

# Influence of behavioural tactics on recruitment and reproductive trajectory in the kittiwake

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**ABSTRACT** Many studies have provided evidence that, in birds, inexperienced breeders have a lower probability of breeding successfully. This is often explained by lack of skills and knowledge, and sometimes late laying dates in the first breeding attempt. There is growing evidence that in many species with deferred reproduction, some prebreeders attend breeding places, acquire territories and form pairs. Several behavioural tactics assumed to be associated with territory acquisition have been described in different species. These tactics may influence the probability of recruiting in the breeding segment of the population, age of first breeding, and reproductive success in the first breeding attempt. Here we addressed the influence of behaviour ('squatting') during the prebreeding period on demographic parameters (survival and recruitment probability) in a long-lived colonial seabird species: the kittiwake. We also investigated the influence of behaviour on reproductive trajectory. Squatters have a higher survival and recruitment probability, and a higher probability of breeding successfully in the first breeding attempt in all age-classes where this category is represented. The influence of behaviour is mainly expressed in the first reproduction. However, there is a relationship between breeding success in the first occasion and subsequent occasions. The influence of breeding success in the first breeding attempt on the rest of the trajectory may indirectly reflect the influence of behaviour on breeding success in the first occasion. The shape of the reproductive trajectory is influenced by behaviour and age of first breeding. There is substantial individual variation from the

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*mean reproductive trajectory, which is accounted for by heterogeneity in performance among individuals in the first attempt, but there is no evidence of individual heterogeneity in the rate of change over time in performance in subsequent breeding occasions*

## 1 Introduction

In species with deferred reproduction, there is growing evidence that activities of individuals during the prebreeding period of life play an important part in selection of a breeding site, territory acquisition, as well as behavioural and social maturation (e.g. Nelson, 1983, 1988; Klomp & Furness, 1990; 1991; Danchin *et al.*, 1991; Cadiou *et al.*, 1994). Different behavioural tactics used by individuals to choose the breeding habitat as a function of its quality, and to acquire a breeding site have been identified (e.g. queuing, floating, sneaking; Zack & Stutchbury, 1992; Ens *et al.*, 1995; Kokko & Sutherland, 1998; Pen & Weissing, 2000). Prebreeders may compete directly with the owners of a territory and attempt to evict them, they may queue until a specific territory becomes available, or establish on any site that becomes available. In this framework, many factors are assumed to play a part in the decision regarding the choice of a tactic, and ultimately in the evolution of these tactics: e.g. the probability of dying before acquiring a territory, individual quality and its influence on competitive ability, the relationship between habitat quality and breeding performance, temporal variation in habitat quality, the probability that a territory becomes available, the number of individuals in a queue. The tactic used is likely to influence age of recruitment, which highlights the relationship with the question of the evolution of deferred breeding. Ens *et al.* (1995) have suggested that the questions of 'when' and 'where' to breed are 'two sides of the same coin'. Lastly, the selective pressures shaping age of first breeding are likely multiple, and the relationships between life-history traits before, and during, reproductive life also have to be considered (Stearns, 1992; Charlesworth, 1994).

One of the difficulties in gaining insight into the selective pressures playing a part in the evolution of these tactics is that individuals in the prebreeding segment of populations are usually more difficult to observe than breeders (Pradel & Lebreton, 1999): little is known about the demographic features of prebreeders. Assessing the influence of behaviour on survival and recruitment probability requires use of capture-recapture models permitting distinction between rates specific to behavioural categories, given that individuals can change category between years (Nichols & Kendall, 1995). Here we addressed the influence of behaviour during the prebreeding period on demographic rates (survival and recruitment probabilities) in a long-lived colonial cliff-nesting seabird species, the kittiwake (*Rissa tridactyla*). Several studies have reported the presence of prebreeders in breeding colonies in this species; some prebreeders were involved in initial stages of the breeding process (i.e. acquisition of a breeding site, pair formation, and nest construction). Detailed behavioural observations have permitted identification of a particular category of prebreeders: squatters (Danchin, 1987; Monnat *et al.*, 1990; Cadiou, 1993; Cadiou *et al.*, 1994; Cadiou & Monnat, 1996).

Squatters are prebreeders or individuals that previously bred. Here we used this terminology for prebreeders resighted on active nests only (i.e. with chicks) whose owners are temporarily absent ('squatters on chicks'; Cadiou *et al.*, 1994). Territorial displays are often observed in squatters, as well as sexual and coordination behaviour involved in pair formation (e.g. Cadiou *et al.*, 1994). Squatters sometimes aggress the chicks or exhibit nest construction behaviour and put

material on their back. Cadiou (1993) has shown that squatters arrive earlier to breeding colonies in the year of recruitment, and thus have more time at the start of the breeding season for coordination stages with their mate. In addition, they have a higher probability of forming pairs with more experienced individuals than non-squatters, which may also be linked to an earlier arrival date.

The interpretation of squatting is complex. First, this behaviour is assumed to play a part in territory acquisition in both prebreeders and failed breeders (Cadiou, 1993, 1999; Cadiou *et al.*, 1994). Squatting prebreeders rarely establish on squatted sites if the owners survive to the following breeding season (they rarely become dominant on these sites and evict owners), but they often do so on a site located close to the squatted sites (Cadiou, 1993). Neighbours often aggress squatters while the owners of the squatted site are absent. Squatting is thought to be part of a process leading to dominance on a site, familiarity with a group of individuals and insertion into a web of social relationships among individuals breeding in dense colonies (Cadiou, 1993). This activity is also thought to play a part in behavioural ontogeny and acquisition of skills specifically related to reproduction (Cadiou, 1993).

We investigated the influence of behaviour and age on the probability that individuals recruit into the breeding segment of the population in the following year. Preliminary results have indicated that squatters have a higher probability of breeding in the next breeding season if they survive than non-squatters. These results are based on observed proportions of individuals that previously were squatters or non-squatters, which returned and were observed in the study area. The recapture probability of breeders is very close to 1 (Cam *et al.*, 1998), which makes inference about the influence of behaviour in the group of individuals that survived and recruited valid. However, the recapture rate of prebreeders is not close to 1 (see results). Consequently, investigation of the influence of behaviour during the prebreeding period on recruitment probability (given that individuals survived) requires incorporation of recapture probability. We also addressed the question of the influence of behaviour and age on survival using the same approach.

The rate of attendance of squatters in breeding colonies is high, which may be associated with energetic stress (as they do not devote this time to foraging). Squatters are frequently involved in fights, which may cause injuries. This may carry costs in terms of survival. In contrast, it has been suggested that individuals adopting offensive tactics (i.e. squatters in this case) may be higher-quality individuals. In this view, we may expect that squatters have a higher survival probability than non-squatters. Lastly, if squatting reflects the degree of 'motivation' of individuals for recruitment into one of the colonies where they were observed, we may expect a higher local survival rate in this category. This hypothesis is based on the idea that non-squatters have a higher probability of dispersing permanently out of the study area.

The second set of questions we addressed concerns the influence of behaviour during the prebreeding period on breeding parameters throughout reproductive life, thereafter referred to as 'individual reproductive trajectory' (i.e. variation in breeding performance as a function of time elapsed since the first breeding attempt). If squatting leads to acquisition of skills and insertion into a local social web before recruitment, we might expect that individuals that previously were squatters perform better than others in the first breeding attempt. This may, or may not hold for the entire breeding trajectory. Individuals that were squatters may perform better throughout the entire reproductive life; in this case a possible

interpretation is that squatting reflects individual quality. Conversely, squatting may be associated with an initial advantage only, which may fade rapidly as all individuals bred and gained the skills underlying the idea of 'experience'.

Assessing differences in fitness components among individuals in populations can be difficult: measurable individual characteristics (e.g. behavioural category, age, etc) may not reflect heterogeneity in a satisfactory manner (Schoenberg, 1985; Trussell & Richards, 1985). This issue has received considerable attention in studies based on longitudinal data (Verbeke & Molenberghs, 2000): differences in the shape of individual trajectories not accounted for by measurable covariates may obscure the phenomenon of interest. Incorporation of individual heterogeneity into models has become a standard approach in studies addressing individual trajectories in many areas of research ('biomedical, educational, pharmacological, psychological, and sociological studies', Morrel, 1998; see also Schoenberg, 1985, Bryk & Raudenbush, 1992; Hedeker & Gibbons, 1994; Dupuis Sammel & Ryan, 1996; Steel, 1996; Weiss *et al.*, 1997). This has been achieved by developing statistical inference approaches based on random effects (Searle *et al.*, 1992), sometimes called 'latent random variables' (Schoenberg, 1985; Dupuis Sammel & Ryan, 1996; Spiegelhalter *et al.*, 1996). Referring to frailty models (i.e. models incorporating individual heterogeneity in survival; Manton *et al.*, 1986; Hedeker *et al.* 2000), Lebreton (1995) described models with random individual effects as models with 'an individual covariate of unknown value' (see also Cooch *et al.* and Pledger & Schwarz, this issue).

