD, Kendall WL (1995) The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* 22:835–840.
- Nichols JD, Brownie C, Hines JE, Pollock KH, Hestbeck JB (1992) The estimation of exchanges among populations or subpopulations. In Lebreton JD, North PM (eds) *Mark Individuals in the Study of Bird Populations*, pp 265–280. Birkhauser-Verlag, Basel, Switzerland.
- Nichols JD, Brownie C, Hines JE, Pollock KH, Hestbeck JB (1993) The estimation of exchanges among populations or subpopulations. In Lebreton JD and North PM (eds) *The Use of Marked Individuals in the Study of Bird Population Dynamics: Models, Methods, and Software*, pp 265–279. Birkhauser Verlag, Berlin, Germany.
- Nol E, Smith JNM (1987) Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology* 56:301–313.
- Nur N (1984) Increased reproductive success with age in the Californian gull: due to an increased effort or improvement of skill? *OIKOS* 43:407–408.
- Nur N (1988) The consequences of brood size for breeding blue tits. . Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. *Evolution* 42(2):351–362.
- Pickering SPC (1989) Attendance patterns and behaviour in relation to the experience and pair-bond formation in the wandering albatross *Diomedea exulans* at South Georgia. *IBIS* 131: 183–195.
- Pledger S, Schwarz CJ (2002) Modeling heterogeneity of survival as a random effect using finite mixtures. *Journal of Applied Statistics* 29 (Special Issue):315–327.
- Porter JM (1988) Prerequisites of recruitment of kittiwakes *Rissa tridactyla*. *IBIS* 130:204–215.
- Pradel R, Lebreton JD (1999) Comparison of different approaches to the study of local recruitment of breeders. *Bird Study* 46:74–81.
- Pradel R, Hines JE, Lebreton JD, Nichols JD (1997) Capture–recapture survival models taking account of transients. *Biometrics* 53(1):60–72.
- Pyle P, Nur N, Sydeman WJ, Emslie SD (1997) Cost of reproduction and the evolution of deferred breeding in the western gull. *Behavioral Ecology* 8(2):140–147.
- Royle JA (2008) Modeling individual effects in the Cormack–Jolly–Seber model: a state-space formulation. *Biometrics* In press.
- Sakamoto Y, Ishiguro M, Kitagawa G (1986) *Akaike Information Criterion Statistics*. KTK Scientific Publishers, Tokyo.
- Schwarz CJ, Schweigert JF, Arnason AN (1993) Estimating migration rates using tag-recovery data. *Biometrics* 49:177–193.
- Stearns SC (1992) *The Evolution of Life Histories*. Oxford University Press, New York.
- Tuljapurkar S (1990) Delayed Reproduction and Fitness in Variable Environments. *Proceedings of the National Academy of Sciences* 87:1139–1143.
- Vaupel JW, Yashin AI (1985) Heterogeneity's ruses: some surprising effects of selection on population dynamics. *American Statistician* 39:176–185.
- Viallefont A, Cooke F, Lebreton JD (1995) Age specific cost of first time breeding. *The Auk* 112(1):67–76.
- White GC, Burnham KP (1999) Program MARK – survival estimation from populations of marked animals. *Bird Study* 46:120–139. Available at: <http://www.cnr.colostate.edu/gwhite/mark/mark.htm>.
- Wiley RH, Rabenold KN (1984) The evolution of cooperative breeding by delayed reciprocity and queuing for favourable positions. *Evolution* 38:609–621.