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

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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
20 species. Apart from physical maturation, this increase may be due to experience accumu-
lated through successive breeding episodes. However, this question has not been much in-
22 vestigated. We show how recent methodological advances allow to account for the number of
previous –possibly unobserved– breeding episodes. Applying this method to the encounter
24 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
26 is always at least 3 times lower than that of same age experienced birds, and that one addi-
tional breeding experience is much more valuable than one additional year of age. Another
28 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
30 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
32 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,
34 manipulative experiments are desirable to confirm this finding.

36 Introduction

The probability that a sexually mature animal breeds is an important component of
38 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
40 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
42 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
44 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
46 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
48 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
50 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
52 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,
54 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
56 effect of experience.

There is surprisingly very little empirical data examining, after controlling for age as a
58 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
60 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).

62 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
64 breeders, while more practical, may miss important factors that act on the decision to breed.
Methodological difficulties faced when estimating breeding probability may explain the
66 contrasted treatment of the two components of overall reproductive success. Indeed, the
few studies examining the link between breeding experience and breeding probability all
68 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*
70 (Cam and Monnat, 2000), but a marked effect in fulmar *Fulmarus glacialis*
(Weimerskirch, 1990) and blue petrel *Halobaena caerulea* (Barbraud and Weimerskirch,
72 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
74 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
76 breeding experience, the obvious impediment is the incomplete breeding information
inherent in most longitudinal studies. Most times, especially in birds, observations are
78 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
80 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
82 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).
84 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
86 structure allow estimating transitions among uncertain states such as the experience status

(multievent models, Pradel, 2005).

88 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*
90 *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
92 breeding probability: Tavecchia, unpublished manuscript; reduced immediate survival:
Tavecchia *et al.*, 2001). Younger birds may thus be encouraged to refrain from expanding
94 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
96 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
98 should increase with age independently of experience. However, if breeding probability is
mainly shaped by constraint, we predict breeding probability to increase markedly with
100 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
102 measurement.

Material and methods

104 Species, study area and data sets

Greater flamingos have bred in the saline lagoons of the Camargue, southern France,
106 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
108 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
110 each year have been marked individually with PVC plastic rings engraved with

alphanumeric codes which can be read through a telescope from a distance of up to 400
112 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
114 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
116 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,
118 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
120 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
122 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
124 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
126 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
128 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
130 encountered during the rearing period, one regression was run per sex and per cohort.

Multi-event modeling of breeding experience

132 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
134 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

136 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
138 non-breeding bird with no experience (state NB_0) will remain so as long as it survives and
does not breed : probability $\phi(1-\beta_0)$. When it starts breeding, it joins the state B_0 :
140 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
142 (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
144 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
146 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
148 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
150 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
152 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
154 implementation may be found in appendices A and B.

Results

156 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
158 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

160 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
162 spell killed several thousand flamingos (Johnson and Cézilly, 2007). Otherwise, survival
was maintained constant over the 'normal' years. Resighting probabilities were time-specific
164 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
166 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
168 (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
170 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
172 (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
174 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
176 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
178 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
180 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
182 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
184 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

186 survival. Survival probabilities of adults were estimated at 0.97 ± 0.001 in normal years and
at 0.84 ± 0.02 during the cold spell. This matches previous estimates (Tavecchia *et al.*,
188 2001). Recapture probabilities did not differ from those found by Balkız (2010).

Breeding probability appeared clearly and strongly enhanced by experience (Figure 2).
190 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
192 experience factor (Balkız, 2006). The breeding probability at age 8 of breeders with one
previous experience (0.49 ± 0.04) was >3 times higher than that of inexperienced
194 breeders. By contrast, breeding probabilities of multiple experienced flamingos increased
continuously until they became systematic breeders around age 15. Through model
196 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.

198 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
200 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
202 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
204 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
206 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
208 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
210 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

212 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
214 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
216 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
218 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
220 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
222 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
224 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
226 being of a lower order of magnitude than the effects of age or experience (Figure 2).

Discussion

228 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
230 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
232 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
234 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

236 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
238 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
240 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
242 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
244 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
246 ignored breeding experience. We review hereafter several common topics with which
breeding experience may interfere, starting with the role of age.

248 **experience vs age**

Age had previously been shown to positively influence flamingo breeding behavior by
250 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.
252 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
254 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
256 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
258 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
260 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.

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

individual heterogeneity

268 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
270 possibly broadly, e.g. genetic differences. Individual heterogeneity usually refers to
preexisting unidentified differences regarded as intrinsic or 'latent', such as those that result
272 from a different genetic background or different conditions experienced during early
development (Lindstrom, 1999). The actual breeding probability will result from this
274 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
276 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
278 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
280 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
282 capture-recapture analysis of breeding probability not involving experience would reflect
pre-existing differences among individuals but also different degrees of experience. In an
284 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

286 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,
288 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
290 consistent with the competition hypothesis (Gauthreaux, 1978), which predicts an
advantage of larger males in better condition for acquiring territory and mate. As for
292 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.
294 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
296 be more risk-prone by attempting to breed earlier. This point, which deserves better
consideration, is beyond the scope of our study.

298 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
300 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
302 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
304 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
306 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
308 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
310 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

312 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
314 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
316 classes but not in the most experienced one seems to indicate that having few experiences
is penalizing after this age.

318 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
320 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
322 period for learning and perfecting display behaviours in flamingos, in a way similar to song
learning in songbirds (Beecher and Brenowitz, 2005).

324 **skipping and trade-offs**

Up to now, we have not discussed trade-offs because, although trade-offs are
326 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.
328 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,
330 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
332 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
334 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
336 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
338 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
340 observed as is common with colonial birds.

The progressive increase of breeding probability in young can be seen as an
342 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
344 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
346 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
348 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
350 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
352 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
354 (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
356 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
358 been put down to individual heterogeneity (Noordwijk and Jong, 1986), but the neglected
role of experience is another possible reason.

360 **implications in terms of life-history strategy**

A turning point in the life history of the Camargue greater flamingos seems to lie
362 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
364 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
366 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
368 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
370 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
372 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
374 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
376 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
378 breeding, senescence playing probably a very minor role in long-lived species.

conclusion

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

384 recognizable (simple generalizations like observations of non-breeders are straightforward).
We have found not only that breeding experience is a factor but actually a major one, at
386 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
388 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
390 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
392 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,
394 possibly through hormonal manipulation (Chuei, 2007), and then comparing their breeding
probability to that of control individuals.

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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 \hat{c} of 2.244 (section C.1.1): Δ QAIC 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	Δ QAIC ($\hat{c}=2.244$)
$\beta_{a.e}$	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 \hat{c} of 1.625 (section C.2.1): $\Delta QAIC$ 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	$\Delta QAIC$ ($\hat{c}=1.625$)
$\beta_{a_2.e+BC.s}$	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

508 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
 510 $i = 0, 1, 2+$. The transition probabilities are expressed in terms of ϕ , the
 probability of surviving to the next breeding season, and β , the probability,
 512 conditional on survival, of breeding the next season. The β 's will always be
 age-dependent in practice. 27

514 2 Breeding probability as a function of age and experience for greater flamin-
 gos breeding in the Camargue, south of France. Plain circle: no previous
 516 breeding episode; empty circle: one previous breeding episode; triangle: 2 or
 more previous breeding episodes. The curve for inexperienced individuals is
 518 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 ab-
 520 sence 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
 522 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 fe-
 524 males would be only slightly smaller. These ranges are independent of age or
 experience level, symmetric around and maximum at 0.5. 28

Figure 1:

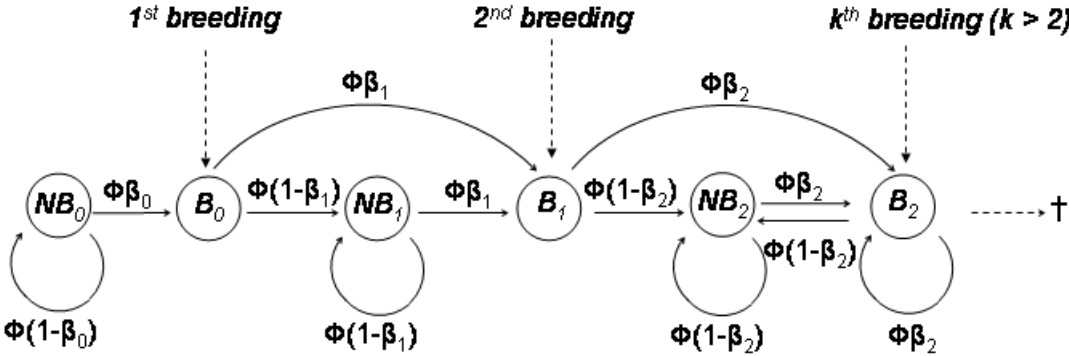


Figure 2:

