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Now you see him, now you don't: experience, not age, is related to reproduction in kittiwakes

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In long-lived species, individuals can skip reproduction. The proportion of breeders affects population growth rate and viability, there is a need to investigate the factors influencing intermittent breeding. The theory predicts that if lack of experience is an important constraint, breeding probabilities should increase with experience for individuals of the same age, whereas under the so-called restraint hypothesis, breeding probabilities should increase with age regardless of experience. However, because the probability of detecting individuals in the wild is generally less than 1, it is difficult to know exactly the number of previous breeding episodes (breeding experience). To cope with this issue, we developed a hidden process model to incorporate experience as a latent state possibly influencing the probability of breeding. Using a 22-year mark-recapture dataset involving 9970 individuals, we analysed simultaneously experience and age effects on breeding probabilities in the kittiwake (*Rissa tridactyla*). We did not detect an influence of age on adult breeding probabilities. We found that inexperienced birds breed less frequently than experienced birds. Our approach enables us to highlight the key role of experience on adults breeding probabilities and can be used for a wide range of organisms for which detection is less than 1.

Keywords: *Rissa tridactyla*; capture–recapture; breeding probability; experience; age; seabirds

1. INTRODUCTION

As animals get older, they should become more successful parents because of improvement of their reproductive performance with age [1]. Two major non-exclusive explanations have been suggested at the individual level [2]. The *restraint* hypothesis [3,4] assumes a trade-off between current reproductive effort and future reproduction and predicts that reproductive effort increases with age as the residual reproductive value decreases, which improves breeding performance with age. By contrast, the *constraint* hypothesis [5,6] assumes age-related improvement of breeding abilities. As animals get older, they become more efficient at obtaining high-quality territories or mates, caring for eggs, nestlings, etc. Recently, it has been suggested that this improvement of abilities may only be owing to progressive acquisition of experience during repeated breeding events [7] regardless of age.

Until now, the majority of previous studies reporting age-related differences in life-history traits of wild vertebrates could not disentangle age and experience effects because of the issue of detection of less than 1 inherent to studies in the wild [8]: what is the state of an unobserved individual? Is it alive or not? Breeding or not? How can we update the number of experience events when we do not see the animal? Here, we used a recent statistical approach [9] to determine the relative influence of age and experience on breeding probabilities in a seabird. We tested two predictions: (i) if lack of experience is an important *constraint*, breeding probabilities will increase with experience for individuals of the same age, and (ii) under the *restraint* hypothesis, breeding probabilities will increase with age regardless of experience.

We analysed 22 years of data on individually marked kittiwake chicks and adults (*Rissa tridactyla*). This seabird has a reproductive cycle exhibiting most of the problems of studies of wild long-lived vertebrates: after delayed recruitment (mostly between ages 3 and 6) [10], individuals can skip breeding events during life [11,12]. Using multi-event capture–recapture models [13], we incorporated experience as a latent state possibly influencing the probability of breeding and estimated survival, and age at first breeding while accounting for imperfect detection. We assessed jointly the influence of age and experience on adult breeding probability, which has rarely been done in natural conditions before.

2. MATERIAL AND METHODS

(a) *Species, study area and data collection*

The kittiwake is a pelagic seabird wintering at sea whose adults usually come back annually to breed on vertical cliffs on the coast line. Breeders lay a clutch of one to three eggs. Individuals show high overall site fidelity if they breed

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successfully or if a large proportion of their neighbours do so [14]. Conversely, they are more likely to skip breeding [15] and disperse [14,16] after a breeding failure and if a high proportion of their neighbours also failed breeding. Individuals are more likely to retain the same mate following a successful breeding event [17]. Individuals leave the colonies at the end of the breeding season at the latest (September), but some may leave earlier (e.g. non-breeders and pre-breeders; see below).

Mark-recapture data were collected in five colonies (a few kilometres apart from each other) in Brittany, France (48°5′ N, 4°36″ W) from 1979 to 2001 for 9970 individuals. Individuals were marked as chicks before fledging using a unique colour combination of plastic bands [12]. Every year, colonies were intensively searched for banded birds from January to August, though the large majority of data come from the more restricted nesting period, mid-April to mid-August. During a breeding season, a bird may be missed (not seen) or seen either as a pre-breeder [18,19], as a breeder or as a non-breeder. An individual was considered as a breeder if its nest reached a completion criterion [20]. From 1979 to 2001, the field effort was high enough to allow identification of the first breeding event and distinction between pre-breeders and non-breeders [10,18,19,21,22]. Indeed, as the annual resighting (or detection) probability of breeders and non-breeders (not pre-breeders) has always been close to 1 during this period [12,18,19], virtually no breeding event was missed in the study area. Non-breeders are individuals known to have previously bred, resighted in the current year, but that did not meet the criterion used to classify individuals as breeders [12,20]. Some individuals that previously bred were resighted but with unknown breeding activity; they were too few to allow consideration of an additional state in capture–recapture models. Individuals that previously bred and were not resighted in the current year (if any [10,18,19]), or with unknown breeding activity were not classified as non-breeders [12]. Note, however, that this unusually high detection probability is not a prerequisite to implement the statistical approach; we propose to assess breeding experience (see §2*b*). Non-breeders do not always establish in a specific place (not confined to a colony or cliff [23,24]), or at least cannot be assigned to a specific location because the resightings are almost equally distributed among different places. However, it is sometimes possible to assign them to a specific site or colony (non-breeders confined to a cliff) if they consistently attend a place, exhibit specific territorial behaviour or get involved in the preliminary steps of the breeding process with a mate (e.g. coordination behaviour). We acknowledge that the assigned state (confined/not confined) is subjective and depends on (i) the rate of attendance of the individual in different locations, (ii) the probability that investigators detect the individual when it is there (location-specific detection probability; among other things, this may depend on whether investigators devote as much effort to the different locations within a breeding season), and (iii) whether the individual exhibits territorial or preliminary breeding behaviour with a mate.

(b) *Dealing with experience when detection is less than 1*

We modelled the whole life cycle of kittiwakes (pre-breeders included). Denoting *i* the number of breeding events in the birds reproductive life, we distinguished individuals with no past experience ($i = 0$), having bred once before ($i = 1$) and with at least two previous breeding events ($i = 2$). In each breeding season, a bird of experience *i* may either breed and gain a point of experience ($i + 1$) at the end of the season, or not and keep experience *i*. In such settings, multi-state capture–recapture models are usually recommended to study transition between states while coping with the issue of detection of less than 1 [25]. However, whenever an individual was not observed in a given breeding season, it was not possible to update its experience counter since we did not know if this bird bred or not. Experience was, therefore, partially known, which demanded a particular treatment. We resorted to multi-event capture–recapture models [13] that were recently developed to deal with situations where there is uncertainty in the assignment of an individual to a particular state, here experience [9].

$$\boxed{1 \longrightarrow 2 \longrightarrow 0 \longrightarrow 3}$$

$$\text{(i)}\quad \overset{p}{\mathrm{PB}} \xrightarrow[\psi_{\mathrm{PB}\text{->}\mathrm{B}_0}]{\Phi_{\mathrm{PB}}} \overset{p}{\mathrm{B}_0} \xrightarrow[\psi_{\mathrm{B}_0\text{->}\mathrm{B}_1}]{\Phi_{\mathrm{B}_0}} \overset{1-p}{\mathrm{B}_1} \xrightarrow[\psi_{\mathrm{B}_1\text{->}\mathrm{B}_2}]{\Phi_{\mathrm{B}_1}} \overset{p}{\mathrm{B}_2}$$

$$\text{(ii)}\quad \overset{p}{\mathrm{PB}} \xrightarrow[\psi_{\mathrm{PB}\text{->}\mathrm{B}_0}]{\Phi_{\mathrm{PB}}} \overset{p}{\mathrm{B}_0} \xrightarrow[\psi_{\mathrm{B}_0\text{->}\mathrm{NB}_1}]{\Phi_{\mathrm{B}_0}} \overset{1-p}{\mathrm{NB}_1} \xrightarrow[\psi_{\mathrm{NB}_1\text{->}\mathrm{B}_1}]{\Phi_{\mathrm{NB}_1}} \overset{p}{\mathrm{B}_1}$$

Figure 1. Probability of an encounter history when the individual is not detected on a particular occasion. Observations ‘1’, ‘2’ and ‘3’ correspond, respectively, to the observation of the individual as a pre-breeder, a breeder with no experience and a breeder with unknown experience. Two scenarios (i) and (ii) may have generated this particular encounter history. Underlying states are denoted PB for pre-breeders, B_0 for breeder with no experience, B_1 for breeder with a single previous breeding event, B_2 for breeder with at least two previous breeding event and NB_1 for non-breeder with a single previous breeding event.

Our model considered nine different states underlying the five possible observations when collecting data: pre-breeder (PB), breeder (B) with no or some experience ($i = 0$, 1 or 2), non-breeder (NB) confined or not to a cliff with some experience ($i = 1$ or 2) and dead bird. Some of these states are directly observable (pre-breeders, breeders and non-breeders confined or not), whereas others are only partially observable (experience) or not observable (dead individuals). The temporal dynamics of states is governed by transitions depending on survival probability (Φ), the probability of breeding in the following year (ψ) and the probability of confinement (ϵ). States were related to the observations through detection probabilities (p). When an individual was not observed during a breeding season, the model considered all possible histories. For instance, let us ignore the confinement and assume that we have only four sampling occasions for simplicity (figure 1). We consider an individual that was seen as a pre-breeder (1), seen as a breeder with no experience (2), not seen (0) and finally seen as a breeder (3). Because this individual was missed at the penultimate occasion, its experience could not be known. Two scenarios are possible (figure 1): (i) this bird was breeder with a single previous breeding event (B_1) during the season, it went undetected and was therefore a breeder with two points of experience (B_2) in the last season (with probability $[p \times \Phi_{\mathrm{PB}} \times \psi_{\mathrm{PB}\text{->}\mathrm{B}_0} \times p \times \Phi_{\mathrm{B}_0} \times \psi_{\mathrm{B}_0\text{->}\mathrm{B}_1} \times (1 - p) \times \Phi_{\mathrm{B}_1} \times \psi_{\mathrm{B}_1\text{->}\mathrm{B}_2} \times p]$), and (ii) this bird was non-breeder with a single previous breeding event (NB_1) when it went undetected, which means that it was a breeder with a single point of experience (B_1) in the last occasion (with probability $[p \times \Phi_{\mathrm{PB}} \times \psi_{\mathrm{PB}\text{->}\mathrm{B}_0} \times p \times$

$\Phi_{B_0} \times \psi_{B_0\text{->}NB_1} \times (1 - p) \times \Phi_{NB_1} \times \psi_{NB_1\text{->}B_1} \times p$]). These two events being exclusive, the probability for this particular encounter history to occur is the sum of the two probabilities. This exercise can be carried out for every individual. The product of these probabilities is the likelihood that needs to be maximized to get maximum-likelihood estimates for all parameters. More details are given in the electronic supplementary material, appendix S1.

(c) *Modelling strategy*

First, we developed a general model reflecting biological processes of interest, which was based on prior studies of these colonies. We considered that, among pre-breeders, recapture probabilities depended on age, whereas survival and transition probabilities to state first-time breeder varied with both age and time additively [10,18]. Adult (hereafter, 'adults' will refer to birds that have recruited) recapture probabilities were repeatedly shown to be high in the study area [12,18,26]. Therefore, we assumed that these probabilities were independent of age and time. Second, we evaluated the fit of the general model to the data using the program U-Care [27]. Goodness-of-fit (GOF) tests are not available for models with permanent transitions (from PB to B here) [28]. Nevertheless, we used the available GOF procedure for the adult part of the resighting histories, which coincides with a standard multi-state capture–recapture model [28].

To test our predictions about the influence of experience on breeding probabilities, we fitted a set of models incorporating several effects (breeding state, age, time, experience and no effect) on each parameter (p, Φ, ψ, ϵ) sequentially while constraints on remaining parameters were held constant. Once the main effect was determined for a parameter, we added each of the remaining effects in an additive and interactive fashion to assess if one of these combinations was relevant. We repeated this until no better model was selected. We started by identifying the most appropriate structure for p, then for ϵ using the previously selected structure for p, then for Φ and finally for ψ using the structures for p, ϵ and Φ selected in the previous steps. In total, we fitted 43 competing models that were compared using Akaike's Information Criteria (AIC) [29]. Two models were considered distinct when their AIC differed by more than 2 units, otherwise we used the simplest one. Once model selection was completed, we checked again that the effects we dropped at earlier stages were not needed. We used the program E-Surge [30].

3. RESULTS

The GOF test of our general model indicated lack of fit ($\chi^2_{92} = 201.06$, $p < 0.001$). We corrected for overdispersion in subsequent analyses using a variance inflation factor ($\hat{c} = 201.06/92 = 2.1854$).

Survival of pre-breeders peaked at age 3. It was maximum in 2001 (0.89, s.e. = 0.02) and minimum in 1998 (0.70, s.e. = 0.02) (figure 2). Recruitment probability between ages 1 and 2 was very close to zero but increased with age up to 5 years old (from 0.27 to 0.68 depending on year), after which it declined (figure 3).

The best model according to AIC (table 1) suggested constant adult survival (0.79, s.e. = 0.01). This contrasts with previous studies on the same population, which detected a time effect [12,18]. We suspect that the use of a coefficient of overdispersion led to conservative results.

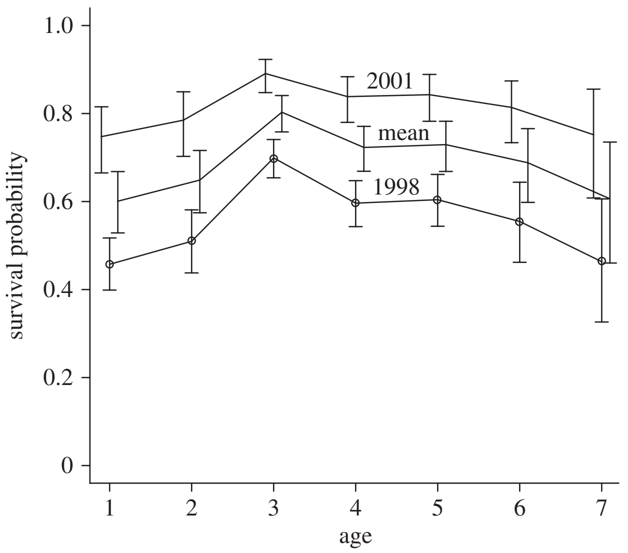

Figure 2. Survival probabilities of pre-breeders according to age (with 95% confidence intervals). The 'mean' line shows survival probabilities for a particular age averaged over the years from 1986 to 2001. After 7 years old, probabilities were not estimated because numbers of pre-breeders were too small. Years prior to 1986 were not included as pre-breeders could not be 7 years old.

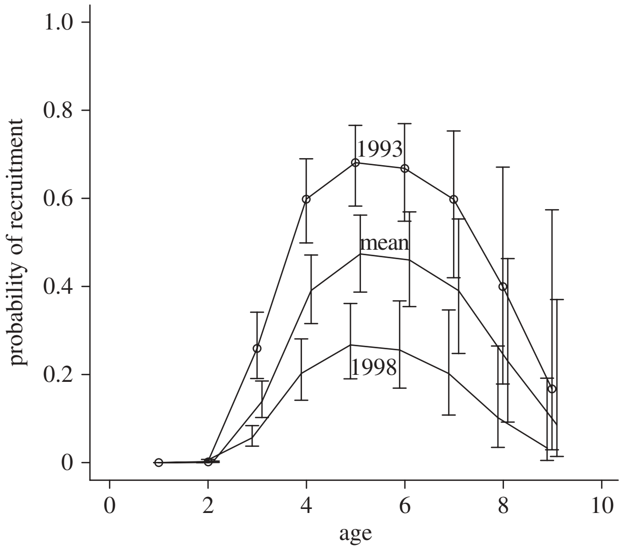

Figure 3. Probabilities of breeding in the following year for pre-breeders according to age (with 95% confidence intervals). The mean line shows survival probabilities for a particular age averaged over the years from 1988 to 2001. After 9 years old, probabilities were not estimated because numbers of pre-breeders were too small. Years prior to 1988 were not included as pre-breeders could not be 9 years old.

Recapture probabilities were constant after recruitment (0.99, s.e. = 0.01), while confinement probabilities were time-dependent (electronic supplementary material, appendix S2). No evidence of an influence of age on the breeding probabilities was found. Following a year without breeding, breeding probability varied by years but was independent of experience. After a year with breeding, breeding probability was influenced by both time and experience, with experienced breeders having a higher probability of breeding in the following year than inexperienced breeders (figure 4). Interestingly, the future breeding

Table 1. List of all models considered with AIC values for each set of parameters. (Best models are in bold. For each set of parameters (detection, confinement, survival and breeding), the best model is in bold. A '—' stands for constant parameter. See text for details on the model selection procedure.)

parameter	effect	AIC	number of estimated parameters
detection p	—	**16 184.79**	88
	breeding state	16 186.73	89
	experience	16 187.37	90
confinement ϵ	—	16 184.79	88
	breeding state	16 177.45	90
	experience	16 186.53	89
	age	16 206.51	104
	time	**16 137.72**	105
	time + state	16 137.05	107
	time + breeder	16 139.05	108
	time + non-breeder confined	16 139.05	108
	time + non-breeder not confined	16 137.05	107
	time + experience	16 139.72	106
	time + age	16 163.03	121
	time × state	16 162.62	126
	time × breeder	16 149.12	100
	time × non-breeder confined	16 193.76	100
	time × non-breeder not confined	16 178.65	99
	time × experience	16 162.69	122
	time × age	16 285.00	205
survival Φ	—	**16 137.72**	105
	breeding state	16 137.24	106
	experience	16 139.82	107
	age	16 169.89	125
	time	16 147.01	125
breeding ψ	—	16 137.72	105
	breeding state	16 119.56	106
	experience	**16 113.72**	107
	age	16 144.94	123
	time	16 123.47	124
	experience + age	16 142.42	125
	experience + time	16 095.90	127
	experience × state	**16 090.01**	109
	experience × breeder	**16 088.70**	108
	experience × non-breeder	16 128.93	112
	experience × age	16 161.70	139
	experience × time	16 146.65	163
	(experience × breeder) + age	16 115.41	126
	(experience × breeder) + time	**16 069.95**	128
	(experience × breeder) × age	16 159.99	140
	(experience × breeder) × time	16 149.84	164
	(experience × breeder) + time + age	16 384.25	144
	(experience × breeder) + time × age	16 094.05	338

probability for non-breeders was uniformly lower than that of inexperienced breeders (figure 4).

4. DISCUSSION

We developed a model accounting for variation in breeding probability with both age and experience, hence discriminating between the two, which has rarely been attempted in situations where detection issues prevent direct measurement of experience. Here, we addressed experience in a synthetic manner (0, 1 or ≥ 2 past breeding events). The approach can be extended to more general situations with a larger number of experience classes, but the influence of age and experience can be separated only in age-classes, where several levels of experience are represented. Moreover, wild vertebrate population studies where detection probability is very high are not so common [8]. For this reason, development of approaches designed to update the number of experience events when the animal is not seen will allow other investigators to address questions about ontogeny and life-history evolution in species, where learning may play an important part in determining fitness [1]. The ability to correctly assign breeding states to individuals may strongly depend on the sampling scheme. For example, unless investigators monitor breeding locations early in the season, breeders that failed their breeding attempt early (e.g. just after laying eggs) may be assigned the state 'non-breeder' (see 'identification of non-breeders' in Cam *et al.* [12]). Studies aiming at assessing breeding activity and success require appropriate sampling design and effort [31]. However, when state can be correctly assigned to part of the studied population, it

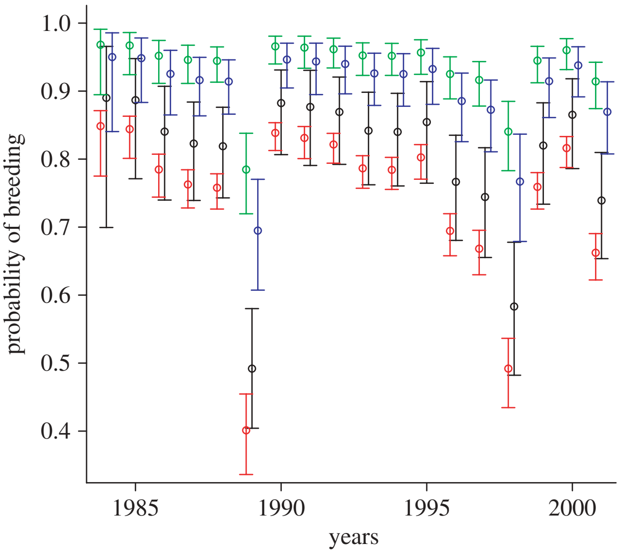

Figure 4. Probability of breeding in the following year for an adult according to state, experience and year: green points for breeders with at least two previous breeding events ($i = 2$), blue points for breeders having bred once before ($i = 1$), black points for breeders with no experience ($i = 0$) and red points for non-breeders.

is possible to estimate the probability of correctly classifying individuals using models handling state uncertainty [13].

Our estimates showed that pre-breeders had the highest probability of recruiting at intermediate age (around age 5). The increase in recruitment probability up to age 5 may reflect acquisition of physiological and behavioural maturity [21]. Other studies of the same population and another system where the recruitment of individuals has been addressed in detail provided evidence that individuals recruiting at intermediate age experienced higher reproductive success in the year of recruitment than those recruiting earlier [10,32]. For kittiwakes, delaying recruitment up to intermediate ages may be associated with fitness advantages that may offset the direct costs of delayed recruitment (i.e. costs such as 'missed' breeding opportunities in comparison with individuals recruiting earlier) [10]. Individuals delaying recruitment benefited from a longer prospecting period during which they may acquire more information and skills related to reproduction [33], which may contribute to favour the evolution of delayed breeding [34]. Besides, in the kittiwake, recruitment is a progressive social process, pre-breeders becoming more and more involved in the reproductive process (i.e. forming pairs, building incomplete nests) without fully meeting the criteria used to classify an individual as a breeder [21,22]. It is difficult to distinguish the effects of age versus experience acquired before first breeding by observing the pre-breeders own first breeding attempts; detailed behavioural studies during the pre-breeding period would be required.

Concerning adults, we first showed an influence of experience on the probability of breeding in the following year in breeders: experienced breeders had a higher probability of breeding in the following year than inexperienced breeders (figure 4). The classical explanation for this pattern is the trade-off between current and future reproduction [35,36]. Investment in current reproduction may have a cost in terms of reduced survival or future reproduction [4], and experienced breeders, having acquired abilities increasing the efficiency of their activities [19], may use less energy than inexperienced breeders to breed. Consequently, some of the inexperienced birds would skip reproduction whereas experienced kittiwakes would not in the next season. Studies of costs of first reproduction accounting for imperfect detection are providing increasing evidence of such costs in long-lived wild vertebrates (e.g. [36]). However, as previously emphasized [19], non-breeders exhibit the lowest probability of breeding in the following year compared with all categories of breeders, which is not consistent with the trade-off hypothesis (a larger cost in individuals investing more energy into reproduction), but is consistent with the heterogeneity one [2,11,12,19,36–39]. In addition, we found evidence of substantial variation of breeding probability with year, mostly characterized by two extreme events during the study (1989 and 1998). It has been hypothesized that the 1989 event was related to climatic conditions (a particularly dry year) that also affected sympatric greater black-backed gulls (*Larus marinus*) [12]. The slight decrease in breeding probability in the years 1996 and 1997 is related to a massive dispersal event within the study area (complete colony desertion by 1997; [24]) following heavy local predation by corvids. Whether extreme events (1989, 1998) coincide with particular climatic and oceanic events either in winter during migration or in the vicinity of colonies is currently being investigated.

Second, we did not detect an influence of age *per se* on adults breeding probability while it was reported in previous studies of the same population [11,23]. We see several explanations for this apparently contradictory result. An age effect can be masked by individual heterogeneity [11], which was not accounted for here, or may be detectable only when accounting for other covariates [23]. Alternatively, while many experienced individuals are reobserved at oldest ages, none of the inexperienced individuals reached old ages. The small range of variation of age in inexperienced birds may explain that we observed a slightly increasing but not significant trend with age of future breeding probability in inexperienced breeders (figure 5). Last, experience may indeed dominate age in driving reproduction, which was not addressed in other studies of the same population that did not consider age and experience simultaneously. We acknowledge that we addressed only a subset of hypotheses concerning breeding probability. The set of models considered can be completed by focusing on specific biological hypotheses and possible issues with sampling design. For example, breeding probability has been shown to be associated with divorce or dispersal in several species [15,24,40]. In addition, in this study population, previous results have provided evidence that the probability of breeding in the following year differs according to previous breeding success (for birds involved in the breeding process) [19,23]. Because of the well-known relationship between breeding success, dispersal and divorce, subsequent breeding probability is likely to vary with any of these covariates, as well as with those associated with breeding success itself [15,16].

Furthermore, lack of independence among individuals (i.e. members of a pair, individuals living in the same location) may create pseudoreplication [41]. To cope with this issue, we estimated a variance inflation factor and accounted for overdispersion in the estimation and

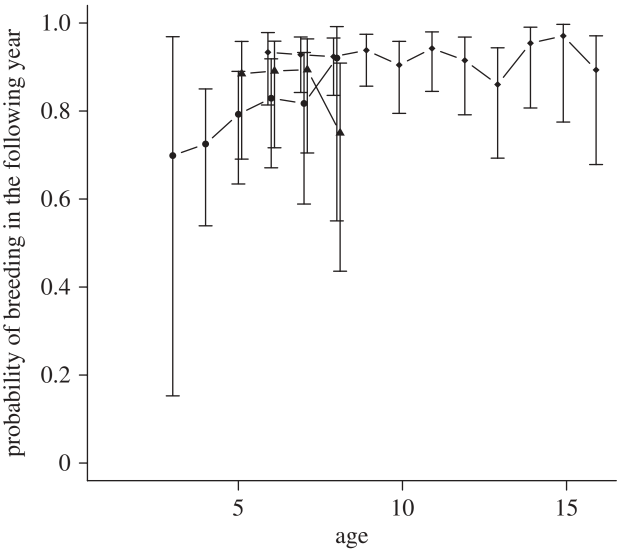

Figure 5. Probability of breeding in the following year for breeders as a function of age (x-axis) and experience: diamonds for breeders with at least two previous breeding events ($i = 2$), triangles for breeders having bred once before ($i = 1$) and filled circles for breeders with no experience ($i = 0$). The estimates are from the best model to which we added an effect of age for illustration.

model selection process [42]. Alternatively, one may want to explicitly account for specific sources of dependency among individuals (e.g. members of a pair could be treated as clusters in mixed models; [23,43]). An earlier study of this population did not provide evidence that results concerning the relationship between previous breeding state and subsequent breeding probability on the one hand, or between age and breeding probability on the other hand, were sensitive to incorporation of a covariance between members of a pair [23]. However, experience had not been considered, and the sample used concerned only members of double-marked pairs. Results cannot be generalized to either a different study period, or a different species, and the analytical approach was designed for situations where detection probability is very high. Methodological development will be needed to build models incorporating specific covariance structures and extend currently available random effect models [44,45].

Similarly, one may want to account for the fact that observations from individuals breeding on neighbouring sites may not be independent. A previous study accounted for the covariance between individuals breeding on the same cliff to address the relationship between previous breeding state and future breeding probability or between age and breeding probability [23]. Again, experience was not taken into account, and the analysis required selection of a specific subset of individuals confined in a given spatial unit. In addition, it was previously suggested that the approach used to define clusters of individuals breeding in the same spatial units (cliffs) was not satisfactory [23]. Indeed, the number of pairs in such units ranged from 10 to 300; unless there was no heterogeneity in breeding activity and success in the unit (e.g. complete breeding failure [24]), the degree of dependency among individual breeding events was likely to depend on distance among sites. Models accounting for distance among sites and perhaps other topographic characteristics within discrete spatial units are likely to reflect spatial processes in a more realistic manner [46]. Further work is required to build autologistic models [47] for spatially referenced capture–recapture data from resightings and breeding activity.

In conclusion, we evaluated the respective role of age and experience on the probability of breeding in a wild vertebrate by simultaneously incorporating these factors and others (time, breeding state and confinement) in our model. Because of the issue of detection of less than 1 inherent in natural conditions, the level of experience of individuals is difficult to assess, but the use of hidden process capture–recapture models allows study of the influence of intrinsic and extrinsic factors possibly playing an important part in the demography of a wide range of organisms.

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