Breeding experience might be a major determinant of breeding probability in long-lived species: the case of the greater flamingo

Roger Pradel, Rémi Choquet, Béchet Arnaud

▶ **To cite this version:**

Roger Pradel, Rémi Choquet, Béchet Arnaud. Breeding experience might be a major determinant of breeding probability in long-lived species: the case of the greater flamingo. 2011. hal-00655507v1

HAL Id: hal-00655507

https://hal.science/hal-00655507v1

Preprint submitted on 29 Dec 2011 (v1), last revised 11 May 2019 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Breeding experience might be a major determinant of breeding probability in long-lived species: the case of the greater flamingo

Roger Pradel:

corresponding author, roger.pradel@cefe.cnrs.fr, Centre d'Écologie Fonctionnelle et Évolutive, Campus CNRS, UMR 5175, 1919 Route de Mende, 34293 Montpellier Cedex 5, France & Institut Mediterrani d'Estudis Avançats, Population Ecology Group, ES-07190 Esporles, Spain

Rémi Choquet:

remi.choquet@cefe.cnrs.fr, Centre d'Écologie Fonctionnelle et Évolutive, Campus CNRS, UMR5175, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

Arnaud Béchet:

bechet@tourduvalat.org, Centre de Recherche de la Tour du Valat, Le Sambuc, 13200 Arles, France

Keywords: constraint, capture-recapture, life history, multievent models, restraint.

Online Appendix A Multi-event modeling of breeding experience

Online Appendix B Implementation of the generic model in E-SURGE

Online Appendix C Results of data analysis

Article

Abstract. The probability of breeding is known to increase with age early in life in many species. Apart from physical maturation, this increase may be due to experience accumulated through successive breeding episodes. However, this question has not been much investigated. We show how recent methodological advances allow to account for the number of previous –possibly unobserved– breeding episodes. Applying this method to the encounter histories of 14716 greater flamingos over 25 years, we get a detailed picture of the interplay of age and experience. Particularly notable is that breeding probability of inexperienced birds is always at least 3 times lower than that of same age experienced birds, and that one additional breeding experience is much more valuable than one additional year of age. Another pattern, that breeding probability of birds with <2 experiences drops after age 8, may point either to phenotypic heterogeneity or to the end of a sensitive period for acquiring behavioral skills. These results hold when controlling for the sex and for individual differences. All in all, the role of experience appears major in this species. Overlooking experience may hamper the detection of trade-offs and the assessment of individual heterogeneity. More importantly, experience may be a major factor in determining the optimal age of first breeding. However, manipulative experiments are desirable to confirm this finding.

Introduction

The probability that a sexually mature animal breeds is an important component of fitness and, as such, has long retained the attention of ecologists (Wynne-Edwards, 1939). In many species, especially long-lived ones, the probability of breeding tends to increase with age. This increase can be predicted on theoretical grounds. One line of reasoning, rooted in the optimal theory of life histories is that reproductive effort should increase with age because the expectation of future reproduction (residual reproductive value) decreases due to senescence (Williams, 1966) (in the details, the theory predicts that age specific reproductive effort differs in growing vs. stable populations and an increase is not always expected in fast-growing populations (see Charlesworth, 1994, p. 218)). Hence, in long-lived species, breeding probability is expected to covary positively with age as a result of increasing efforts, younger animals breeding less frequently because they ”restrain” from doing so (restraint hypothesis). At the other extreme, another theory puts forward the lack of foraging and breeding efficiency in young, individuals only progressively acquiring the skills required to breed successfully. In this view, younger individuals would breed less frequently because they are incapable of doing so (constraint hypothesis: Curio, 1983). Under this second theory, experience might be more important than age per se in determining breeding probability (Table 1). Indeed, appropriate breeding skills (e.g., nest site defense, coordination of incubation duties between partners) are particularly likely to be acquired in the course of repeated breeding episodes. By contrast, the restraint hypothesis predicts no effect of experience.

There is surprisingly very little empirical data examining, after controlling for age as a proxy for physical maturation, whether individuals with previous breeding experience are more likely to breed. This is in sharp contrast with the score of studies examining a related but distinct question, whether individuals with previous breeding experience are more likely

to succeed when they do breed (reviews in Clutton-Brock, 1988; Wooller *et al.*, 1990).
Overall reproductive success, the interesting parameter from an evolutionary perspective, is the combination of the two; hence, studying the conditional reproductive success of the sole breeders, while more practical, may miss important factors that act on the decision to breed. Methological difficulties faced when estimating breeding probability may explain the contrasted treatment of the two components of overall reproductive success. Indeed, the few studies examining the link between breeding experience and breeding probability all rely on bird populations where capture probability is virtually equal to 1. Results are contrasted: no effect of breeding experience has been found in kittiwakes *Rissa tridactyla* (Cam and Monnat, 2000), but a marked effect in fulmar *Fulmarus glacialoides* (Weimerskirch, 1990) and blue petrel *Halobaena caerulea* (Barbraud and Weimerskirch, 2005). However, in the first two studies, experience was measured as the number of years elapsed since the first breeding, which is different from the number of actual breeding experiences because the birds do not breed systematically every year. In the latter, age was unknown and thus not controlled for. In the endeavor to relate breeding probability to breeding experience, the obvious impediment is the incomplete breeding information inherent in most longitudinal studies. Most times, especially in birds, observations are conducted on the breeding area during the breeding season. Then, the non-observation of an animal can result either from the individual not being present and not breeding, or the individual being missed by the observer. The resulting data are then analyzed by treating non-breeding as an unobservable state. This common two-state approach (e.g. Kendall and Nichols, 2002; Rivalan *et al.*, 2005) allows testing the influence of age and of breeding investment during the previous season on breeding probability (Tavecchia *et al.*, 2005). However, because breeding experience is not observable, it is inadequate to examine the role of breeding experience. Today, new capture-recapture models with a hidden Markov structure allow estimating transitions among uncertain states such as the experience status

(multievent models, Pradel, 2005).

In this paper, we use the multievent framework to evaluate simultaneously the effects of age and experience on the breeding probability of the greater flamingos *Phoenicopterus roseus* breeding in the Camargue, southern France. Previous studies had suggested that breeding is a costly decision in this species especially in young age classes (reduced breeding probability: Tavecchia, unpublished manuscript; reduced immediate survival: Tavecchia *et al.*, 2001). Younger birds may thus be encouraged to refrain from expanding maximal parental effort to forestall the associated risk of dying and, hence, future reproduction. On the other hand, because breeding coordination is an important component of breeding outcome in flamingos, we expect experience to play an important role in the ability of breeding. If breeding probability is solely shaped by restraint, breeding probability should increase with age independently of experience. However, if breeding probability is mainly shaped by constraint, we predict breeding probability to increase markedly with experience in birds of the same age. We examine this question both on a large data set and on a restricted data set where we can control for individual differences through biometrical measurement.

Material and methods

Species, study area and data sets

Greater flamingos have bred in the saline lagoons of the Camargue, southern France, for centuries (Johnson and Cézilly, 2007). Since 1974, they have bred regularly on an artificial island located in a complex of commercial salt pans where water levels are managed for salt production, except in 1996 when the birds settled on a nearby island following adverse conditions. Since 1977, on average 12% (7-30%) of the chicks reared each year have been marked individually with PVC plastic rings engraved with

alphanumerical codes which can be read through a telescope from a distance of up to 400 m. In 1983, a tower hide was erected near the breeding island, 70 m from the closest nest. Every spring throughout the breeding season, this hide is occupied by observers who record breeding activities of ringed birds. Flamingos are recorded as breeders when they are seen (i) at a nest with an egg, (ii) $>$24h at the same position on the island (flag sticks allow precise positioning of each banded bird on the island), (iii) with a chick or (iv) sometimes only much later in the season feeding a chick in the creche. In 1996, observation of breeding birds were performed from a distant dyke and using a floating hide. Since 1985, the ringing protocol includes biometrical measurement of chicks providing a mean to calculate a proxy for individual differences in quality. In 2002, the monitoring was discontinued and restarted fully only 2 years later. The longest period when the data were collected continuously is thus 1977-2001. The restricted period starting in 1985 has more detailed data and no exceptional weather conditions. We decided to run a main analysis of the effects of age and experience on the extended period and a second analysis on the restricted period where we checked the effects of the possibly confounding factors of sex and body condition. As a measure of individual quality, we calculated a body condition index at fledging as the residual of the log-log regression of weight on tarsus length which has been shown to be a good predictor of recruitment in great tits (Both *et al.*, 1999). To account for differences in body shape between males and females as well as for different conditions encountered during the rearing period, one regression was run per sex and per cohort.

Multi-event modeling of breeding experience

Let us consider a bird of experience i, i.e. having bred exactly i times before. For the purpose of our study, we limit the range of experience to three levels: birds with no experience ($i = 0$), birds having bred once before ($i = 1$) and birds with multiple previous breeding experiences ($i = 2$). At each breeding occasion, a bird of experience i can either

breed (state B_i) or not (state NB_i). We denote ϕ the survival probability from one breeding season to the next and β_i the breeding probability of a bird of experience level i. A non-breeding bird with no experience (state NB_0) will remain so as long as it survives and does not breed : probability ϕ(1-β_0). When it starts breeding, it joins the state B_0 : probability $\phi\beta_0$. Because at this time it gains one point of experience, this state is only transitory. At the next occasion, it will be either a breeder with one previous experience (state B_1) : probability $\phi\beta_1$; or a non-breeder with one previous experience (state NB_1) : probability $\phi(1-\beta_1)$. A bird in state NB_1 will remain in this state as long as it skips breeding : probability $\phi(1-\beta_1)$. The acquisition of further experiences ($i=2$) through subsequent breeding episodes follows the same pattern (Figure 1). When the colony is visited, there are just two possible events for a particular bird : either it is seen breeding (code 1) or not (code 0). We assume that a non-breeding bird is not present on the colony and thus cannot be observed and that, if the bird is breeding, it has a probability $p<1$ of being seen. After several seasons, the set of events make up a resighting history. The event on a particular occasion does not allow to know the exact state of the bird. However, under a particular resighting history, some states are more likely than others. This renders the estimation of the model parameters possible in a probabilistic framework (for details on multievent modelling, see Pradel, 2005). Details on the current model and its implementation may be found in appendices A and B.

Results

We first analyzed the capture histories of 14716 flamingos marked from 1977 to 1997 and resighted until 2001. In order to focus on the breeding probabilities, we first decided on a survival and capture structure incorporating all the major known effects (see section C.1.2 for a test of these effects). Building upon previous studies, we distinguished two ageclasses

for survival probabilities, first-year and adult ($>$1 year-old). Survival probabilities were free to differ between the two age classes but also during the year 1984-1985 when a severe cold spell killed several thousand flamingos (Johnson and Cézilly, 2007). Otherwise, survival was maintained constant over the 'normal' years. Resighting probabilities were time-specific and fixed to 0 for the first two years of life because sexual maturity is only reached at 3 years. Finally the breeding probabilities (β) were calculated for each combination of age and experience with three levels of experience: inexperienced birds, birds that had bred once, birds that had bred at least two times. Using a hybrid symbolic-numeric method (Rouan *et al.*, 2009, section 3), we found that the first year survival could not be estimated separately from the breeding probabilities of inexperienced birds. Consequently, we decided to fix the first-year survival in normal years to a known value. This solved the identifiability problem. The model was implemented and run using program E-SURGE (Choquet *et al.*, 2009a), which uses a quasi-Newton algorithm to minimize the deviance.

Based on a sex-ratio of 1/1 and the sex-specific estimates of Balkız (2006), we computed a value of 0.763 for the first-year survival in normal years. With this value for normal years, first-year survival during the cold spell was estimated at 0.589, much lower than the sex-averaged estimate from Balkız: 0.697. However, because Balkız made her study with observations from the whole mediterranean range of the species, her estimate unlike ours is unaffected by the dispersal of young from the Camargue, which may have been particularly high after the cold spell. Assuming that Balkız estimate is the true survival of young, this means roughly 16 % dispersal of young. We nonetheless decided to try lower values of the normal-year first-year survival to examine the effect of emigration from the Camargue in normal years. Figure 2 shows estimates of breeding probabilities of inexperienced individuals for two values of the normal-year first-year survival : 0.763 (which assumes no emigration of young) and 0.632 (assuming 17% emigration of young). Estimates of other parameters were completely independent of the value of the first-year

survival. Survival probabilities of adults were estimated at 0.97 $\pm$ 0.001 in normal years and at 0.84 $\pm$ 0.02 during the cold spell. This matches previous estimates (Tavecchia *et al.*, 2001). Recapture probabilities did not differ from those found by Balkız (2010).

Breeding probability appeared clearly and strongly enhanced by experience (Figure 2). Breeding probabilities of birds with < 2 breeding experiences present a right skewed shape with a peak at age 8. This peak was also found in recent analyzes not including the experience factor (Balkız, 2006). The breeding probability at age 8 of breeders with one previous experience (0.49 $\pm$ 0.04) was $>$3 times higher than that of inexperienced breeders. By contrast, breeding probabilities of multiple experienced flamingos increased continuously until they became systematic breeders around age 15. Through model selection (Table 2), we checked that the model could not be simplified and in particular that experience and age were both important in determining the probability of breeding.

In order to control for possibly confounding factors, we next ran a more detailed analysis of the subset of cohorts ringed from 1985 where body measurements were available and after which no cold spell happened. This restricted data set is made of 3727 females, 3547 males and 5069 unknown-sex individuals. Sex has been found to have a limited influence on flamingo survival except for a marked cost of the first breeding in young females (Tavecchia *et al.*, 2001). We were particularly wary about the possible interference of this latter effect with the estimation of breeding probability. Sex also influences the probability of detection to a small extent (Pradel *et al.*, 1997). We decided to include these known effects of sex in the analysis and further to test its influence on breeding probability. To do so, the unknown sex individuals were assumed to have an equal chance of being of either sex and were introduced in the analysis following the methodology of Pradel *et al.* (2008) to which we refer the interested reader. The body condition index at fledging was introduced in the model as a covariate of breeding probability. Its effect was assessed separately for males and females. We ran a series of models (Table 3) where the structures of survival and

capture probabilities, based on previous knowledge, did not change. Sex-specific survival values for the first two years of life were fixed to the values estimated by Balkız (2006) to solve the identifiability problem (see above). Capture probabilities were made additively time- and sex- dependent. Once we had found the best possible description of breeding probability, we ran an additional model to test whether individuals with different body conditions had different baseline survivals by incorporating body condition as a covariate of survival separately for each sex; no effect was detected (increase in QAIC of 3.70, section C.2.3). As in the previous analysis, the best model indicates that breeding probability is influenced by age and experience. Sex is not retained as a main factor of breeding probability. However, body condition has a small but significant effect which differs between males and females: large males but small females being more likely to breed (Figure C2). These results were robust to the removal of four apparent outliers. Otherwise, the general shape of the pattern of variation of breeding probability with age and experience is very similar to that of the previous analysis, the difference between large and small individuals being of a lower order of magnitude than the effects of age or experience (Figure 2).