The most common objectives when incorporating random individual effects are to address the possible covariance between observations from the same individual, or to investigate individual variation from the average population pattern (Bryk & Raudenbush, 1992; Verbeke & Molenberghs, 2000). According to Chan & Kuk (1997), 'incorporation of random effects to models is useful in accounting for population heterogeneity, overdispersion, and intracluster correlation'. This type of approach is based on assessment of the distribution of the unobservable latent response variable (where 'latent' reflects the fact that one addresses 'unobserved realizations of an underlying random variable'; Steele, 1996). Models with random individual effects permit investigation of deviation of 'subject-specific' responses about the response assessed at the level of the 'overall population' (Verbeke & Molenberghs, 2000) (i.e. 'subject-specific inference as opposed to population-averaged inference'; Chan & Kuk, 1997). These underlying individual characteristics are not observable or measurable and are sometimes called 'true ability' (e.g. Bryk & Raudenbush, 1992). Here, they can be viewed as variables describing underlying individual quality. We used this approach to investigate the influence of behavioural tactic on individual trajectories.

## 2 Methods

### 2.1 Data collection

Data were collected from 1987 to 1999 in Brittany, France (Danchin & Monnat, 1992; Cam *et al.*, 1998; Danchin *et al.*, 1998). Each year chicks were marked before fledging using a unique combination of colour bands. Detailed behavioural data were collected from April to August. The frequency of field sessions increased from twice a week to daily observations in summer. Observations from each individual were summarized in order to identify its yearly breeding status. Breeding

states are: prebreeder (individuals that never previously bred and that are not breeding in the current year), breeder, and non-breeder (individuals that previously bred but are not breeding in the current year). Breeders are individuals that built a nest that reached the completion criterion (Maunder & Threlfall, 1972). Successful breeders raised at least one chick to independence, and failed breeders built a nest that reached the completion criterion but that failed to raise any chick to independence.

The recapture probability of breeders and non-breeders is very close to one (Cam *et al.*, 1998). This permits determination of age of first reproduction: it is the age of first observation as a breeder in one of the colonies. We recognize, however, that recruitment into another population outside Brittany (e.g. the British Isles or Spain) before recruitment in Brittany is possible, but probably unlikely. The majority of prebreeders attend colonies in the year(s) before recruitment and it is unlikely that birds breeding in colonies located hundreds of kilometres from Brittany are also so frequently observed in colonies in Brittany. However, in a few cases, individuals were not resighted at all before recruitment, or were resighted very late in the breeding season preceding local recruitment, possibly after attempting to breed outside Brittany and failing that breeding attempt.

A specific monitoring programme whose objective was to study squatting started in 1989. This permitted specification of a set of behavioural codes systematically used during subsequent observation sessions. The yearly individual behavioural state of prebreeders (squatter versus non-squatter) was determined during the chick-rearing period. Here we used behavioural data from prebreeders only, as the main focus was on recruitment. In addition, we restricted the definition of 'squatters' to individuals resighted on unattended nests built by other individuals and which were active at the time of observation (i.e. contained chicks). We selected data from birds marked from 1987 to 1999. Individuals born in 1987 were 2 years old in 1989, which is the minimum age at which squatting has been observed (1-year-old kittiwakes are physically different from older individuals in terms of plumage, and are physiologically immature).

## 2.2 Biological hypotheses and approach to modelling

*2.2.1 Influence of squatting on survival in prebreeders and recruitment probability.* We used multistate capture-recapture models (e.g. Nichols & Kendall, 1995) to address the influence of squatting on survival in prebreeders and recruitment probability. Analyses were performed using program MSSURVIV (Hines, 1994), with data from 4075 birds. Difficulties in fitting models with a large number of parameters played an important part in specification of the initial model. We sought a model in which every parameter and the corresponding standard error were estimated. In this step, we focused on prebreeding stages and ignored differences in yearly state in individuals that bred at least once (i.e. non-breeding, and reproductive performance in breeders). Recapture, survival, and transition probabilities varied according to state: two categories of prebreeders (squatters and non-squatters), and 'adults' (which we define as recruits or individuals that bred at least once). Although previous studies have shown that breeding state influences survival and transition probability to reproduction in the following year in 'adults' (breeding activity and performance, Cam *et al.*, 1998; Cam & Monnat, 2000a,b), sample sizes were too small when stratifying the data according to year, age, behavioural tactic and breeding activity and success in order to estimate all the survival and

transition probabilities. We did not consider the influence of time on parameters, although models would have been biologically more realistic if this factor had been incorporated. However, the low recapture probability of the youngest prebreeders (see results) prevented us from considering year specificity. Lastly, as the study of behaviour started in 1989, we selected data from only some cohorts (marked in 1987 or later). Inference about the effect of time and age would necessarily be restricted to combinations of age-classes and years represented in the data set. Because first breeding occurs relatively late in some individuals (6 years old or more), we believe that data collection should be continued for several additional years before addressing this question.

Parameters were age-specific in initial models. Because of the main focus on recruitment, we considered age-classes represented in prebreeders: from 0 to 6 years or higher (owing to small sample sizes, we pooled data from prebreeders older than 6). Other models allowed age-specificity in parameters corresponding to 'adults', but this is beyond the scope of this paper (Cam & Monnat, 2000b). The initial model with three states, seven age-classes and 13 occasions included 972 parameters. Some of these parameters were fixed to 0, e.g. transition probabilities corresponding to impossible successions of states, such as transition from adult to prebreeder, or survival and recapture probabilities corresponding to strata progressively appearing as individuals age and thus not represented in younger age-classes (e.g. no breeder was released at age 0).

*2.2.2 Influence of squatting on reproductive trajectory.* To account for a possible difference between the influence of squatting on reproduction in the first and subsequent breeding attempts, we used 'hockey stick' models (Littell *et al.*, 1996) to describe individual trajectory. These models include two 'intercepts' corresponding to the initial state (i.e. success or failure) at first reproduction, a possible 'jump' between the first and the second breeding occasions ('second intercept'), and a linear influence of time elapsed since the second occasion on breeding performance. The second part of the individual trajectory is usually longer than the first, which gives the shape of a 'hockey stick' to most individual trajectories (i.e. a short 'initial' segment, and then a longer one; see Littell *et al.*, 1996, p. 421 for illustrations).

We analysed individual reproductive trajectories using random-coefficients models. In these models, each individual is assumed to have 'its own initial state' at first reproduction (the probability of an initial breeding performance of a given level), 'its own state' at breeding occasion 2 (performance in the occasion following the first breeding attempt), and 'its own slope' for the influence of time elapsed since the occasion 2 on reproductive performance. Importantly, comparisons between models with and without individual random effects address individual heterogeneity in the dependent variable. Hence, inference about 'underlying' differences among individuals was based on evidence that incorporation of such effects was needed, or not, to account for the process that gave rise to the data. In addition, we designed models where individual effects were correlated. This permits investigation of the relationship between initial state, state in occasion 2, and the rate of variation of breeding performance in subsequent occasions. This approach has been used in studies of development to address the relationship between initial 'ability' and subsequent rate of development (e.g. Bryk & Raudenbush, 1992). In situations where the response variable has an upper limit (e.g. a probability), improvement is possible only in cases where the probability of a higher-level initial performance is low. The idea that there is a relationship between initial state and

the shape of subsequent breeding trajectory may thus seem obvious. However, it is possible to envision situations where performance remains low in individuals with lower initial state, and high in individuals with higher initial state.

We addressed the influence of behaviour in prebreeding stages on breeding performance in the first attempt and in subsequent breeding trajectory using the software program MIXOR (Hedeker & Gibbons, 1996). Performance was modelled using ordinal complementary log-log models (Agresti, 1990). This link function considerably reduced the time needed to run models and led to results similar to those obtained using logit models. The dependent variable had three modalities: breeding failure; one chick raised to independence; two or more chicks raised to independence. There were  $i = 1 \dots N$  individuals ('subjects', or 'level-2 observations'; Hedeker & Gibbons, 1996) and  $j = 1 \dots n_i$  repeated observations per individual ('level-1 observations', nested within each level-2 unit; Hedeker & Gibbons, 1996). Let  $y_{ij}$  be the observation associated with level-2 unit and level-1 unit  $j$ . Latent, unobservable responses,  $y_{ij}$ , were modelled as follows. The initial model included three random effects: (I) an initial intercept corresponding to initial state at first reproduction ( $a_i^*$  in equation (2)), (II) a variable distinguishing the first breeding occasion from subsequent occasions ( $d_i^*$  in equation (2)) (which can account for a 'jump' upward or downward in performance between attempts 1 and 2), (III) a modified measure of 'experience' (with a slope parameter  $b_i^*$  in equation (2)) equal to the number of breeding occasions since occasion 2. In the initial model, the three random effects were correlated. For the simple case where there is only one fixed effect (behaviour, a dummy variable 'SQ'), the model can be expressed as (see Verbeke & Molenberghs, 2000):

$$y_{ij} = a_i + (d_i + \lambda_2 SQ_i) t_{ij} + (b_i + \lambda_3 SQ_i) t'_{ij} + \lambda_1 SQ_i + \varepsilon_{ij} \tag{1}$$

where  $a_i$ ,  $d_i$  and  $b_i$ , are assumed to be normally distributed, with means  $\alpha$ ,  $\delta$  and  $\beta$  respectively, and covariance matrix  $\Omega$ .  $\varepsilon_{ij}$  are the model residuals; they are assumed to be normally distributed, but independent, with mean 0 and variance  $\sigma^2$ .  $t_{ij}$  is equal to 0 at first reproduction, 1 otherwise. This term forms the basis for the 'hockey stick' structure, that is, the initial 'jump' in performance between occasions 1 and 2 (the shorter segment of the reproductive trajectory).  $t'_{ij}$  is equal to 0 for occasions 1 and 2, and is equal to 1, 2, ...,  $k$  for subsequent breeding occasions. This term corresponds to the linear trend with 'experience' (computed as actual experience - 2). SQ is a dummy variable that takes value 0 or 1 for individual  $i$ , depending on behaviour.

The model in (1) can be expressed as (see Littell *et al.*, 1996, p. 254):

$$y_{ij} = (\alpha + a_i^*) + (\delta + d_i^* + \lambda_2 SQ_i) t_{ij} + (\beta + b_i^* + \lambda_3 SQ_i) t'_{ij} + \lambda_1 SQ_i + \varepsilon_{ij} \tag{2}$$

where  $a_i^*$ ,  $d_i^*$  and  $b_i^*$  is the random effects part of the model, with mean 0 and covariance matrix  $\Omega$ ,

$$\Omega = \begin{bmatrix} \sigma_a^2 & \text{symmetric} \\ \sigma_{ad} & \sigma_d^2 \\ \sigma_{ab} & \sigma_{db} & \sigma_b^2 \end{bmatrix}$$

Concerning fixed effects, in addition to the mean of random effects, the model also included age of first breeding (four modalities corresponding to age-classes 2-3, 4, 5,  $\geq 6$ ), behaviour (two modalities: squatter and non-squatter), and pairwise

interactions. This initial model permitted investigation of the influence of behaviour on reproductive performance in the first, second and subsequent breeding attempts while accounting for age of first breeding. Small sample sizes for the youngest and the oldest first-time breeders constrained us to pool data (we specified two age-classes: 2 and 3-year-old first time breeders, and individuals aged 6 or more).

Breeding performance in the first attempt and subsequent attempts cannot be described using the same number of states: there is an additional state after first reproduction: non-breeding (i.e. individuals that skip a breeding occasion). Previous work on the same biological model has shown that the proportion of non-breeders varies from 0.10 to 0.30, depending on year (Cam *et al.*, 1998). The probability of non-breeding is higher immediately after the first breeding attempt than later in reproductive life (Cam & Monnat, 2000a). Non-breeding can be considered as the lowest level of reproductive performance. Incorporation of this state in an analysis of the type described above is very likely to lead to a negative influence of 'experience' on performance relative to the initial status, as this level can be observed only in experienced breeders. In order not to exclude observations of non-breeders from the present study, we performed an additional analysis addressing the influence of behaviour on breeding trajectory, starting at occasion 2. The dependent variable had four modalities: non-breeding, breeding failure, one chick raised to independence, two or more chicks raised to independence. As above, we used a random-coefficients model with a hockey stick structure moved forward one breeding occasion (i.e. the first breeding attempt was excluded from the set of responses). We incorporated an additional covariate in the initial model: breeding performance in the first attempt. In doing so, our hope is to gain insight into the relationship between the two analyses (i.e. based on three or four states), especially if the first analysis provides evidence of an influence of squatting on the first occasion, but not the others. The following fixed effects were included in the initial model: the mean of random effects, age of first breeding (four modalities corresponding to age-classes 2-3, 4, 5,  $\geq 6$ ), behaviour, reproductive success in occasion 1, and second-order interactions.

### 2.3 Model selection

The approach to estimation used in all the analyses was based on maximum likelihood (marginal maximum likelihood for the random effects models built with the program MIXOR; Hedeker & Gibbons, 1996). We used Akaike's Information Criterion (AIC) for model selection (Akaike, 1973; Sakamoto *et al.*, 1986; Burnham & Anderson, 1998; Verbeke & Molenberghs, 2000). When possible, we estimated an overdispersion parameter using a bootstrap approach; note that MIXOR does not offer that possibility. For analyses focusing on the prebreeding period, capture-recapture multistate models were built in a sequential manner according to specific hypotheses. In analyses focusing on reproductive trajectory, we built a set of models including all the main effects plus a combination of second-order interactions. We then built all the models including all these effects except one interaction. This permitted selection of a set of candidate models including some interactions; we used these models and deleted one more interaction. This led to a set of models including a minimum number of relevant interactions. In the following step, we considered models without the main effects not involved in interactions. We used this approach because the number of possible models was very large, and the various biological hypotheses about squatting and age of first breeding specified

earlier did not permit us to specify a set of *a priori* predictions about combinations of interactions that may be more relevant than others. Lastly, we did not consider model uncertainty (Burnham & Anderson, 1998) in the model selection process. Finding the ‘best’ estimates was not our objective: we were mostly interested in assessing specific biological hypotheses. This, however, is not in contradiction with approaches accounting for model uncertainty (Burnham & Anderson 1998). We conducted model selection in a sequential manner and systematically sought the most parsimonious models. We recognize that other approaches are possible and that conclusions may differ according to the approach.

### 3 Results

#### 3.1 Influence of behaviour on survival in prebreeders and on recruitment probability

We started with a model where the recapture probability of adults and squatters was not age-specific (M0, Table 1). The recapture probabilities of adults and squatters were high, which raised convergence problems: we constrained them to be constant over age in order that MSSURVIV converges. The estimated extra-dispersion parameter corresponding to the initial model was equal to 1.94 (100 simulations). According to Burnham & Anderson (1998), this does not provide strong evidence of overdispersion. However, as this may be sufficient to influence the model selection process, we used QAIC for model selection. We set recapture rates equal, or fixed them to 1 (M1, M2 and M3); the latter constraint was retained only for adults, but the estimated recapture probability of squatters was also high (Table 2). We found evidence of an influence of age on the recapture probability of non-squatters, but not after age 3 (M4 to M9, Table 1). We used model M8 to continue model selection.

Survival varied according to age and state (M10 and M11). Models where the survival rates of individuals in different states but in the same age-class were set equal were not retained (M12 to M14). Note that not all states were represented in every age-class: the constraints of equality of survival rates among states were restricted to the age-classes where the states considered were represented. The survival probability of adults varied with age (M15), but not after age 4 (M17 and M18). The highest values (in 2-year-old adults) should be considered with caution (Table 2): these estimates are based on few observations. There was no evidence of an influence of age on survival in squatters (M19 to M21, Table 1). Concerning non-squatters, there was no evidence that survival varied according to age in individuals older than 3 (M23 to M25), but the model with constant parameters over age was not a good candidate (M22). The models with no influence of age in younger prebreeders were not good candidates either (M26 and M27). Squatters have the highest survival rate, compared with both adults and non-squatters (Table 2). We chose the model with lower QAIC (M25, Table 1) to continue model selection.

Transition probabilities varied with age and state (M28 and M29). Non-squatters did not have equal probability of becoming breeders or squatters in the following age-class (M30). In addition, the probability that non-squatters become breeders in the following age-class differs from that of squatters (M31). Finally, squatters did not have equal probability of recruiting in the following age-class or to be resighted as non-squatters (M32). The characteristics of the lowest-QAIC model (M41) were the following: there was no influence of age on transition rates in

TABLE 1. Influence of behavior on survival and recruitment into the breeding segment of the population

Model name	Recapture probability	Survival probability	Transition probability	NP	QAIC
M0	$p_a^1$ $p^2$ $p^3$	$S_a^1$ $S_2^2, S_3^2, S_4^2, S_{\geq 5}^2$ $S_a^3$	$\psi_a^{12}$ $\psi_1^{13}, \psi_2^{13}, \psi_3^{13}, \psi_4^{13}, \psi_{\geq 5}^{13}$ $\psi_2^{21}, \psi_3^{21}, \psi_4^{21}, \psi_{\geq 5}^{21}$ $\psi_2^{23}, \psi_3^{23}, \psi_4^{23}, \psi_{\geq 5}^{23}$ $\psi_a^{33}$	43	1429.2
M1 <sup>¥</sup>	$p_a^1, p^2, p^3 = 1, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			42	1427.1
M2	$p_a^1, p^2 = 1, p^3 = 1, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			41	1428.5
M3	$p_a^1, p^2 = p^3, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			42	1430.5
M4	$p^1, p^2, p^3 = 1, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			37	2349.7
M5	$p_s, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			36	1848.6
M6	$p_1^1, p_2^1, p_3^1, p_4^1, p_{\geq 5}^1, p^2, p^3 = 1, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			41	1425.6
M7	$p_1^1, p_2^1, p_3^1, p_{\geq 4}^1, p^2, p^3 = 1, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			40	1424.1
M8	$p_1^1, p_2^1, p_{\geq 3}^1, p^2, p^3 = 1, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			39	1422.8
M9	$p_1^1, p_{\geq 2}^1, p^2, p^3 = 1, S_a^r(\text{M0}), \psi_a^{rr}(\text{M0})$			38	1589.1
M10	$p_a^r(\text{M8}), S_a, \psi_a^{rr}(\text{M0})$			29	1442.6
M11	$p_a^r(\text{M8}), S_a^r, \psi_a^{rr}(\text{M0})$			26	1439.6
M12	$p_a^r(\text{M8}), S_a^1(\text{M0}), S_a^2 = S_a^3, \psi_a^{rr}(\text{M0})$			37	1427.5
M13	$p_a^r(\text{M8}), S_a^1 = S_a^2, S_a^3(\text{M0}), \psi_a^{rr}(\text{M0})$			35	1446.8
M14	$p_a^r(\text{M8}), S_a^1 = S_a^3, S_a^2(\text{M0}), \psi_a^{rr}(\text{M0})$			34	1428.7
M15	$p_a^r(\text{M8}), S_a^1(\text{M0}), S_a^2(\text{M0}), S^3, \psi_a^{rr}(\text{M0})$			35	1525.5
M16	$p_a^r(\text{M8}), S_a^1(\text{M0}), S_a^2(\text{M0}), S_2^3, S_3^3, S_4^3, S_{\geq 5}^3, \psi_a^{rr}(\text{M0})$			38	1420.8
M17	$p_a^r(\text{M8}), S_a^1(\text{M0}), S_a^2(\text{M0}), S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			37	1418.9
M18	$p_a^r(\text{M8}), S_a^1(\text{M0}), S_a^2(\text{M0}), S_2^3, S_{\geq 3}^3, \psi_a^{rr}(\text{M0})$			36	1426.8
M19	$p_a^r(\text{M8}), S_a^1(\text{M0}), S^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			34	1415.7
M20	$p_a^r(\text{M8}), S_a^1(\text{M0}), S_2^2, S_3^2, S_{\geq 4}^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			36	1417.4
M21	$p_a^r(\text{M8}), S_a^1(\text{M0}), S_2^2, S_{\geq 3}^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			35	1416.1
M22	$p_a^r(\text{M8}), S^1, S^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			28	1492.7
M23	$p_a^r(\text{M8}), S_0^1, S_1^1, S_2^1, S_3^1, S_{\geq 4}^1, S^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			33	1413.7
M24	$p_a^r(\text{M8}), S_0^1, S_1^1, S_2^1, S_3^1, S_{\geq 4}^1, S^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			32	1412.2
M25	$p_a^r(\text{M8}), S_0^1, S_1^1, S_2^1, S_{\geq 3}^1, S^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			31	1411.9
M26	$p_a^r(\text{M8}), S_0^1, S_1^1, S_{\geq 2}^1, S^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			30	1421.9
M27	$p_a^r(\text{M8}), S_0^1, S_{\geq 1}^1, S^2, S_2^3, S_3^3, S_{\geq 4}^3, \psi_a^{rr}(\text{M0})$			29	1426.5
M28	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a$			20	1480.2
M29	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{rr}$			18	3956.9
M30	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{12} = \psi_a^{13}, \psi_a^{21}(\text{M0}), \psi_a^{23}(\text{M0}), \psi_a^{33}(\text{M0})$			27	1438.1
M31	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{13} = \psi_a^{23}, \psi_a^{21}(\text{M0}), \psi_a^{12}(\text{M0}), \psi_a^{33}(\text{M0})$			28	1431.5
M32	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{21} = \psi_a^{23}, \psi_a^{13}(\text{M0}), \psi_a^{12}(\text{M0}), \psi_a^{33}(\text{M0})$			28	1481.3
M33	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{12}(\text{M0}), \psi_a^{13}(\text{M0}), \psi_a^{21}, \psi_a^{23}(\text{M0}), \psi_a^{33}(\text{M0})$			28	1409.1
M34	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{12}(\text{M0}), \psi_a^{13}(\text{M0}), \psi_a^{21}, \psi_a^{23}, \psi_a^{33}(\text{M0})$			25	1404.1
M35	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{12}(\text{M0}), \psi_a^{13}, \psi_a^{21}, \psi_a^{23}, \psi_a^{33}(\text{M0})$			22	1450.8
M36	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{12}(\text{M0}), \psi_2^{13}, \psi_3^{13}, \psi_{\geq 4}^{13}, \psi_2^{21}, \psi_3^{21}, \psi_{\geq 4}^{21}, \psi_a^{33}(\text{M0})$			24	1402.2
M37	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{12}(\text{M0}), \psi_2^{13}, \psi_{\geq 3}^{13}, \psi_{\geq 3}^{21}, \psi_2^{23}, \psi_a^{33}(\text{M0})$			23	1400.3
M38	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_a^{12}, \psi_2^{13}, \psi_{\geq 3}^{13}, \psi_a^{21}, \psi_2^{23}, \psi_a^{33}(\text{M0})$			19	3911.3
M39	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_1^{12}, \psi_2^{12}, \psi_3^{12}, \psi_{\geq 4}^{12}, \psi_2^{13}, \psi_{\geq 3}^{13}, \psi_a^{21}, \psi_a^{23}, \psi_a^{33}(\text{M0})$			22	1401.1
M40	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_1^{12}, \psi_2^{12}, \psi_{\geq 3}^{12}, \psi_2^{13}, \psi_{\geq 3}^{13}, \psi_a^{21}, \psi_a^{23}, \psi_a^{33}(\text{M0})$			21	1400.0
M41	$p_a^r(\text{M8}), S_a^r(\text{M25}), \psi_1^{12}, \psi_{\geq 2}^{12}, \psi_2^{13}, \psi_{\geq 3}^{13}, \psi_a^{21}, \psi_a^{23}, \psi_a^{33}(\text{M0})$			20	1399.5

State notation: 1 = nonsquatter (prebreeder), 2 = squatter (prebreeder), 3 = 'adult' (first-time breeder or individual that bred at least once).

Age-classes 6 includes individuals aged 6 or more.

Age-classes represented by subscript  $a$  (in brackets):  $p_a^1(1-6)$ ,  $p_a^2(2-6)$ ,  $p_a^3(2-6)$ ,  $S_a^1(0-6)$ ,  $S_a^2(2-6)$ ,  $S_a^3(2-6)$ ,  $\psi_a^{12}(1-5)$ ,  $\psi_a^{13}(1-6)$ ,  $\psi_a^{21}(2-6)$ ,  $\psi_a^{23}(2-6)$ ,  $\psi_a^{33}(2-6)$ .

Transition probabilities fixed to 0:  $\psi^{31}$  and  $\psi^{32}$ .

NP = Number of estimated parameters

¥ in brackets: name of the model whose structure was retained for the specified parameters

TABLE 2. Influence of behavior and age on survival, transition and recapture probability.

State	Age	Parameter estimate	Estimated standard error
<i>Survival probability</i>			
Nonsquatter	0	0.72	$6.43 \cdot 10^{-2}$
	1	0.53	$4.87 \cdot 10^{-2}$
	2	0.80	$1.63 \cdot 10^{-2}$
	$\geq 3$	0.69	$1.66 \cdot 10^{-2}$
Squatter	0 & 1	***	***
	$\geq 2$	0.92	$1.80 \cdot 10^{-2}$
Adult	0 & 1	***	***
	2	1.00	$2.02 \cdot 10^{-5}$
	3	0.76	$3.58 \cdot 10^{-2}$
	$\geq 4$	0.81	$1.17 \cdot 10^{-2}$
<i>Transition probability</i>			
Nonsquatter—squatter	0	***	***
	1	$4.25 \cdot 10^{-18}$	$3.10 \cdot 10^{-2}$
	$\geq 2$	0.16	$9.94 \cdot 10^{-3}$
Nonsquatter—adult	0 & 1	***	***
	2	0.13	$1.11 \cdot 10^{-2}$
	$\geq 3$	0.35	$1.93 \cdot 10^{-2}$
Squatter—nonsquatter	0 & 1	***	***
	$\geq 2$	0.28	$3.02 \cdot 10^{-2}$
Squatter—adult	0 & 1	***	***
	$\geq 2$	0.53	$3.23 \cdot 10^{-2}$
<i>Recapture probability</i>			
Nonsquatter	1	$4.65 \cdot 10^{-2}$	$5.69 \cdot 10^{-3}$
	2	0.55	$1.59 \cdot 10^{-2}$
	$\geq 3$	0.90	$1.31 \cdot 10^{-2}$
Squatter	1 & 2	***	***
	$\geq 3$	0.99	$1.73 \cdot 10^{-2}$
Adult	1	***	***
	$\geq 2$	1 (fixed)	***

\*\*\*Parameter not estimated

squatters, the probability that non-squatters become breeders in the following age-class did not vary after age 3, and the probability that they become squatters stabilized at age 2.

### 3.2 Relationship between behaviour and age of first breeding

We assessed the relationship between behaviour and age of first breeding (in the subset of individuals that survived and attempted to breed). We used a baseline-category logit model (Agresti, 1990) with age of first breeding as a categorical dependent variable (four levels corresponding to the age-classes: 2-3, 4, 5,  $\geq 6$ ), and behaviour as the covariate ( $N = 467$  individuals). The analysis was performed using SAS (1988). The likelihood ratio test provided evidence of a relationship between squatting and age of first breeding ( $\chi^2 = 27.14$ ,  $df = 3$ ,  $P < 0.0001$ ). The estimated proportions of squatters that recruited in age-class  $a$  were:  $a = 2-3$ ,  $\hat{\phi} = 0.14$  (estimated standard error:  $\hat{SE} = 0.03$ );  $a = 4$ ,  $\hat{\phi} = 0.57$  ( $\hat{SE} = 0.04$ );  $a = 5$ ,

$\hat{\phi} = 0.20$  ( $\hat{SE} = 0.03$ );  $a = 6$  or more,  $\hat{\phi} = 0.09$  ( $\hat{SE} = 0.02$ ). For non-squatters:  $a = 2-3$ ,  $\hat{\phi} = 0.40$  ( $\hat{SE} = 0.03$ );  $a = 4$ ,  $\hat{\phi} = 0.43$  ( $\hat{SE} = 0.03$ );  $a = 5$ ,  $\hat{\phi} = 0.12$  ( $\hat{SE} = 0.02$ );  $a = 6$  or more,  $\hat{\phi} = 0.05$  ( $\hat{SE} = 0.01$ ). The mean age of first breeding was higher in squatters. Squatters: 4.28 (standard deviation: 0.92,  $N = 130$ ); non-squatters: 3.83 (standard deviation: 0.91,  $N = 337$ ). We found evidence of an influence of behaviour on the mean age of first breeding: Generalized Linear Model—SAS (1998);  $F_{(1,465)} = 23.67$ ,  $P = 0.0001$ .

The proportion of squatters recruiting in the first age-class (2- and 3-year old birds) is lower than the proportion of non-squatters. However, squatters are not represented in 1-year-old individuals and are poorly represented in 2-year-old individuals. The relationship between age of first breeding and behaviour reflects the fact that squatting is not expressed in the youngest prebreeders.

### 3.3 Influence of behaviour on reproductive trajectory

**3.3.1 First breeding and subsequent attempts.** We first addressed individual variation (i.e. the random effects) in the various components of the model (M0 to M5, Table 3). As initial status is likely to have a substantial influence on the shape of subsequent reproductive trajectory, we built models that included the intercept as a random effect, plus a combination of other random effects. Models including random components for the second intercept and the influence of time elapsed since occasion 2 only (either independent or correlated) did not converge.

**Model selection.** We did not find evidence of individual variation in the second intercept or in the influence of experience on breeding performance (M0 to M4, Table 3). In contrast, the model without the individual effect on initial status performed poorly (M5). This shows that there was substantial heterogeneity in initial performance among individuals, and that variation in reproduction trajectories was better accounted for by a model incorporating individual variation in initial state.

We then built a set of models including all the effects but one interaction (M6 to M10, Table 3), retained the two lowest-AIC models (M7 and M8), and then deleted one more interaction (M11 to M17). Several models had low AIC values (M11, M12, M13, and M15). We used these models as starting points and dropped one more interaction (M18 to M25). Two models from this step had AIC values close to the lowest value: M18 and M19. When deleting one additional interaction, AIC values increased (M26 to M28). The difference between these values and the lowest value ranged between 3.8 and 8.0, so we decided to retain models M18 and M19. In addition, the model without any interaction was not a good candidate (M29). The data were not able to provide definitive results, as several models have AIC values close to the minimum value. All these models include two or three interactions. The most parsimonious models with AIC values closest to the lowest value were models M18 and M19; we present the corresponding parameter estimates.

**Parameter estimates.** Both models included the variables: behaviour, age of first breeding, and the modified measure of experience. The interactions retained differed. The reference category corresponded to the first breeding attempt in the youngest non-squatters. Positive parameter estimates indicate that the covariate considered had a positive influence on the probability of raising two chicks to

TABLE 3. Influence of behavior, age of first breeding, and experience on reproductive trajectory (first reproduction included). Response variable: breeding failure, 1 chick raised to independence, 2 or more chicks raised to independence

Model	Fixed effects $\Psi$	$\Omega$	AIC	NP
M0	ESQAJE*ASQ*ASQ*ESQ*JA*J	$\sigma_1^2, \sigma_I^2, \sigma_E^2, \sigma_{IE}, \sigma_{IE}, \sigma_{JE}$	2327.1	24
M1	ESQAJE*ASQ*ASQ*ESQ*JA*J	$\sigma_1^2, \sigma_E^2, \sigma_{IE}$	2330.2	21
M2	ESQAJE*ASQ*ASQ*ESQ*JA*J	$\sigma_1^2, \sigma_E^2$	2329.8	20
M3	ESQAJE*ASQ*ASQ*ESQ*JA*J	$\sigma_1^2, \sigma_I^2, \sigma_{IJ}$	2329.6	21
M4	ESQAJE*ASQ*ASQ*ESQ*JA*J	$\sigma_1^2$	2327.9	19
M5	ESQAJE*ASQ*ASQ*ESQ*JA*J	—	2365.0	18
M6	ESQAJESQ*ASQ*ESQ*JA*J	$\sigma_1^2$	2328.6	16
M7	ESQAJE*ASQ*ASQ*JA*J	$\sigma_1^2$	2325.9	18
M8	ESQAJE*ASQ*ESQ*JA*J	$\sigma_1^2$	2322.7	16
M9	ESQAJE*ASQ*ASQ*ESQ*J	$\sigma_1^2$	2328.5	16
M10	ESQAJE*ASQ*ASQ*EA*J	$\sigma_1^2$	2330.0	18
M11	ESQAJESQ*ESQ*JA*J	$\sigma_1^2$	2323.3	13
M12	ESQAJE*ASQ*JA*J	$\sigma_1^2$	2320.7	15
M13	ESQAJE*ASQ*ESQ*J	$\sigma_1^2$	2323.3	13
M14	ESQAJE*ASQ*EA*J	$\sigma_1^2$	2325.0	15
M15	ESQAJESQ*ASQ*JA*J	$\sigma_1^2$	2323.3	15
M16	ESQAJE*ASQ*ASQ*J	$\sigma_1^2$	2326.6	15
M17	ESQAJE*ASQ*AA*J	$\sigma_1^2$	2329.3	17
M18	ESQAJESQ*JA*J	$\sigma_1^2$	2321.2	12
M19	ESQAJE*ASQ*J	$\sigma_1^2$	2321.3	12
M20	ESQAJE*AA*J	$\sigma_1^2$	2324.4	14
M21	ESQAJE*ASQ*E	$\sigma_1^2$	2328.8	12
M22	ESQAJESQ*EA*J	$\sigma_1^2$	2325.1	12
M23	ESQAJESQ*ESQ*J	$\sigma_1^2$	2330.7	10
M24	ESQAJESQ*ASQ*J	$\sigma_1^2$	2334.3	12
M25	ESQAJESQ*AA*J	$\sigma_1^2$	2329.4	14
M26	ESQAJE*A	$\sigma_1^2$	2328.1	11
M27	ESQAJA*J	$\sigma_1^2$	2324.5	11
M28	ESQAJESQ*J	$\sigma_1^2$	2328.7	9
M29	ESQAJ	$\sigma_1^2$	2337.1	8

$\Psi$  Intercept (I) always included

Notation: E = experience, SQ = behavior, A = age of first breeding, J = second intercept. Interactions are indicated with an asterisk.

$\Omega$ : terms included in the variance-covariance matrix of random effects

independence. Squatters had a higher probability of raising two chicks than non-squatters at baseline (i.e. first breeding) ('Behaviour'; Table 4). There was a 'jump' upward in performance between the first and the second breeding occasions ('Int. 2'), and a slight improvement in performance with time elapsed since occasion 2 ('Time'). Performance was poorer in the youngest first-time breeders (2 and 3 years old) than in older first-time breeders ('Age (a)'). Both models included the interaction between behaviour and the second intercept ('Behaviour  $\times$  Int. 2'): the initial jump in performance depended on behaviour. The corresponding estimate was negative: the jump in performance between the first and the second occasions was less pronounced in squatters, that is, in those that had a higher probability of raising two chicks in the first breeding attempt.

Model M18 included the interaction between age of first breeding and the second intercept ('Int. 2  $\times$  Age (a)'): the 'jump' in performance between occasions 1 and 2 depended on age of first breeding. All estimated parameters were negative: the jump in performance between occasions 1 and 2 was less pronounced in individuals

TABLE 4. Estimates of parameters in the linear model (models M18 and M19)

Parameter	Estimate	Estimated standard error	Z statistic	P
<i>Model M18</i>				
Int. 1	-0.68	0.11	-6.06	0.00
Int. 2	0.98	0.13	7.51	0.00
Behavior	0.23	0.15	1.52	0.13
Time	0.05	0.02	2.03	0.04
Age (4)	0.51	0.14	3.53	0.00
Age (5)	0.62	0.21	2.96	0.00
Age ( $\geq 6$ )	0.45	0.27	1.64	0.10
Behavior*Int. 2	-0.38	0.17	-2.21	0.00
Int. 2*Age (4)	-0.62	1.17	-3.63	0.00
Int. 2*Age (5)	-0.59	0.25	-2.34	0.02
Int. 2*Age ( $\geq 6$ )	-0.30	0.43	-0.70	0.48
Random effect (Int. 1)	0.52	0.08	6.85	0.00
<i>Model M19</i>				
Int. 1	-0.53	0.12	-4.86	0.00
Int. 2	0.61	0.10	6.25	0.00
Behavior	0.30	0.15	1.98	0.05
Time	0.13	0.04	3.20	0.00
Age (4)	0.26	0.12	2.21	0.03
Age (5)	0.44	0.17	2.53	0.01
Age ( $\geq 6$ )	0.24	0.22	0.95	0.34
Behavior*Int. 2	-0.49	0.16	-2.99	0.00
Time*Age (4)	-0.13	0.05	-2.65	0.01
Time*Age (5)	-0.24	0.07	-3.55	0.00
Time*Age ( $\geq 6$ )	0.06	0.12	0.48	0.63
Random effect (Int. 1)	0.54	0.08	6.96	0.00

Notation: Int. 1 = first intercept, Int. 2 = second intercept, time = time elapsed since breeding occasion 2 (years)

Random effect: expressed in terms of standard deviation. The *P* value corresponds to a one-tailed test (two-tailed tests for the other parameters).

that bred for the first time at age 4, 5, 6 or more (i.e. those that started with a better performance) than in birds that started breeding at 2 or 3. The smallest absolute value corresponded to the oldest first-time breeders ('Int. 2  $\times$  age ( $\geq 6$ )'). The latter individuals had a lower probability of raising two chicks in the first breeding occasion than 4- or 5-year-old individuals. However, the subsequent jump was more substantial than in 4 and 5-year-old first-time breeders, which shows that they partly 'caught up' with younger first-time breeders in terms of performance.

Model M19 included the interaction between age of first breeding and experience (i.e. from occasion 2; 'Time  $\times$  Age (a)'): the influence of experience varied according to age of first breeding. The coefficients corresponding to categories of birds that recruited at age 4 or 5 were negative. The largest absolute value corresponded to 5-year-old first-time breeders: this category had the best performance at occasions 1 and 2, and then performance decreased after occasion 2. The influence of experience was either virtually non-existent or positive in the other categories. The last estimate was positive, which indicates that the influence of experience was positive in birds that started breeding at an older age ( $\geq 6$ ), and that they partly 'caught up' with intermediate age first-time breeders.

*Summary and preliminary interpretations.* Squatters perform better than others in the first breeding attempt, regardless of age of recruitment. The youngest and the oldest recruits performed less well than recruits of intermediate age. The probability of raising two chicks increased between the first and the second attempt; this was more pronounced in birds whose initial performance was poorer (i.e. non-squatters versus squatters, and youngest and oldest recruits versus others). The positive influence of behaviour during the prebreeding period is particularly marked in the first breeding attempt. In preliminary analyses, we used models without the 'second' intercept, with a simple linear trend in performance starting at first reproduction (these results are not shown). In this case, the variable describing behaviour was not retained. This supports the idea that the main role played by this variable in the description of the process that gave rise to the data is to account for the difference in the performance of the two behavioural categories in the first breeding attempt.

### 3.3.2 Second breeding and subsequent attempts.

*Model selection.* As above, we first addressed individual variation in initial breeding success, the second intercept (the jump in performance between occasions 2 and 3), and the subsequent influence of experience. We did not find evidence of individual variation in the two latter effects (Table 5). The lowest-AIC model in this subset of models included the intercept and experience as correlated random effects (M1), but the AIC value of the model with a single random effect (M5) was close. We retained the most parsimonious model to continue model selection. The model without any random effect was not a good candidate (M6).

Models M7 to M13 included all main effects and all second-order interactions except one. One of these models had an unambiguously lower AIC value: M12. We used this model and built the six models obtained by dropping one additional interaction (M14 to M19). We chose the minimum-AIC model from this subset: M15, and then built the five models including one interaction fewer (M20 to M24). All these models except one (M20) had similar fit. This model was the only one that did not include the interaction between performance in occasion 1 and the second intercept. As dropping the other interactions seemed to have little influence on the fit of models, we deleted all the interactions but the one that distinguished model M20 from the others. The resulting model (M25) had a lower AIC value than all the others. The model including main effects exclusively was not a good candidate (M26). We then deleted one of the main effects not involved in the interaction. Model M27 was retained in this step. We deleted the second main effect not involved in the interaction: this model had the lowest AIC value (M30). As above, the data did not provide definitive results, as several models had similar fit (e.g. M30 and M27). However, when considering the most parsimonious model, it did not include the variable describing behaviour during the prebreeding period. We present the corresponding parameter estimates.

*Parameter estimates.* The reference category corresponded to individuals that failed in the first breeding attempt. As above, a positive estimate indicates that the covariate considered had a positive influence on the probability of raising two chicks. Individuals that performed well in the first reproduction had a higher probability of performing well in the second breeding occasion ('Perf (p)', Table 6). The estimated parameter corresponding to the second intercept (the 'jump' in performance between occasions 2 and 3; 'Int. 2') was negative, with a small absolute value. This provides evidence that there was no substantial variation in breeding success

TABLE 5. Influence of behavior, age of first breeding, and experience on reproductive trajectory (first reproduction excluded). Response variable: nonbreeding, breeding failure, 1 chick raised to independence, 2 or more chicks raised to independence.

Model	Fixed effects ¥	$\Omega$	AIC	NP
M0	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2, \sigma_7^2, \sigma_E^2, \sigma_{IJ}, \sigma_{IE}, \sigma_{JE}$	2495.3	29
M1	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2, \sigma_E^2, \sigma_{IE}$	2492.5	27
M2	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2, \sigma_E^2$	2495.2	26
M3	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2, \sigma_7^2, \sigma_{IJ}$	2494.7	26
M4	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2, \sigma_7^2$	2494.9	26
M5	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2$	2493.2	25
M6	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*PP*J	—	2543.2	23
M7	ESQAJPE*A SQ*ASQ*ESQ*JA*JSQ*P	$\sigma_1^2$	2500.7	23
M8	ESQAJPE*A SQ*ASQ*ESQ*JA*JP*J	$\sigma_1^2$	2489.6	23
M9	ESQAJPE*A SQ*ASQ*ESQ*JSQ*PP*J	$\sigma_1^2$	2491.4	22
M10	ESQAJPE*A SQ*ASQ*EA*JSQ*PP*J	$\sigma_1^2$	2491.2	24
M11	ESQAJPE*A SQ*ASQ*JA*JSQ*PP*J	$\sigma_1^2$	2491.2	24
M12	ESQAJPE*A SQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2$	2487.5	22
M13	ESQAJPSQ*ASQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2$	2490.8	22
M14	ESQAJPE*A SQ*ESQ*JA*JSQ*P	$\sigma_1^2$	2495.0	20
M15	ESQAJPE*A SQ*ESQ*JA*JP*J	$\sigma_1^2$	2483.8	20
M16	ESQAJPE*A SQ*ESQ*JSQ*PP*J	$\sigma_1^2$	2485.5	19
M17	ESQAJPE*A SQ*EA*JSQ*PP*J	$\sigma_1^2$	2485.5	21
M18	ESQAJPE*A SQ*JA*JSQ*PP*J	$\sigma_1^2$	2485.5	21
M19	ESQAJPSQ*ESQ*JA*JSQ*PP*J	$\sigma_1^2$	2485.1	19
M20	ESQAJPE*A SQ*ESQ*JA*J	$\sigma_1^2$	2491.4	18
M21	ESQAJPE*A SQ*ESQ*JP*J	$\sigma_1^2$	2481.4	17
M22	ESQAJPE*A SQ*EA*JP*J	$\sigma_1^2$	2481.9	19
M23	ESQAJPE*A SQ*JA*JP*J	$\sigma_1^2$	2481.9	19
M24	ESQAJPSQ*ESQ*JA*JP*J	$\sigma_1^2$	2481.6	17
M25	ESQAJPP*J	$\sigma_1^2$	2479.5	12
M26	ESQAJP	$\sigma_1^2$	2491.7	10
M27	ESQJPP*J	$\sigma_1^2$	2473.7	9
M28	EAJPP*J	$\sigma_1^2$	2479.1	11
M29	SQAJPP*J	$\sigma_1^2$	2487.0	11
M30	EJPP*J	$\sigma_1^2$	2473.3	8

¥ Intercept (I) always included

Notation: E = experience, SQ = behavior, A = age of first breeding, J = second intercept, P = reproductive performance in the first breeding attempt. Interactions are indicated with an asterisk.

$\Omega$ : terms included in the variance-covariance matrix of random effects

between occasions 2 and 3 in birds that failed the first breeding attempt (note that the previous analysis provided evidence that there is a jump upward in performance in those individuals between occasions 1 and 2). Estimates of the interaction terms between the second intercept and the initial reproductive performance (in the first breeding attempt; ‘Int. 2 × Perf (p)’) show that after occasion 2, breeding success decreased in individuals that performed well in the first and second attempt. The difference between individuals that started with a higher-, or a lower-level breeding performance lessened after occasion 2, mostly because of deterioration in performance of individuals with a higher-level initial performance. Lastly, the influence on experience (from occasion 3; ‘Time’) on breeding success was positive.

*Summary and preliminary interpretations.* We did not find evidence of an influence of behaviour on reproduction. This supports the idea proposed above: the influence of behaviour was particularly marked in the first breeding attempt. This conclusion

TABLE 6. Estimates of parameters in the linear model (model M30)

Parameter	Estimate	Estimated		
		standard error	Z statistic	P
Int. 1	1.62	0.09	17.70	0.00
Int. 2	-0.04	0.11	-0.39	0.69
Time	0.13	0.03	4.21	0.00
Perf (2)	0.60	0.18	3.25	0.00
Perf (3)	1.24	0.45	2.78	0.00
Int 2*Perf (2)	-0.38	1.18	-2.10	0.03
Int 2*Perf (3)	-0.74	0.43	-1.73	0.08
Random effect (Int. 1)	0.59	0.07	8.90	0.00

Notation: Int. 1 = first intercept, Int. 2 = second intercept, time = time elapsed since breeding occasion 3 (years), Perf. = breeding performance in the first breeding attempt (2 = raised 1 chick to independence, 3 = raised 2 or more chicks to independence).

Random effect: expressed in terms of standard deviation. The *P* value corresponds to a one-tailed test (two-tailed tests for the other parameters).

must be considered carefully though. The first breeding attempt was excluded from the trajectory (i.e. from the set of responses), but was incorporated into the model as a covariate. Performance in the first breeding attempt influenced the shape of the individual trajectory in subsequent occasions: the better the individual performed initially, the higher the probability of performing well in the second attempt. In addition, the previous analysis (trajectories starting at first reproduction) provided evidence that squatters had a higher probability of performing well at first reproduction. To some extent, initial performance could reflect behaviour during the pre-breeding period.

Unlike in the analysis of trajectories starting at first reproduction, there was a decrease in the probability of a higher-level performance between the second and the third attempt at baseline (i.e. individuals that failed the first breeding attempt). The decrease was more pronounced in individuals with a higher initial performance (i.e. birds that performed well in occasion 1). A possible interpretation is that this corresponds to a delayed expression of the higher cost of the first reproduction described in several species (Viallefont *et al.* 1995ab), but in the present case, this would reflect cumulative costs (e.g. Nichols & Kendall, 1995).

Lastly, the probability of raising two chicks increased as a function of time elapsed since the third breeding attempt. We also built models including the latter variable squared to account for a possible deceleration in the rate of variation in the probability of a performance of higher level, but this variable was not retained (these results are not shown). This may be linked to the fact that the maximum age of individuals in the cohorts selected for this study is 12: if such deceleration occurs, it is possible that it is expressed only in older individuals.

#### 4 Discussion

We found evidence that squatters have a higher survival probability than non-squatters, and if they survive, a higher probability of recruiting in the following year. This was observed in all age-classes. An individual was classified as a squatter only if investigators observed the bird while exhibiting specific behaviour. Daily observations have shown that individuals seldom behave as squatters on a single

occasion (or day; Cadiou, 1999), which increases the probability that investigators detect squatters. However, it is likely that some squatting events have been missed and that some individuals have been erroneously classified as non-squatters. In spite of this, our results show that squatters and non-squatters had unambiguously different demographic characteristics. As the state 'non-squatter' includes both true non-squatters and misclassified squatters, the corresponding estimated demographic parameters are probably too close to those of squatters (assuming that there is no relationship between the ability of investigators to classify individuals and the demographic parameters of those individuals). That is, the magnitude of the differences between the two state-specific survival rates or the two state-specific transition rates is likely underestimated.

The interpretation of most of our results relies on several non-exclusive hypotheses. One of these results is of critical importance to the interpretation of most others. In the analyses of reproductive trajectory, the models incorporating individual heterogeneity (i.e. a random individual effect) in initial state had the best fit. This provides evidence that there was substantial individual variation in reproductive performance from the population average performance (Hedeker & Gibbons, 1996). In addition, although our data were not able to provide definitive answers, we did not find evidence that the other random effects were needed to describe the process that gave rise to the data. Individual variation in the rate of change in reproductive performance over time (after the first breeding attempt) from the population average rate of change was not substantial. Lastly, this rate and the initial state (or 'initial potential for reproduction') were not correlated. Incorporation of initial heterogeneity was sufficient to describe the process that gave rise to the individual trajectories, and the single random effect retained in both analyses was additive in the model. That is, for a reproductive trajectory of a given shape (which depends on age of first reproduction and behaviour), differences among individuals in a different initial state were 'expressed' in the entire trajectory. Individuals that started reproductive life with a higher latent probability of raising two chicks consistently performed better than others afterward. These results support the hypothesis that this population includes individuals of different quality, as proposed in previous studies using data from the same population (Cam *et al.*, 1998, 2002; Cam & Monnat, 2000ab).

A classic difficulty in interpreting the influence of covariates on survival is the contribution of mortality to local survival: the interpretation strongly depends on the weight of permanent emigration out of the study area and true mortality. Two hypotheses can be proposed to explain the higher survival rate in squatters compared with adults. First, a higher probability of dispersing in adults (i.e. first-time breeders and individuals that bred at least once), which is in contradiction with patterns described in the literature (e.g. Greenwood & Harvey, 1982), would cause the appearance of higher survival in squatters than adults. However, it is possible that the probability of dispersing out of the study area is particularly low in prebreeders involved in the recruitment process (i.e. squatters), even lower than in individuals that already recruited. The latter category includes non-breeders, unsuccessful and successful breeders, and it has been shown that breeding performance substantially influences the probability of dispersing within the study area (e.g. Danchin & Monnat, 1992; Danchin *et al.*, 1998). The survival rate closest to true survival probably corresponds to successful breeders, while the rate corresponding to 'adults' in general may reflect permanent emigration to some extent. The data used in this study come from five colonies located in Brittany, while the

range of the species covers the entire North Atlantic. To date, the conditions are not met to assess emigration out of the study area.

The second hypothesis relies on the idea of differences in individual quality, assuming that local survival reflects true survival. Cam *et al.* (in press), and Link *et al.* (this issue) have found evidence that there is substantial heterogeneity in latent survival probability in this population. We suggest that the hypothesis of differences in individual quality can be proposed to explain differences in survival among groups defined on the basis of observable characteristics (e.g. behaviour): these groups would be composed of individuals of different latent quality. The group of adults may be more heterogeneous in terms of individual quality than squatters, the latter being mostly composed of higher-quality individuals, while the former would include a non-negligible proportion of lower-quality individuals.

Several non-exclusive hypotheses can also be put forward to explain the influence of age and behaviour on reproduction. The interpretation of our results raises another classic difficulty: the respective influence of intrinsic individual characteristics and environmental factors on breeding success. The first hypothesis that can be proposed to explain the higher probability of an initial higher performance in squatters is that squatters are individuals of higher intrinsic quality. The second is based on the results obtained in studies of behavioural tactics associated with recruitment and habitat selection (Ens *et al.*, 1995). It is possible that squatters acquire higher-quality breeding sites. This would be consistent with studies conducted in other colonies that have suggested that there is a relationship between individual quality and the quality of breeding sites (e.g. Coulson, 1966, 1968). The substantial improvement of performance of non-squatters between the first and the second breeding attempt, and the overall increase in the probability of a higher-level performance over life, may also rely on acquisition of higher-quality sites. Individuals may disperse and establish on higher-quality sites, or the characteristics of individuals may change throughout life. The conditions are not met to address questions about the relationship between breeding site quality, behaviour and individual breeding trajectory. This requires assessment of the quality of breeding sites independently of individual breeding performance; how to do this in species that breed in dense colonies, such as the kittiwake is not clear. In addition, Boulinier & Lemel (1996) have used an indirect measure of habitat quality and have suggested that the quality of the breeding habitat measured at a larger spatial scale is autocorrelated over a few years, but not longer periods of time. The relationship between the long-term consistency in breeding performance and the quality of breeding sites will require additional investigations.

Understanding variation of breeding performance over life in iteroparous species with definite growth requires consideration of two aspects: age and experience (Pärt, 1995). Disentangling the two factors is not possible: while individuals with different experience (measured by the number of breeding attempts) may be represented in some age-classes, the intrinsic relationship between these factors forbids investigation of variation in reproductive parameters as a function of the entire range of combinations of values (very young individuals cannot be very experienced). We recognize that the influence of time elapsed since first breeding on reproduction combines both effects (age and experience).

In addition, in situations where there is individual heterogeneity in survival, within-generation phenotypic mortality selection (Vaupel & Yashin, 1985ab) can lead to an apparent positive influence of age on survival and reproduction (Curio, 1983; Vaupel & Yashin, 1985ab; Forslund & Pärt, 1995; MacDonald *et al.*, 1996;

Service, 2000; Cooch *et al.* this issue). Here we found evidence of heterogeneity among individuals in latent breeding performance, which supports the hypothesis of differences in individual quality (Cam *et al.*, 1998, in press; Cam & Monnat 2000a). Moreover, Cam *et al.* (in press), and Link *et al.* (this issue) have found evidence that there is heterogeneity in latent survival probability and in latent reproductive rates, and that these rates are positively correlated at the individual level. The following scenario can be proposed (see also Cooch *et al.* this issue): individuals with lower survival and poorer reproductive performance die earlier, which results in an apparent increase in performance (Curio, 1983; Forslund & Pärt, 1995). As individual trajectories are of unequal length, it is possible that 'missing data' (at the end of shorter trajectories) are not 'missing at random' (Hedeker & Gibbons, 1996; Littell *et al.*, 1996; Verbeke & Molenberghs 2000), that they are not independent of the unobserved response, and that they mostly correspond to poor performance. This would lead to a situation where the average breeding performance of older individuals would be higher than the average reproductive performance of younger birds (Cooch *et al.*, this issue), but this would not necessarily mean that performance improves in individuals that survived longer. Investigating this question requires use of a modelling approach incorporating the correlation between latent survival and reproductive parameters (Cam *et al.*, 2002; Link *et al.*, this issue; Link *et al.*, 2002).

Lastly, our results lead to several considerations relevant to studies of behavioural tactics associated with recruitment and the evolution of deferred breeding. First, the time required to recruit is often considered as an intrinsic characteristic of behavioural tactics (e.g. direct competition and eviction of the owners of a site versus waiting until a site becomes available). Squatting can be considered as an offensive tactic. However, it is possible that not all the tactics are open to individuals in all age-classes; offensive tactics probably require a strong competitive ability that younger individuals do not have, and may be open only to individuals that are behaviourally more mature. Squatting is associated with 'fast' recruitment once individuals have become squatters, but not with recruitment at a younger age. This suggests that the time required to attain behavioural maturity may also be an important component to take into account when specifying the conceptual framework used to address the evolution of tactics.

Secondly, squatters are more successful than others at least in the early years of reproductive life. It has been suggested that if delaying breeding is associated with a higher probability of success at the start of reproductive life, this may play a part in the evolution of deferred breeding (e.g. Charlesworth, 1994). If tactics open to behaviourally more mature individuals (older prebreeders only) are more successful, it is possible that behaviour is part of the process contributing to favour deferred breeding. In addition, our results show that behaviour during prebreeding stages is associated with an unambiguous initial advantage in terms of reproduction, but we did not find evidence that the variables measured before, or at the start of reproductive life (behaviour and age of first breeding) have long-term effects on the reproductive trajectory. This may reflect the fact that other important variables have been omitted in our analyses (temporal variation in environmental characteristics for example). This suggests that one of the assumptions commonly made in studies of the evolution of behavioural tactics should be considered carefully: the fact that the costs and benefits associated with the different tactics are reflected during the entire reproductive life (e.g. that individuals that obtained a higher-quality site do not disperse, and that the quality of the site does not vary over time).

As stated by Clobert (1995), Lebreton (1995), and Nichols & Kendall (1995), development of multistate capture-recapture models is an important step for studies of life histories. These models permit investigation of processes taking place during part of the individual history, which is the case in prebreeding stages in species with deferred reproduction, and also transitions between stages (e.g. Woods *et al.*, 1998; Pradel & Lebreton, 1999). In cases where state describes behaviour, the risk of misclassifying individuals observed on a few occasions may be high: the development of multistate robust-design models may offer new possibilities (Kendall & Nichols personal communication). Finally, the questions addressed here are relevant to the general theme of 'development' and changes in individual characteristics over life (Bryk & Raudenbush, 1992). According to Bryk & Raudenbush (1992), inferences about the shape of trajectories have often been plagued by failure to account for heterogeneity among individuals. Another major difficulty is linked to individual heterogeneity in survival probability, the correlation between survival and reproductive rates at the individual level, and their effects on the apparent influence of age on both survival and reproductive rates (Curio, 1983; Vaupel & Yashin, 1985ab; Forslund & Pärt, 1995; Service, 2000; Cam *et al.*, in press). This highlights the need for development of modelling tools permitting distinction between mortality selection and changes actually expressed at the individual level in situations where recapture probability is lower than one (e.g. Burnham & Rexstad, 1993; Lebreton, 1995; Cooch *et al.*, this issue; Pledger & Schwartz, this issue).

### Acknowledgements

We are grateful to the Conseil Général du Finistère and the Société pour l'Etude et la Protection de la Nature en Bretagne for allowing us to work in the nature reserve of Goulien Cap-Sizun (Brittany, France). We thank D. Hedeker for advising us concerning the use of the program MIXOR. We also thank M. Conroy and an anonymous referee for their constructive comments on this manuscript, and all the researchers and students who helped with the field work.

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