

# Using multistate recapture modelling to assess age-specific bottlenecks in breeding success: a case study in the greater flamingo *Phoenicopterus roseus*

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Bird reproductive performance often increases with age or experience as a result of improved foraging skills, increased reproductive effort, improved coordination between partners, or a selection process. However, it remains unclear whether age and/or experience affect equally the successive steps of the breeding process, from egg laying to incubation and chick rearing. Using data from a long-term study of the Camargue (southern France) population of the greater flamingo *Phoenicopterus roseus*, we studied the influence of age on step-specific breeding performances during a single breeding season. We used, for the first time, multistate recapture models to evaluate the effect of age on breeding attendance (as a surrogate for breeding success) during incubation, early chick rearing and late chick rearing. Our results show a significant positive influence of age on breeding attendance, but only during the incubation period. Older parents had a higher probability than younger ones of completing incubation, whereas after the chick had hatched, the influence of parental age on breeding attendance was no longer significant. Although a high rate of nest desertion by younger flamingos during the middle of the incubation period coincided with a period of heavy rainfall, including rainfall level as a covariate did not improve the fit of the models. We discuss our results in relation to the evolution of life-history strategies in long-lived bird species and the influence of environmental instability.

Across a wide range of iteroparous species, breeding performance strongly depends on parental age with young and first-time breeders performing less successfully than older and experienced breeders (Clutton-Brock 1988, Newton 1989). In birds, breeding performance generally increases with age during the first reproductive years, stabilizes at middle age and, in some species, declines later in life (Clutton-Brock 1988, Forslund and Pärt 1995). The improvement of breeding performance with age during the early years of reproductive life is well described, and usually interpreted in relation to four non exclusive hypotheses: (1) the age-related improvement of competence due to breeding experience (Sydeman et al. 1991, Pyle et al. 2001, Bregnballe 2006), or foraging skills enhancement (Laaksonen et al. 2002, Wheelwright and Templeton 2003), (2) improved coordination between pair-members through mate fidelity (Cézilly and Nager 1996), (3) the optimization of reproductive effort (Williams 1966), or (4) the progressive appearance or disappearance of different quality phenotypes among cohorts with time (Curio 1983; Forslund and Pärt 1995, Cam and Monnat 2000).

Even though the question of age-related difference in breeding performance has been widely discussed, so far only a few studies have attempted to evaluate the influence of parental age on the successive steps of breeding so as to

understand which step(s) of the breeding process is (are) the most limiting for young individuals. A successful breeding attempt depends upon the completion of three consecutive steps: egg laying, incubation and chick rearing. Parental age can potentially influence breeding success at each of those three steps, for instance through differences in egg composition and size (Bogdanova et al. 2007), length of incubation (Komdeur 1996, Massaro et al. 2004, Bogdanova et al. 2006), or provisioning rate during brood care (Weimerskirch 1990). Although chick-rearing has often been considered as the most demanding breeding step (Monaghan and Nager 1997), increasing evidence indicates that early breeding steps are also relatively costly, especially in younger individuals, and likely to influence age-specific trade-offs affecting parental investment (Massaro et al. 2004, Bogdanova et al. 2006, 2007).

Partitioning the influence of parental age between the different steps of reproduction can be difficult in practice, in particular when field conditions only allow intermittent instead of continuous monitoring of breeders. Under such conditions, it might be difficult to ascertain whether breeding failure occurred before or after hatching. In this context, multistate capture-recapture models may provide an alternative to more conventional statistical tools. Multistate capture-recapture models allow the testing of

hypotheses in evolutionary ecology, while taking into account variation in resighting probability between groups (Clobert 1995, Nichols and Kendall 1995). Such models have been previously used to investigate the effect of age on breeding performance through comparing age-specific breeding probabilities and survival over several breeding seasons (Cam and Monnat, 2000, Beauplet et al. 2006). Here, we propose that they could be advantageously used over shorter periods of time (Schaub et al. 2001, B  chet et al. 2003), particularly within a single breeding season.

We developed such a transversal approach using data from a long-term study of the greater flamingo *Phoenicopterus roseus* breeding in the Camargue (southern France). The greater flamingo is a long-lived species which shows no mate fidelity between consecutive breeding seasons (C  zilly and Johnson, 1995, Johnson and C  zilly 2007) but strong age-assortative mating (C  zilly et al. 1997, Johnson and C  zilly 2007). Females lay a single egg, and incubation and chick-rearing duties are shared by both sexes (Johnson 1983, C  zilly 1993, C  zilly et al. 1994). Although the breeding success increases with age, some evidence suggests that the effect might be limited to incubation (C  zilly 1993, C  zilly et al. 1994, Johnson and C  zilly 2007). In addition, age may interact with environmental parameters, such as temperature or level of rainfall. Indeed, climatic conditions can affect different components of breeding success in birds, such as number of fledging (Monadjem and Bamford 2009), feeding rates of nestling (Pasinelli 2001), or offspring quality (Dawson 2008), and evidence exists that the costs of reproduction for young individuals or first-time breeders of long-lived species can be particularly marked under harsh conditions (Barbraud and Weimerskirch 2005). Among the climatic parameters flamingos faced during their breeding, rainfall is suspected to be the most likely to negatively affect their breeding performances (Johnson and C  zilly 2007), and thus to underline temporal variation of nest attendance. In particular, episodes of heavy rainfalls are likely to affect flamingo breeding success through increasing the risk of abandonment following nest flooding. However, the interaction between parental age and local weather conditions has not been assessed so far in flamingos, although results obtained on other bird species suggest that the age effect on breeding performance might be more pronounced under poor climatic conditions (Sydeman et al. 1991, Ratcliffe et al. 1998, Laaksonen et al. 2002).

## Materials and methods

### Study area and data collection

Since 1974, greater flamingos have bred on an artificial island located in the commercial salt pans of Salin-de-Giraud (Camargue, southern France). Incubation generally starts in April and lasts 29 days. At the age of 10 d, chicks gather in small cr  ches on the breeding island, before moving into the water to join a larger cr  che which numbers up to several thousand individuals (Johnson and C  zilly 2007). Since 1977, on average 12% of the chicks fledged in the Camargue have been ringed each year with PVC rings engraved with alphanumeric codes that can be read from a distance up to 300 m. We analysed the

resightings of the 1991 breeding season when an average of >10 h per day were spent observing the colony from the tower from April 2 (first egg obs.) to July 16 and >2 h per day at the cr  che, from July 16 to September 8 (end of obs.). Resightings of ringed birds were done with a telescope from a hide situated 70 m from the colony. Only flamingos observed at least once as breeders were considered. The location and the breeding status of each ringed individual were recorded (Tavecchia et al. 2001). Flamingos are considered as breeders, when they were seen at the same location of the breeding island for  $\geq 48$  h, observed incubating an egg, or feeding a chick on the breeding island or in the cr  che.

### Statistical methods

We divided the breeding season into 16 intervals of 10 days corresponding to 16 resighting occasions. We considered three successive breeding steps: 1 = incubation, when a flamingo was seen at the same position on the breeding island for at least 48 hours or seen with an egg, 2 = early chick rearing, when a flamingo was seen feeding a chick on the breeding island and 3 = late chick rearing, when a flamingo was seen feeding a chick in the cr  che, outside the island. Using the multistate capture-recapture approach, we estimated three different parameters (Nichols et al. 1994):

- $P_t^r$  resighting probability: probability that an individual is resighted at time  $t$  in step  $r$ , given that it is present on the colony at time  $t$ .
- $S_t^r$  survival probability: probability that an individual in step  $r$  at time  $t$  survives until  $t+1$ .
- $\Psi_t^{rs}$  conditional transition probability: probability that an individual in step  $r$  at time  $t$  is in step  $s$  at time  $t+1$ , given that it survived to  $t+1$ .

Since flamingos' yearly survival is very high (> 90% for adults in Tavecchia et al. 2001) and, unlike other species where nest abandonment can be confounded with adult mortality (e.g. Roche et al. 2010), adults have no predators in the Camargue, we assumed that no flamingo died during the breeding season. Therefore, in our case  $S$  does not represent survival but breeding attendance (its complement being breeding desertion or breeding failure). The higher breeding attendance is at a given breeding step, the higher the probability is to complete this step successfully. Breeding attendance can thus be considered here as a surrogate for breeding success.

Because breeding is a unidirectional process, we fixed all reverse transitions to zero. We also fixed resighting probabilities to one when flamingos could not be observed in a particular state (Choquet et al. 2005). By doing this we ensure that if the birds are in a particular state they cannot be missed and then that if there are no observations of any bird in a given state it is because none are in this state. Maximum age of breeders was 14 yr in 1991, whereas very few breeding attempts by birds <4 year-old were recorded that year. In flamingos, physiological maturity is reached at 3-years old (Johnson and C  zilly 2007), recruitment peaks at 8-years old (Balk  z 2006) and there is a cost of first reproduction for females breeding before age 7 (Tavecchia et al. 2001).

Therefore, we considered three a priori age-classes, (4 to 8 years old, 9 to 11 years old and 12 to 14 years old), resulting in a balanced sample size allocation (see Results).

Our most general model was thus written  $[S_{t^*g}^r P_{t^*g}^r \Psi_{t^*g}^r]$  where  $(t,s)$  indicates breeding steps,  $(t)$  the time effect and  $(g)$  the age-class effect (see Lebreton et al. 1992). The latter effects are connected with an  $(*)$  if they are in interaction and with a  $(+)$  if they are additive.

We first tested whether our starting global model provided an adequate description of the data, using GOF tests for multistate models (Pradel et al. 2003) implemented in U-CARE (version 2.2.5; Choquet et al. 2003). We first tested the fit of the JollyMove (JMV) model (survival, transition and recapture probabilities time- and step-dependent, see Brownie et al. 1993) for each age-class. Since the general model was not rejected, we then fitted more constrained models using M-SURGE (version 1.8. 1; Choquet et al. 2004).

Model selection relied on the second-order Akaike's information criterion corrected for overdispersion and small sample (QAICc; Burnham and Anderson 2002). Throughout the analysis, whenever the difference between two models in QAICc ( $\Delta$ QAICc) was greater than 2, the model with the lower QAICc was preferred, whereas when  $\Delta$ QAICc values were lower than 2 we considered models as fairly similar in their ability to describe the data (Lebreton et al. 1992).

## Rainfall and breeding attendance

The 1991 breeding season was characterized by harsh rainfall accompanied by strong winds at the end of April/beginning of May, reported in details by observers at the colony. The amount of precipitation (in mm per day) was available from the meteorological station of Salin-de-Giraud located 7.9 km from the breeding island. We first examined the relationship between rainfall and breeding attendance by including rainfall as a covariate. In this modelling, we held the same structure as the reference model for recapture and transition probabilities. As recommended by White and Burnham (1999), the covariate was centred on the average and standardized by its standard deviation. After harsh weather, observations at the colony are very difficult either because the observation tower is inaccessible or because mud makes rings unreadable. Hence, we expected the effect of heavy rainfall to be only detectable in the period following the rainfall event.

Because we explored the effect of a discrete climatic event with only two strong rainfall events over ten periods with almost no rainfall at all, obtaining a significant statistical correlation was unlikely. We thus used an alternative approach by contrasting breeding attendance between periods with different rainfall conditions (Lebreton et al. 1992, Cézilly et al. 1996). We first contrasted periods of "heavy rainfalls" (i.e. time periods with at least one day with rainfall  $> 30$  mm) and those with "normal weather". We also contrasted periods of "exceptional rainfalls" (i.e. time periods with at least one day with rainfall  $> 50$  mm), and those with "normal weather". In both modelling approaches, we allowed incubation attendance to vary with time from period 9 to period 15, when birds are no

longer incubating, in order to allow relevant comparisons with the reference model.

## Results

### Goodness of fit and model selection

From April 2 to September 8 1991, 967 greater flamingos were observed as breeders at least once. Among them, 338, 346 and 283 were in the first, second and third age-class, respectively. The GOF test for the JMV model provided evidence of overdispersion, especially for the first and third age-classes (first:  $\hat{c} = 1.380$ ,  $\chi^2 = 75.52$ , DF = 55,  $p < 0.05$ ; second age-class:  $\hat{c} = 1.026$ ,  $\chi^2 = 63.61$ , DF = 62,  $p < 0.10$ ; third age-class:  $\hat{c} = 1.282$ ,  $\chi^2 = 78.26$ , DF = 61,  $p < 0.05$ ). We thus used the average values of  $\hat{c}$  (1.220) calculated over the age-classes to correct for overdispersion in model selection.

From our most general model  $[S_{t^*g}^r P_{t^*g}^r \Psi_{t^*g}^r]$  we first intended to simplify transitions and recapture probabilities, allowing breeding attendance parameters to vary with time and breeding steps, and among age-classes. The best model thus obtained only considered time- and step-dependent recapture and transitions probabilities:  $[S_{t^*g}^r P_t^r \Psi_t^r]$  ( $\Delta$ QAICc with the most general model = 86.4). In a second step, we investigated the effect of age on breeding attendance.

### Age effect on breeding attendance and model selection procedure

We first modelled breeding attendance as a function of both age and time, with full interaction between the two variables (M9 – Table 1). Modelling a constant additive effect of age over time on breeding attendance resulted in better models (M1 to M5, M7 and M8). M5 considers an additive age effect similar for the three breeding steps, and provides evidence for an age effect (M5 vs M6). Relaxing this constraint to let the additive effect of age differ between the three breeding steps (M3 vs M5) improved the fit. Hence, age influenced breeding attendance differently between successive breeding steps. Therefore we tested for an age effect on the three different breeding steps (M2, M7 and M8). M7 and M8 were not well supported, suggesting that age does not influence chick-rearing performance, neither on the island nor in the crèche. By contrast, M2, in which only incubation attendance is age-dependent, provided a good fit of our data. Finally, M1 in which breeding attendance does not depend on being in step 2 or 3, was the best model out of our set of candidate models (Table 1).

### Transition and resighting probabilities

Transition probabilities from incubation to chick rearing on the island remained low ( $< 0.04$ ) until period 5 when they progressively increased up to  $0.48 \pm 0.04$  at period 8 marking the peak of hatching. Transition probabilities from incubation to rearing a chick in crèche or from rearing a chick on the island to rearing a chick in the crèche followed the same pattern with a peak at period 10.

Table 1. Modelling breeding attendance ( $S_t^i$ ) as a function of time, age, rainfall and breeding states for greater flamingo in the Camargue, South France. Resighting ( $P_t^i$ ) and transitions ( $\psi_t^{i^s}$ ) probabilities are step- and time-dependent ( $t, s$ : breeding steps at time  $t$  and  $t+1$  for all models described). Results of model selection include: number of parameter estimated ( $k$ ), Deviance, Akaike Information Criterion value corrected for overdispersion and small sample size (QAICc),  $\Delta$ QAICc and Akaike weights  $\omega_i$ .

No.	Models	Constraints and biological hypothesis (in italics)	k	Deviance	QAICc	$\Delta$ QAICc	$\omega_i$
M1	$S_{t+g}^1, S_t^{2=3}$	Additive age effect on breeding attendance in step 1 - Age only influences the probability of continuing incubation Breeding attendance equal in step 2 and 3 ( $S_2 = S_3$ )	66	8964.4	7471.9	0	0.73
M2	$S_{t+g}^1, S_t^2, S_t^3$	Additive age effect on breeding attendance in step 1 - Age only influences the probability of continuing incubation	68	8962.3	7474.2	2.3	0.23
M3	$S_{t+g}^i$	Additive age effect on breeding attendance different for each step - Age effect on breeding attendance is different along the breeding process	71	8960.8	7478.9	7	0.02
M4	$S_{t+g}^1, S_{t+g}^{2=3}, S_t^2, S_t^3$	Additive age effect on breeding attendance in step 1 - Age only influences the probability of continuing incubation Same age effect on breeding attendance in state 1 after 9 years old ( $g_2 = g_3$ ) Breeding attendance equal for individuals from 9 to 14 years old	66	8975.1	7480.7	8.8	0.01
M5	$S_{t+G}^i$	Additive age effect equal for each step (G) - Age effect on breeding attendance is the same whatever the breeding step	68	8971.7	7481.9	10	0
M1E	$S_{E+g}^1, S_t^{2=3}$	2 levels of time-periods: exceptional rainfalls vs normal weather - Probability of continuing incubation is affected by exceptional rainfall Breeding attendance equal in step 2 and 3 ( $S_2 = S_3$ )	62	8996.1	7489.9	18	0
M1C	$S_g^1, S_t^{2=3}$	Constant breeding attendance at step 1 - Age but not time influences the probability of continuing incubation Breeding attendance equal in step 2 and 3 ( $S_2 = S_3$ )	61	9005.1	7495.3	23.4	0
M6	$S_t^i$	No age effect	66	9001.7	7502.5	30.6	0
M7	$S_{t+g}^2, S_t^1, S_t^3$	Additive age effect on breeding attendance in step 2 - Age only influences the probability to raise a chick in his first 10 days on the breeding island	68	8999.9	7505.1	33.2	0
M8	$S_{t+g}^3, S_t^1, S_t^2$	Additive age effect on breeding attendance in step 3 - Age only influences the probability to raise a chick in crèche	69	8998.9	7506.2	34.3	0
M1H	$S_{H+g}^1, S_t^{2=3}$	2 levels of time-periods: Heavy rainfalls <i>versus</i> normal weather - Probability of continuing incubation is affected by heavy rainfall Breeding attendance equal in step 2 and 3 ( $S_2 = S_3$ )	59	9018.1	7507.9	36	0
M1 covariate	$S_{rainfall+g}^1, S_t^{2=3}$	Breeding attendance in step 1 in function of rainfall - Probability of continuing incubation varies with rainfall amount Breeding attendance equal in step 2 and 3 ( $S_2 = S_3$ )	61	9048	7530.4	58.5	0
M9	$S_{t*g}^i$	Age effect in interaction with time on breeding attendance - Breeding attendance at each step varies as a function of both age-classes and time, with full interaction between the two	118	8923.4	7542.4	70.5	0

Interaction and additivity among variables are written (\*) and (+), respectively.

Breeding steps: 1: flamingo incubation; 2: flamingo observed feeding a chick on the breeding island; 3: flamingo observed feeding a chick in the crèche outside the breeding island.

G: group effect (age) equal for each step; g: group effect (age) different for each step; Age-classes: 4–8 years ( $g_1$ ), 9–11 years ( $g_2$ ) and 12–14 years ( $g_3$ );  $t$ : time effect.

Rainfall is for rainfall as a covariate for breeding attendance; H=2 levels of time periods Heavy rainfalls vs normal weather; E=2 levels of time periods Exceptional rainfalls vs normal weather.

Note: If breeding attendance could be estimated for all periods in both state 2 and state 3, models M1 and M2 should differ by 15 parameters. However, because state 2 is only observable from period 3 to 10 and state 3 only from period 9 to 15 this difference is reduced to the two temporarily overlapping parameters, namely parameters 9 and 10. Thus, models M1 and M2 only differ by two parameters.

Resighting probabilities in incubation dropped ( $<0.15$ ) at period 3 and 4 because of harsh weather conditions then raised up to  $0.81 \pm 0.02$  at period 7 and dropped again ( $0.16 \pm 0.06$ ) at hatching in period 9. As expected, resighting probabilities of a flamingo rearing a chick on the island remained high ( $>0.77$ ) until period 9 while resighting probabilities of a bird feeding a chick in the crèche was much lower (range  $0.16 \pm 0.01$  to  $0.27 \pm 0.04$ ).

### Age effect on the probability of continuing incubation

M1 gave reliable estimates of the probability of continuing incubation until the 8th period. After period 8, it is no longer possible to observe a bird with an egg because of hatching. Estimation at the upper boundary of the probability of continuing incubation at period 3 ( $S=1$ ) is likely linked to the lack of resightings during this period because of harsh weather conditions preventing observers to reach the observation tower.

The probability of completing incubation increased with age (Fig. 1a). As M1 and M2 provide a better fit than M4 (grouping age-classes 2 and 3), the probability of continu-

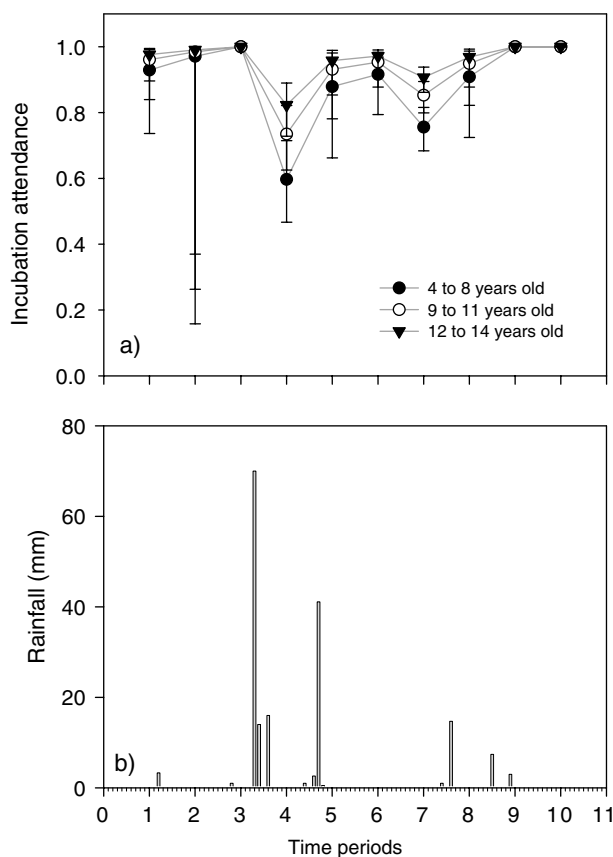


Figure 1. Probability to continue incubation for three age-classes of the greater flamingo in the Camargue, south of France compared to climatic conditions from April 4 (start of period 1) to July 10 (end of period 10). a) Incubation attendance ( $\pm$  95% CI) as a function of age estimated from model M1 (Table 1). b) Daily rainfall accumulations (mm).

ing incubation is likely to increase with age at least until 12 year-old, the start of the older age category of our dataset. Interestingly, nest desertion or failure showed a strong increase at period 4 irrespective of the age of the breeders. The other observed decrease in the probability of continuing incubation, period 7, corresponds to the peak of the hatching period when most birds transited from step 2 to 3.

### Effect of rainfall

Heavy rainfall occurred: (1) from 25 to 28 April (period 3) with 100 mm accumulated (70 mm on April 25 only), and (2) 9 May (period 4) when it rained up to 41.1 mm (Fig. 1b). There was no significant rainfall event outside the incubation period, with only 17.8 mm on the 10th of August (period 14).

Including rainfall as a covariate to explain incubation attendance variation was not retained by model selection as this model provided less support than the invariant model considering an absence of temporal variation of incubation attendance (Table 1). Hence, there was no evidence for a direct correlation of rainfall with incubation attendance probability.

As an alternative approach, we first considered periods 4 and 5 together as periods following “heavy rainfalls” and the others as “normal weather”. Then, we considered only period 4 as a period following “exceptional rainfall”, while all other periods were considered as “normal weather”. We held the same structure as the reference model for recapture and transition probabilities. Both model M1H (Heavy rainfall), and model M1E (Exceptional rainfall; Table 1) failed to confirm that variation in breeding attendance was a direct consequence of variation in rainfall levels during incubation. Even though M1E was better supported than a model in which the probability of continuing incubation was constant (M1C), the  $\Delta\text{QAICc}$  with the reference model M1 was large ( $>10$ ), thus providing no support for an effect of exceptional climatic event on incubation attendance.

### Discussion

Our study shows that, in the greater flamingo, breeding performance continues to increase with age until 12-14 y, with the probability for this age-class to successfully complete incubation being up to 20% higher than that of younger birds. This confirms preliminary results obtained by Johnson and Cézilly (2007). This long process of improvement of breeding performance might be related to the extreme longevity of greater flamingos that can live up to 30 y in the wild, and even over 50 yr in captivity (Johnson and Cézilly 2007).

The effect of parental age was critical during incubation, with young birds having a higher probability of breeding desertion than older ones only at this step. In colonial waterbirds, breeding failure mainly occurs during incubation because of nest desertion (Jouventin 1975, Davis and

McCaffrey 1986, Warham 1990, Cézilly 1993, Tveraa et al. 1997). Contrary to the “peak demand hypothesis”, stating that energy expenditure is maximal when parents are delivering food to young, our results are rather in accordance with recent reappraisals suggesting that incubation is an energetically demanding period of equal importance as the nestling period (Williams 1993, Piersma and Morrisson 1994, Tinbergen and Williams 2002, de Heij et al. 2006). Hence, the capacity of a bird to cope with this energetic demand may improve with age, increasing the chance to achieve incubation with success.

A selective process on low-quality phenotypes and the improvement of competence and/or experience are the two hypotheses most likely to be involved in the positive influence of age observed. According to the appearance/disappearance of phenotypes hypothesis, lower quality individuals are less likely to survive, resulting in an increase of the proportion of well-performing birds in the older age-classes (Curio 1983, Forslund and Pärt 1995). In flamingos, females starting to breed before the age of 7 pay a cost in terms of survival compared to those starting to breed later (Tavecchia et al. 2001). This could be explained by the fact that the first breeding attempt selects for females of high quality, therefore contributing to the apparent improvement of performances with age. Alternatively, individuals of high quality, with a high probability of survival, could delay first reproduction to avoid reproductive costs. Parents could also improve their incubation performances with age as they improve some competences and/or acquire further breeding experience. Constraints on foraging skills (Bildstein et al. 1991), a better access to breeding sites for older parents (Rendón et al. 2001), or the attenuation of stress hormone production with age (Angelier et al. 2007) could also contribute to explain the observed age difference. Although our analysis does not allow us to distinguish between these different hypotheses, previous evidence (Cézilly 1993, Tavecchia et al. 2001) suggests that the energetic demands of egg laying and incubation could be the ultimate cause of age-related improvement of breeding success in greater flamingos. Our results thus provide an addition to previous empirical evidences of a positive effect of age on incubation performance (Massaro et al. 2004, Bodgdanova 2006, 2007).

Our results also suggest that after hatching, parents seem to be equally able to cope with chick rearing whatever their age. Incubation may then act as a bottleneck, eliminating individuals of poorest quality, such that the remaining birds are equally likely to be successful. Indeed, although several studies have observed better offspring-rearing capacities in older parents (e.g. Weimerskirch 1990, Pugsek 1995), it had been shown that flamingo parental age had no effect on feeding bout length (Cézilly et al. 1994). Our results are thus in accordance with this previous study and suggest that incubation in itself is the main cause of age differences in breeding attendance. In addition, according to life-history theory (Roff 1992, Stearns 1992), parental effort in long-lived species should vary with the residual reproductive value of the adult, the cost of reproductive investment and the value of the current offspring (Ackerman and Eadie

2003, Bourgeon et al. 2006). In that context, the value of an egg is supposedly lower than that of a hatched chick. In addition, the cost of reproduction is likely to be higher for adult flamingos during the incubation period than during the chick-rearing period. Indeed, incubating implies fasting for long periods of time, whereas breeding adults are free to move and feed for themselves once the chick has joined the crèche (Johnson and Cézilly 2007). Therefore, young adult flamingos facing adverse conditions during the breeding season might be more likely to desert an egg (see Cézilly 1993) than to abandon a chick that has already survived to the crèching stage.

## Effect of rainfall

The pattern of nest attendance was marked by a strong decrease at period 4 (Fig. 1a), indicating a high rate of nest desertion and/or nest failure. There was a good correspondence between this decrease and the occurrence of heavy rainfall (Fig. 1a, b). Nest attendance dropped strongly at period 4 following two days of strong winds and 100 mm rainfall accumulation in period 3. This pattern is confirmed by the comments made by observers at the colony who mentioned massive egg losses in periods 3 and 4. Still, we failed to obtain any significant statistical evidence for a direct effect of rainfall on breeding attendance, either using rainfall level as a covariate or time categories models. This does not mean, however, that breeding attendance is unaffected by climatic conditions. First, the effect of rainfall might be modulated by other factors, such as wind speed and temperature that were not included in our analysis. Second, considering only a single year with a particular pattern of rainfall may limit the statistical power of the analysis. Third, the effect of adverse climatic conditions may vary according to the age and experience of breeders (Barbraud and Weimerskirch 2005). Interestingly, age-specific differences in nest attendance were accentuated during the periods of heavy rainfall, with younger flamingos being much more affected than older ones (incubation attendance  $0.59 \pm 0.06$  for 4–8 yr-old,  $0.73 \pm 0.05$  for 9–11 yr-old and  $0.82 \pm 0.04$  for 12–14 yr-old). Rainfall is harsh conditions for incubating flamingos causing nest flooding, facilitating predation by gulls (Salathé 1983), and decreasing foraging efficiency. This type of climatic event generally increases nest desertion rates (Cézilly 1993). Older flamingos might be able to settle on higher nest sites or to secure higher nests with a lower risk of flooding. In chinstrap penguins *Pygoscelis antarctica*, nest maintenance has been shown to prevent nest flooding and, hence, decrease egg and chick mortality (Moreno et al. 1995). In addition, the ability to maintain the nest through regular stone provisioning appears to reflect both parental abilities and individual quality in penguins (Fargallo et al. 2001). A similar behaviour can be observed in flamingos, with incubating individuals often seen scraping off the mud at available neck distance to the top of their nest (Johnson and Cézilly 2007). This, in addition to the variability of nest height on the island, suggests that individuals of better quality or being more experienced could allocate more

effort to nest maintenance, thus increasing egg survival under detrimental condition. Finally, when the weather became favourable again, differences in incubation attendance were reduced. Weather severity may thus modulate the probability to achieve incubation, especially in young flamingos.

### Methodological considerations

To our knowledge, our study is the first example of the use of multistate capture-recapture modelling to evaluate breeding performance within the short period of a single breeding season. We believe it could be advantageously used for other species in which the continuous monitoring of breeding attempts is impossible. In this case, the approach is robust to capture/resighting heterogeneity encountered along the breeding season.

Our first aim was to evaluate the efficiency of multi-state modelling at assessing the effect of age on breeding success over different steps during reproduction. To that end, we concentrated on a limited data set, considering one year during which the observation pressure was particularly high. One obvious limitation here is that the age effect could be confounded by a cohort effect. However, given that we considered age categories consisting of several consecutive age classes, the possibility of a cohort effect remains moderate. Still, the approach deserves to be extended over several years in order to ascertain the generality of our results. It would then be possible to assess whether breeding success has an influence on subsequent adult survival and future reproductive success.

In addition, for the purpose of our analysis, all resightings were distributed in 16 periods. The effect of pooling data on parameter estimates has not been yet fully explored as well as a related problem concerning the fact that occasions were continuous rather than discrete (i.e. no interval between occasions as assumed by the CJS model). Because in standard survival analysis, Hargrove and Borland (1994) showed that this only induced a small positive bias in survival estimates, we are confident that this should not affect our results too severely. Furthermore, estimates for resightings and transition probabilities reflected our expectations regarding variations of observation effort and tracked the directional dynamics of breeding phenology. Finally, this work should be explored more thoroughly in the future by using multi-event models (Pradel 2005). This would allow distinguishing events (the observation of a bird in a given behaviour) from the underlying state of the birds (breeding with success or in failure). This would thus give the possibility to properly integrate uncertainty in state assignment.

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