Discussion

Breeding experience emerges from our analysis as the major factor determining breeding probability in our study population. This rules out a pure restraint hypothesis which predicts no effect of experience (Table 1). On the other hand, our results are consistent with the constraint hypothesis. The decline in breeding probability in the least experienced past 8 years could be due to an increasing inability to acquire needed skills in older birds (e.g. displays involved in pair formation, Groothuis, 1992). The prominent role of experience is in stark contrast with the almost nonexistent role given to it in the theoretical literature on life history. For instance, Stearns, in his reference book, does not even mention breeding

experience when considering the benefits of early maturity (Stearns, 1992, p123-124). Practitioners seem to have been more aware of the potential influence of breeding experience on breeding probability (Clutton-Brock, 1988) but, for lack of a practical solution, they have generally made simplifying assumptions like assuming that breeding was systematic after the first reproduction (e.g. Pyle *et al.*, 1997). Yet, with the greater flamingo, we have a species where skipping is probably frequent. We estimate here that full breeding is attained only at age 15, and only for the individuals with at least two previous breeding experiences (Figure 2). Given the found large magnitude of the effect of breeding experience on breeding probability, one may wonder whether studies of generally weaker effects, like the cost of reproduction, have been affected in their conclusions when they ignored breeding experience. We review hereafter several common topics with which breeding experience may interfere, starting with the role of age.

experience vs age

Age had previously been shown to positively influence flamingo breeding behavior by ensuring better access either to breeding site (Rendon *et al.*, 2001) or to mate (Cézilly *et al.*, 1997). However, the confounding effect of experience could not be separately assessed. Here, we can examine the interplay of age and experience by picking a point on the lowest curve in Figure 2. This point corresponds to an inexperienced individual. An inexperienced individual with one more year of age lies at the next point on the same curve; an individual with one previous experience but the same age is found at the corresponding point of the intermediate curve. It appears that, from age 5 to age 17, it is always better to have one previous experience than one more year of age (age 4 is an apparent exception but see trade-offs below). After age 17, the data become too scarce to be reliably interpreted. For an individual with one previous experience (a point on the intermediate curve), it would similarly be better to have one more experience than to be one year older. In fact, past age

7, age has essentially a negative effect on breeding probability in this experience class.
Several studies have demonstrated an increase of survival and breeding success from first-time breeders to experienced breeders (Weimerskirch, 1990; Beckerman *et al.*, 2002; Barbraud and Weimerskirch, 2005; Nevoux *et al.*, 2007), but, to our knowledge, only another recent study has demonstrated the favorable cumulative effect of breeding experiences on breeding probability (Desprez *et al.*, 2011).

individual heterogeneity

Individuals in a population differ in many ways: some conspicuous, like sex and age; some hidden but identified, like breeding experience; and some unidentified, except possibly broadly, e.g. genetic differences. Individual heterogeneity usually refers to preexisting unidentified differences regarded as intrinsic or 'latent', such as those that result from a different genetic background or different conditions experienced during early development (Lindstrom, 1999). The actual breeding probability will result from this individual component superimposed on changing characteristics such as age and breeding experience. Because it is generally viewed as the cumulative result of a great number of individually tiny effects, individual heterogeneity is usually modeled as a normal random effect. For instance, we could consider that, independently of age or experience, each individual flamingo has its own personal latent breeding probability, the logit of which is normally distributed in the population. However, an unspecified individual random effect behaves essentially as a residual and tends to capture whatever individual differences are absent from the model structure. For instance, an individual random effect in a capture-recapture analysis of breeding probability not involving experience would reflect pre-existing differences among individuals but also different degrees of experience. In an attempt to control for individual differences, we rather incorporated an index of body condition. This was done on a restricted range of years because the information was not

available for the whole duration of the study. Body condition did influence breeding probability but to a lesser extent than experience (Figure 2). In presence of this covariate, experience was still retained as a major factor (Table 3). If body condition at fledging does predict body size and condition at recruitment, the effect detected in males would be consistent with the competition hypothesis (Gauthreaux, 1978), which predicts an advantage of larger males in better condition for acquiring territory and mate. As for females, the counterintuitive result that females in low body condition at fledging breed more may stem from the survival cost of first breeding present in very young females. Because of the lower physiological costs of egg laying in females with higher body size expected under the energetic hypothesis (Ketterson and Nolan, 1976), these females may be more risk-prone by attempting to breed earlier. This point, which deserves better consideration, is beyond the scope of our study.

Another interesting element on which to reflect is the shape of the three curves corresponding to the three classes of experience: while breeding probability increases with age in the three classes up to age 8, it then decreases in the two least-experienced classes while still going up to eventually reach 1 in the most experienced one (Figure 2). The original increase up to age 8 can be explained by the process of physiological maturation in young. This process must eventually slow down and end at some point. Then, with each passing year, the inexperienced class (lowest curve) loses its best elements which join the intermediate class by starting to breed. The average quality of the remaining individuals consequently goes down, which may explain why breeding probability decreases with age in this class after age 8. The same happens to the intermediate class whose best elements tend to join the upper class first; additionally, the new individuals that join it from the lower class are on average worse than the individuals already present. Thus, the average quality in the intermediate class is again expected to decrease with age, which is consistent with the decrease in breeding probability observed after age 8. Now, the continuous increase of

breeding probability in the upper class cannot be explained by individual differences. Here again individual heterogeneity causes a decrease with age of the average quality because of the continuous arrival from the intermediate class of individuals worse than those already present. The decrease in breeding probability after age 8 in the two least experienced classes but not in the most experienced one seems to indicate that having few experiences is penalizing after this age.

A possible scenario is that, of all the individuals with similar latent breeding probabilities, those which by chance do not start to breed when the others do, have the next year a lower chance of breeding, then an even lower one the year after, and so on; they are caught in a downward spiral. This scenario could for instance rests on the existence of a sensitive period for learning and perfecting display behaviours in flamingos, in a way similar to song learning in songbirds (Beecher and Brenowitz, 2005).

skipping and trade-offs

Up to now, we have not discussed trade-offs because, although trade-offs are phenomenons of major importance in the understanding of the evolution of life histories, in terms of magnitude they are second-order effects, except possibly in the very young. Trade-offs are commonly studied in relation to skipping behaviour (e.g. Cam *et al.*, 1998; Rivalan *et al.*, 2005). It is often assumed that skipping is common among young breeders, then becomes less frequent and eventually there is an age of full breeding after which every individual still alive will breed systematically. The notion of a progressive acquisition of a regular breeding activity is well supported by our results because breeding probability increases with age until age 8 for every individual. However, past age 8, this holds only for individuals that have bred at least twice. The frequently held belief that there is an age of full breeding may stem from field observations that recognizable old individuals are breeding systematically year after year. However, our model predicts that there are old

individuals almost never present on the breeding grounds because they breed only once or twice during their lives (see also sparrowhawk, Newton, 1989, pp. 279-296). These individuals may easily pass unnoticed during field studies where only breeders are observed as is common with colonial birds.

The progressive increase of breeding probability in young can be seen as an ontogenetic process by which individuals first acquire the physiological capacity to breed, then behavioural or social skills. This provides a rationale for a cost of early breeding. As soon as physiological maturation is achieved, reproduction becomes possible but it is inefficient and costly because some other skills have not been acquired or sufficiently perfected. An individual that nonetheless engages in breeding at an early age may thus have difficulties recovering and hence may have a reduced breeding probability the next year. This trade-off between successive breedings is difficult to examine from our analysis. Nonetheless, we note that flamingos having bred at age 3 do not breed at age 4 (9 birds were actually observed breeding at 3), although other still inexperienced individuals start breeding then. At this very early age, the cost of reproduction appears thus to cancel the advantage of acquired experience. But this hierarchy of effects is rapidly reversed. At age 6, the individuals with two previous breeding episodes have necessarily bred at age 5 (because breeding at 3 precludes breeding at 4). Yet, they exhibit a higher breeding probability than individuals with just one experience of which at least some have not bred at 5. Thus, as early as 6, experience appears to override the potentially negative effect of a recent breeding. The difficulty of establishing the existence of trade-offs in the wild has long been put down to individual heterogeneity (Noordwijk and Jong, 1986), but the neglected role of experience is another possible reason.

implications in terms of life-history strategy

A turning point in the life history of the Camargue greater flamingos seems to lie somewhere around age 8, probably earlier. Prior to that age, trade-offs have been found (reduced breeding probability: this study and Tavecchia, unpublished manuscript; reduced immediate survival: Tavecchia *et al.*, 2001). Both costs are strongest in the youngest breeders and then diminish rapidly to become undetectable around age 6. Because of this pattern, breeding at the earliest possible age is probably not optimal because the associated costs are then too high to be compensated for by expected higher future breeding outcomes as a result of experience. Yet, a pivotal age must exist where the long-term gain coming with experience balance the short-term cost of reproduction. Apart from the greater flamingos, there is accumulating evidence that trade-offs are especially strong early in life when reproduction seems to be costly, particularly the first time (Cam and Monnat, 2000; Barbraud and Weimerskirch, 2005; Beauplet *et al.*, 2006; Nevoux *et al.*, 2007; Sanz-Aguilar *et al.*, 2008). On the other hand, the generality of our result on the importance of experience in breeding probability must be confirmed. Yet, if experience is confirmed as a major factor acting on breeding probability, the way we understand life history strategy may have to be changed. Experience and cost of reproduction would then appear as the two dominant opposite forces vying to determine the optimal age of first breeding, senescence playing probably a very minor role in long-lived species.

conclusion

Among the natural candidate factors potentially determining the breeding probability of an individual, breeding experience had scarcely been assessed for lack of suitable methods. Using novel statistical tools for capture-recapture data, we have developped a simple and universal model applicable to any species where individuals can be made

recognizable (simple generalizations like observations of non-breeders are straitforward). We have found not only that breeding experience is a factor but actually a major one, at least for the studied species. We have then drawn the consequences of our finding in relation to major topics of the life history theory. It appears that the difficult and yet central point in studies of breeding probability is to unequivocally separate what pertains to experience from what stems from individual heterogeneity taken in the meaning of preexisting differences inherited or acquired during early life. Progress in statistical models could help in this respect. However, we believe that it is only through manipulative experiments that the exact part of each factor can be assessed. A possible approach could be to prevent a random sample of young individuals from breeding for several years, possibly through hormonal manipulation (Chuei, 2007), and then comparing their breeding probability to that of control individuals.

Acknowledgments

This work is part of a long-term study of greater flamingos initiated by Dr L. Hoffmann, carried on by A. Johnson and supported by Tour du Valat. We are grateful to the field assistants of the flamingo project, in particular A. Arnaud, and to C. Germain for maintaining the high quality of the database. We also acknowledge all the voluntary observers who read rings in the field. This work would not have been possible without the authorization given by the company Salins for access to the saltpans. We also thank Tom Sherratt, Marco Festa-Bianchet, and an anonymous reviewer for their stimulating comments on a previous version.

References

406 Balkız, Ö. 2006. Dynamique de la métapopulation de flamants roses en Méditerranée: implications pour la conservation. Ph.D. thesis, Univ Montpellier II, Montpellier, France.

408 Balkız, Ö., Béchet A., Rouan L., Choquet R., Germain C., Aguilar Amat J., Rendón-Martos M., Baccetti N., Nissardi S., Özesmi U. and Pradel R. in press. Experience-dependent 410 natal philopatry of breeding Greater flamingos. Journal of Animal Ecology.

Barbraud, C., and H. Weimerskirch. 2005. Environmental conditions and breeding 412 experience affect costs of reproduction in blue petrels. Ecology 86:682–692.

Beauplet, G., C. Barbraud, W. Dabin, C. Kussener, and C. Guinet. 2006. Age-specific 414 survival and reproductive performances in fur seals: Evidence of senescence and individual quality. Oikos 112:430–441.

416 Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology and Evolution 418 17:263–269.

Beecher, M. D., and E. A. Brenowitz. 2005. Functional aspects of song learning in 420 songbirds. Trends in Ecology and Evolution 20:143–149.

Both, C., M. E. Visser and N. Verboven. 1999. Density-dependent recruitment rates in great 422 tits: the importance of being heavier. Proceedings of the Royal Society of London Series B-Biological Sciences 266:465–469.

424 Cam, E., J. E. Hines, J. Y. Monnat, J. D. Nichols, and E. Danchin. 1998. Are adult nonbreeders prudent parents? the kittiwake model. Ecology 79:2917–2930.

426 Cam, E., and J. Y. Monnat. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. Journal of Animal Ecology 69:380–394.

428 Cézilly, F., V. Boy, C. J. Tourenq, and A. R. Johnson. 1997. Age-assortative pairing in the greater flamingo phoenicopterus ruber roseus. Ibis 139:331–336.

430 Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge, UK.

432 Choquet, R., L. Rouan, and R. Pradel. 2009a. Program E-SURGE: a software application for fitting multievent models. Pages 845–865 *in* D. L. Thomson, E. G. Cooch, and M. J.
434 Conroy, editors. Modeling demographic processes in marked populations. Environmental and Ecological Statistics. Volume 3. Springer, Berlin, Germany.

436 Choquet, R., J. Y. Lebreton, O. Gimenez, A. M. Reboulet, and R. Pradel. 2009b. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data.
438 Ecography 32:1071–1074.

Chuei, J. Y., C. S. Asa, M. Hall-Woods, J. Ballou, and K. Traylor-Holzer. 2007. Restoration
440 of reproductive potential after expiration or removal of melengestrol acetate contraceptive implants in tigers (Panthera tigris). Zoo Biology 26:275-288.

442 Clutton-Brock, T. 1988. Reproductive success. University Press, Chicago, USA.

Curio, E. 1983. Why do young birds reproduce less well? Ibis 125:400–404.

444 Desprez, M., R. Pradel, E. Cam, J. Y. Monnat, and O. Gimenez. 2011. Now you see him, now you don't: experience, not age, is related to reproduction in kittiwakes. Proceedings
446 of the Royal Society of London Series B-Biological Sciences 278:3060–3066.

Gauthreaux Jr, S. 1978. The ecological significance of behavioral dominance. Perspectives
448 in ethology, 3:17–54.

Groothuis, T. 1992. The influence of social experience on the development and fixation of
450 the form of displays in the black-headed gull. Animal Behaviour 43:1–14.

Johnson, A., and F. Cézilly. 2007. *The Greater Flamingo*. T & AD Poyser, London, UK.

Kendall, W. L., and J. D. Nichols. 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. Ecology 83:3276–3284.

Ketterson, E., and V. Nolan. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (Junco hyemalis hyemalis). Ecology 57:679–693.

Lindstrom, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology and Evolution 14:343–348.

Nevoux, M., H. Weimerskirch, and C. Barbraud. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. Journal of Animal Ecology 76:159–167.

Newton, I. 1989. lifetime reproductive success in birds. Academic Press, San Diego, California, USA.

Noordwijk, A. J. v., and G. D. Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

Pollock, K. H. 1981. Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics*, 37, 521–529.

Pradel, R. 2005. Multievent: an extension of multistate capture-recapture models to uncertain states. Biometrics 61:442–447.

Pradel, R., L. Maurin–Bernier, O. Gimenez, M. Genovart, R. Choquet, and D. Oro. 2008. Estimation of sex-specific survival with uncertainty in sex assessment. Canadian Journal of Statistics 36:29–42.

Pradel, R., A. R. Johnson, A. Viallefont, R. G. Nager, and F. Cézilly. 1997. Local recruitment in the greater flamingo: a new approach using capture-mark-recapture data. Ecology 78:1431–1445.

Pyle, P., N. Nur, W. J. Sydeman, and S. D. Emslie. 1997. Cost of reproduction and the evolution of deferred breeding in the western gull. Behavioral Ecology 8:140–147.

Rendon, M. A., A. Garrido, J. M. Ramirez, M. Rendon-Martos, and J. A. Amat. 2001. Despotic establishment of breeding colonies of greater flamingos, phoenicopterus ruber, in southern spain. Behavioral Ecology and Sociobiology 50:55–60.

Rivalan, P., A. C. Prevot-Julliard, R. Choquet, R. Pradel, B. Jacquemin, and M. Girondot. 2005. Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. Oecologia 145:564–574.

Rouan, L., R. Choquet, and R. Pradel. 2009. A general framework for modeling memory in capture-recapture data. Journal of Agricultural, Biological and Environmental Statistics 14:338–355.

Sanz-Aguilar, A., G. Tavecchia, R. Pradel, E. Minguez, and D. Oro. 2008. The cost of reproduction and experience-dependent vital rates in a small petrel. Ecology 89:3195–3203.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Tavecchia, G., T. Coulson, B. J. T. Morgan, J. M. Pemberton, J. C. Pilkington, F. M. D. Gulland, and T. H. Clutton-Brock. 2005. Predictors of reproductive cost in female soay sheep. Journal of Animal Ecology 74:201–213.

Tavecchia, G., R. Pradel, V. Boy, A. R. Johnson, and F. Cézilly. 2001. Sex- and age-related

variation in survival and cost of first reproduction in greater flamingos. Ecology
496 82:165–174.

Weimerskirch, H. 1990. The influence of age and experience on breeding performance of
498 the antarctic fulmar, fulmarus glacialoides. Journal of Animal Ecology 59:867–875.

Williams, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of lack's
500 principle. American Naturalist 100:687–690.

Wooller, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1990. Reproductive success of
502 short-tailed shearwaters puffinus tenuirostris in relation to their age and breeding
experience. Journal of Animal Ecology 59:161–170.

504 Wynne-Edwards, V. C. 1939. Intermittent breeding of the fulmar (fulmarus glacialis), with
some general observations on non-breeding in sea-birds. Proceedings of the Zoological
506 Society of London 109A:127–132.

Table 1: The role of experience in the increase of breeding probability with age under the restraint and the constraint hypotheses. Under a pure restraint hypothesis, breeding probability is hypothesized to increase as a response to the decline in residual reproductive value with age due to senescence : thus, it increases with age but no effect of experience is expected. Under a pure constraint hypothesis, breeding probability increases through improved skills: the experience acquired is thus the relevant factor; age still acts positively in young due to the process of physiological maturation.

Hypothesis	driver of increase in breeding probability	role of experience predicted
pure restraint	senescence	no
pure constraint	behavioral improvement	yes

Table 2: Modeling the effects of age and breeding experience on the breeding probability β of greater flamingos marked as chicks from 1977 to 1997 and resighted as breeders in the Camargue, southern France, until 2001. Taking as a reference the fully age- and time-dependent survival and capture probabilities model (Pollock, 1981), we calculated with program U-CARE (Choquet *et al.*, 2009b) a variance inflation factor ĉ of 2.244 (section C.1.1): ΔQAIC is the Quasi Akaike Information Criterion relative to the best model; k is the model rank. Experience is a factor with 3 levels (e): no experience, 1 previous experience, >1 previous experience; or 2 levels (e_2): no experience, some previous experience. Age (a) is a categorical variable. First-year survival in normal years is fixed to 0.763, which is the sex-averaged value of Balkız (2006) estimates; first-year survival for the cold spell year 1984 is estimated separately; adult survival is estimated separately for the cold spell year and the 'normal' years. Capture probability is time-dependent. Only the breeding probability part of the model varies.

Model	Assumptions of best model or – difference from best model	Deviance	k	ΔQAIC (ĉ=2.244)
$\beta_{a.e}$	Breeding probability varies with age within 3 levels of previous breeding experience	53763.22	87	0
$\beta_{a.e_2}$	– only 2 levels of previous breeding experience	54047.69	67	86.76
β_a	– no effect of experience	54707.50	47	340.79
β_e	– no age effect	54926.11	29	402.20
$\phi_{a.t}\ p_{a.t}$	reference model for fit assessment	53883.71	439	757.69

Table 3: Model selection of the effects of sex (s), age, breeding experience and body condition as a chick (BC) on the greater flamingo breeding probability β. Analysis carried out on the 1985-2001 restricted data set. Taking as a reference the fully age- and time-dependent survival and capture probabilities model (Pollock, 1981), we calculated with program U-CARE (Choquet *et al.*, 2009b) a variance inflation factor ĉ of 1.625 (section C.2.1): ΔQAIC is the Quasi Akaike Information Criterion relative to the best model; k is the model rank. Experience is a factor with 3 levels (e): no experience, 1 previous experience, >1 previous experience; or 2 levels (e_2): no experience, some previous experience. Age (a) is generally a categorical variable; smoothed effects of age, namely linear and quadratic on the logit scale, were tested respectively on the highest level of experience (a_2) and on both the highest and the intermediate levels (a_{12}). First-year and second-year survivals are fixed to the values estimated by Balkız (2006): 0.779 and 0.944 respectively for females, and 0.747 and 0.921 respectively for males; adult survival is sex-specific with an additive age-specific smoothed effect of first breeding for females, namely linear effect of log-age on the logit scale canceling at 6. Capture probability is additively time- and sex-dependent. Only the breeding probability part of the model varies.

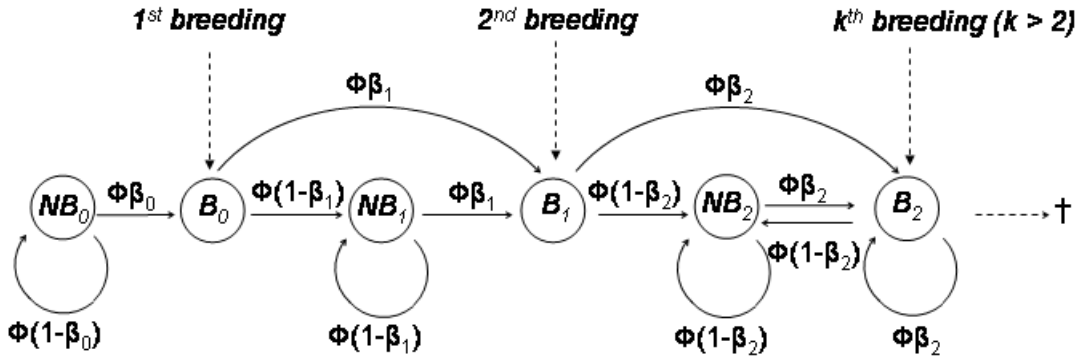
Model	Assumptions of best model or – difference from best model	Deviance	k	ΔQAIC (ĉ=1.625)
$\beta_{a_2.e+BC.s}$	Smoothed age effect on the highest level of experience; age and experience interact fully on the 2 lower levels; additive linear effect of body condition separately for females and males	17575.27	49	0
$\beta_{a.e+BC.s}$	– age and experience interact fully on all levels	17571.45	58	15.66
$\beta_{a.e}$	– no effect of body condition	17583.12	57	20.83
$\beta_{a.e_2+BC.s}$	– only 2 levels of experience fully interacting with age	17613.38	48	21.45
$\beta_{a_{12}.e+BC.s}$	– smoothed age effect on the intermediate level of experience	17655.74	39	29.52
$\beta_{a+BC.s}$	– no effect of experience	17717.29	34	57.39
$\beta_{a.e.s+BC.s}$	– main effect of sex	17528.26	98	69.07
$\beta_{e+BC.s}$	– no age effect	18134.07	23	291.88

List of Figures

1 General pattern of transitions between breeding states : B_i, breeder with i previous experiences and NB_i, non-breeder with i previous experiences for $i = 0, 1, 2+$. The transition probabilities are expressed in terms of ϕ, the probability of surviving to the next breeding season, and β, the probability, conditional on survival, of breeding the next season. The β's will always be age-dependent in practice. 27

2 Breeding probability as a function of age and experience for greater flamingos breeding in the Camargue, south of France. Plain circle: no previous breeding episode; empty circle: one previous breeding episode; triangle: 2 or more previous breeding episodes. The curve for inexperienced individuals is that obtained with a normal-year first-year survival of 0.632; the dashed curve below is for a value of 0.763 of the same parameter corresponding to an absence of emigration (see text for details). The amount of variation linked to body condition, as estimated from the restricted data set (see text), is shown on the right panel for values of breeding probabilities of 0.8, 0.5 and 0.2. The range corresponds to where 95% of the males are situated, the range for females would be only slightly smaller. These ranges are independent of age or experience level, symmetric around and maximum at 0.5. 28

Figure 1:


1st breeding
2nd breeding
kth breeding (k > 2)
Φβ1
Φβ2
NB0
Φβ0
B0
Φ(1-β1)
NB1
Φβ1
B1
Φ(1-β2)
NB2
Φβ2
B2
†
Φ(1-β2)
Φ(1-β0)
Φ(1-β1)
Φ(1-β2)
Φβ2

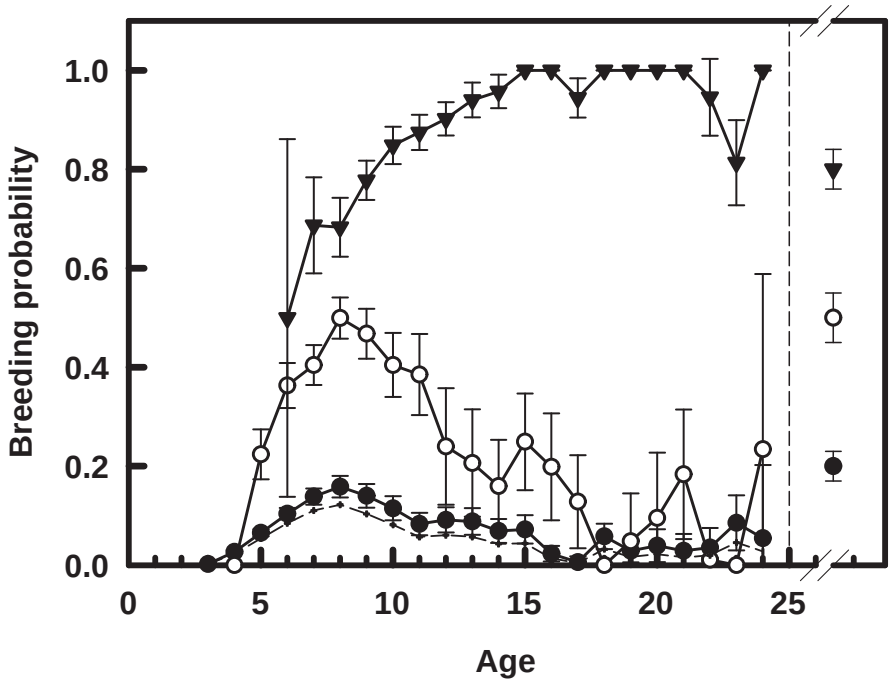



Figure 2: