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Experience-dependent natal philopatry of breeding greater flamingos

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Summary

1. Contrary to the generally high level of natal philopatry (i.e. likelihood that individuals breed at their natal colony) found in first-breeding colonial birds, little is known of natal philopatry later in life. Most hypotheses advanced to explain natal philopatry are valid at all ages. However, for young and inexperienced birds, the benefits of natal philopatry may be counterbalanced by the costs of intraspecific competition at the natal colony making dispersal temporarily advantageous. In turn, experience may increase competitive ability and make natal philopatry advantageous again.

2. We evaluated this hypothesis on the large-scale dispersal of greater flamingos *Phoenicopterus roseus* breeding among three colonies comprising $>85\%$ of the Western Mediterranean metapopulation. The Camargue (France) and Fuente de Piedra (Spain) are large and saturated colonies while Molentargius (Sardinia) is a recent and growing colony.

3. We used a 20-year capture-mark-resighting dataset of 4900 flamingos ringed as chicks in Camargue and Fuente de Piedra and breeding at the three colonies. We assessed the effects of natal colony and breeding experience (first-time observed breeders *versus* confirmed experienced breeders) on dispersal using multistate capture-recapture models. Dispersal to an unobservable state accounted for temporary emigration.

4. Fidelity was higher at the natal colony ($>84\%$) than elsewhere. Fidelity increased with experience in the two large colonies (Camargue and Fuente de Piedra) suggesting a large-scale experience-related despotic distribution. Breeding dispersal was significant (up to 61% and 52% for first-time breeders and experienced breeders, respectively) so that colony dynamics is affected by exchanges with other colonies. Except for Fuente-born breeders leaving Molentargius, dispersal to the natal colony was higher than to any other colonies.

5. Survival was not higher at the natal colony. Inexperienced birds likely had lower breeding success at the Camargue and skipped reproduction after having emigrated to the other large colony but not to Molentargius. Breeding at Molentargius could allow avoiding queuing (and non-breeding) at the large colonies while gaining experience and competitive ability for future attempts.

6. Natal philopatry appears as an important driver of large-scale breeding dispersal in the Greater flamingo. The fitness advantage of natal philopatry is likely experience-dependent and mediated by the variations of intraspecific competition.

Key-words: breeding dispersal, ideal despotic distribution, intraspecific competition, M-SURGE, outbreeding, flyway, phenotype matching

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Introduction

Should I stay or should I go now? That is the question, posed in a famous song of The Clash rock band (1981), that most animals have to address to optimize their foraging, mating or breeding success. While moving allows escaping poor environmental conditions or prospecting for better ones, not moving facilitates increased familiarity with the environment avoiding the costs and risks associated with travelling (Greenwood 1980; Pärt & Gustafsson 1989; Beletsky & Orians 1991; Pärt 1995; Forero *et al.* 1999). Among the variety of movements organisms can make, dispersal movements – those which end with a reproductive event – are particularly important because they affect both population genetics and population dynamics (review in Clobert *et al.* 2001). Traditionally, two types of dispersal movements are distinguished: dispersal from the birth site to the first-breeding site (namely natal dispersal), and dispersal between successive breeding sites (namely breeding dispersal; Greenwood 1980; Greenwood & Harvey 1982). Studies of natal dispersal are far more common and detailed than studies of breeding dispersal (Spear, Pyle & Nur 1998; Altwegg, Ringsby & Saether 2000; Forero, Donazar & Hiraldo 2002; Blums *et al.* 2003; Serrano *et al.* 2003; Sternalski *et al.* 2008).

In colonial birds, many species present a high level of *natal philopatry* (defined as the likelihood that individuals -whatever their previous breeding experience- breed at their natal colony), by often recruiting at their natal colony and sometimes very close to the area of the colony where they were born (review in Prevot-Julliard *et al.* 1998). They also present a moderate to high level of *breeding site fidelity* (defined as the likelihood that breeding adults remain on a given colony from one year to another; Spendelow *et al.* 1995; Forero *et al.* 1999; Serrano *et al.* 2001; Lecomte, Gauthier & Giroux 2008). Natal philopatry is expected to be advantageous in heterogeneous environment (i) because it minimizes costs of prospecting for new breeding sites and of gaining an appropriate knowledge of new mates and foraging areas (Switzer 1993; Danchin & Cam 2002) and (ii) because it favours genetically-based local adaptation (Shields 1982). However, in a growing population, natal philopatry may be costly and maladaptive if increased competition for food and nesting places decrease per capita resource acquisition (Cooch *et al.* 1993; Spear, Pyle & Nur 1998). The advantage of natal philopatry *versus* dispersal is thus context-dependent both relative to the individual internal state and to external conditions (Clobert *et al.* 2008) and may thus vary during the lifetime of an individual, especially in long-lived species.

To benefit the potential advantages of natal philopatry, birds must be able to settle freely at their natal site. This may often be thwarted by intraspecific competition for a territory or a nesting place within the colony (Forero, Donazar & Hiraldo 2002), forcing subordinates to disperse to lower quality sites following an ideal despotic distribution (Rendón *et al.* 2001; Serrano *et al.* 2003; Oro 2008). Dispersal may then become temporarily advantageous by avoiding the cost of competing for a nesting place or of not being able to breed a given year and delaying recruitment (Pradel *et al.* 1997a). In turn, if natal philopatry remains advantageous on the long-term, experience gained elsewhere may increase competitive ability and make dispersal back to the natal site possible again. However, studies of breeding dispersal have not examined the role of the natal site. This omission may result from the use of birds ringed as adults of which, the natal site is unknown (e.g. Spendelow *et al.* 1995). Another difficulty with this kind of data is that age is also ignored. However, in long-lived species, age generally increases an individual's ability to compete for nesting places, and this may result in higher levels of breeding site fidelity in older individuals (Switzer 1993), as supported by empirical results (Payne & Payne 1993). It is unclear yet if age *per se* or experience is the proximal factor for this increase of fidelity (Pärt & Gustafsson 1989).

In this article, we examined the hypothesis that natal philopatry lasts long and remains an important driver of breeding dispersal modulated by breeding experience, i.e. individuals unable to recruit directly on their natal site tend to come back later after having gained experience elsewhere. We explored this issue using a long-term and large-scale ring-resighting study of the greater flamingo (*Phoenicopterus roseus*) in the Western Mediterranean. Here, flamingos belong to a metapopulation *sensu lato* with significant rates of natal and breeding dispersal among a few colonies (Nager *et al.* 1996; Balkız *et al.* 2007). Three of these colonies account on average for $>85\%$ of the breeding pairs: the Camargue in France, Fuente de Piedra in Spain and Molentargius in Sardinia. The Camargue and Fuente de Piedra colonies are long-established, large and saturated, i.e. younger individuals queue to breed at these sites (Cézilly & Johnson 1995; Cézilly *et al.* 1996; Nager *et al.* 1996; Pradel *et al.* 1997a; Rendón *et al.* 2001). Molentargius is a more recent and growing colony suggesting that it is still not saturated. We used multistate capture-mark-resighing models to estimate dispersal from individual-based encounter information over the three colonies (Spendelow *et al.* 1995; Lindberg *et al.* 1998; Lebreton & Pradel 2002; Blums *et al.* 2003; Cam *et al.* 2004). These models allow dealing with temporary emigration, a potential source of bias of dispersal estimates (Burnham 1993; Kendall, Nichols & Hines 1997).

We tested the following predictions: (i) breeding site fidelity is higher at the natal colony, (ii) breeding site fidelity increases with experience and (iii) breeding dispersal back to the natal colony is higher than to other colonies. We also took advantage of a quasi experiment caused by an exceptional cold spell in 1985 which caused the death of >3000 flamingos in the Camargue. After this severe winter, colony size did not change which suggest that a pool of individuals queuing for a nesting place replaced the missing birds (Ens, Weissing & Drent 1995; Pradel *et al.* 1997a). The availability of new breeding opportunities may thus have facilitated increased fidelity, especially for inexperienced birds, in the Camargue the year after. We thus tested the associated prediction (iv) that in the Camargue, fidelity for first-time breeders was higher following the cold spell than in other years.

Finally, to assess the fitness advantage of natal philopatry, we evaluated if breeding at the natal colony was positively correlated with two surrogates of fitness, survival and breeding success.

Materials and methods

STUDY AREA AND FIELD OBSERVATIONS

In the Camargue (southern France, 43°25′N, 04°38′E; Fig. 1) flamingos have been breeding on an artificial island in a large commercial saltpan since 1974 (Johnson & Cézilly 2007). During the study period (1983–2002), breeding occurred every year and the colony size fluctuated between 8600 and 22,200 pairs. The colony of Fuente de Piedra (southern Spain, 37°06′N, 04°45′W; Fig. 1) is located in a natural saline lake. While the number of breeding pairs in Fuente de Piedra is often higher than in the Camargue, frequent drought prevents annual reproduction (Rendón *et al.* 2001). From 1983 to 2002, breeding occurred in 15 out of 20 years and colony size varied from 2083 to 19,500 pairs.

Since 1993, several smaller colonies have established in the Western Mediterranean (Johnson & Cézilly 2007). Molentargius is the largest of these and the third largest flamingo colony in the Western Mediterranean. It is located in a semi-natural lagoon in Sardinia (Italy, 39°13′N, 09°08′E; Fig. 1). It has been occupied every year but once (2001) since it first appeared (Johnson & Cézilly 2007). Colony size varied from 700 to 4400 pairs with a growth rate of 265 additional pairs per year. In 1999, flamingos failed breeding at Molentargius but bred successfully at the nearby Saline di Macchiareddu.

Since 1977 in the Camargue and 1986 in Fuente, about 10% of the chicks have been ringed with a metal ring and a plastic ring bearing a unique alphanumeric code readable from up to 300 meters (Johnson & Cézilly 2007), thus enabling assessing individual breeding status. An individual is recorded as a breeder when incubating an egg, attending a chick, or observed on the same nest > 24 hours (assessed using numbered landmarks). Greater flamingos were monitored at all three colonies but the observation effort differed from one colony to another. In the Camargue, observations were made almost every day from a tower located 70 m from the colony (Johnson & Cézilly 2007). In Fuente de Piedra, surveys were done at least 4 days a week either from a hide located about 300 m from the colony or from vantage points around the lake (Rendón *et al.* 2001). Finally in Molentargius, flamingos were usually observed from dikes < 200 m from the colony; no professional effort was dedicated to read rings, and observations relied on volunteers.

DATASET AND PARAMETERS OF INTEREST

The encounter histories of 4900 individuals ringed as chicks in the Camargue and Fuente de Piedra until 1997 and observed breeding in the Camargue, Fuente de Piedra and Molentargius from 1983 to 2002 were analysed. Of these individuals, 3665 were born and ringed in the Camargue (1791 males, 1702 females and 172 of unknown sex) and 1235 in Fuente de Piedra (588 male, 578 female and 69 of unknown sex). In comparison with the previous study on the breeding dispersal of this species (Nager *et al.* 1996), individuals born and ringed at Fuente de Piedra and resightings done at Molentargius were added. Also, the encounter period was extended from [1986–1992] to [1983–2002].

Encounter histories start with the first observed breeding at one of the three colonies (coded differently for each colony) and continues with the subsequent observations as breeder. The individual's natal colony is indicated by sorting encounter histories in different groups. This approach allows the estimation of three parameters of interest following the notation of Lebreton & Pradel (2002):

P_t^s: The probability that an individual is encountered breeding at time t at site s given that it is alive and breeding at site s at time t ('encounter probability', hereafter).

F_t^s: The probability that an individual alive at site s and time t is still alive at time $t + 1$ ('survival probability', hereafter).

ψ_t^{sz}: The probability that an individual moves from breeding site s at time t to breeding site z at time $t + 1$, given that it survived from time t to $t + 1$ ('movement probability', hereafter, with movements back to the same colony representing 'fidelity' and movements to a different colony representing 'breeding dispersal'). See Appendix S1 for the transition matrices.

Contrary to other bird species, there do not seem to be significant differences in movements of males and females in flamingos (Nager

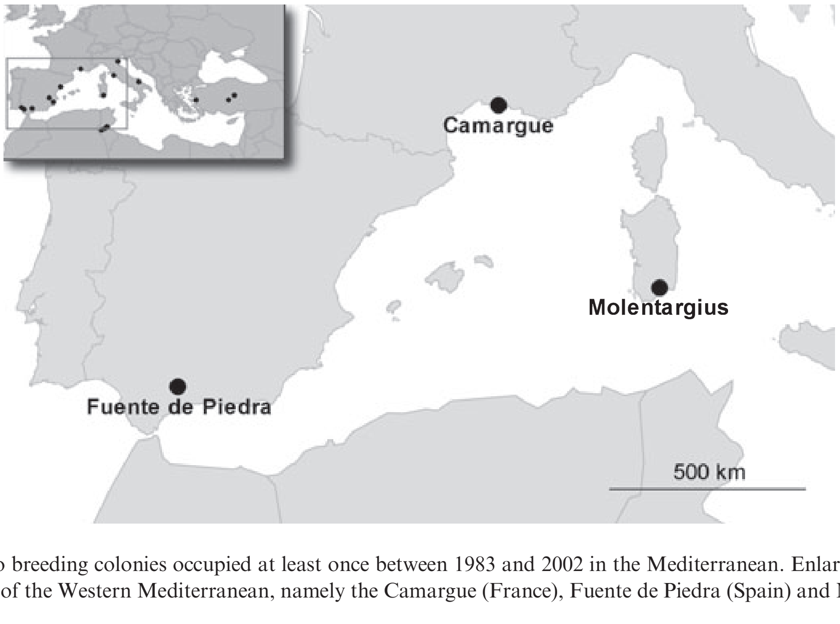

Fig. 1. Greater flamingo breeding colonies occupied at least once between 1983 and 2002 in the Mediterranean. Enlarged are the locations of the three main colonies of the Western Mediterranean, namely the Camargue (France), Fuente de Piedra (Spain) and Molentargius (Sardinia) considered in the study.

et al. 1996; Barbraud, Johnson & Bertault 2003). Therefore, the sex effect was excluded on movement probabilities and we included individuals of unknown sex in the analysis. Taking into account only the individuals of known sex can possibly positively bias the survival probabilities, because the individuals of unknown sex tend to be the individuals observed less frequently.

GOODNESS-OF-FIT TESTS AND MULTISTATE CAPTURE-MARK-RESIGHTING MODELLING

The goodness-of-fit tests of the Jolly Move Model (JMV; Brownie *et al.* 1993; Pradel, Wintrebert & Gimenez 2003) was run using U-CARE (Choquet *et al.* 2009) treating individuals from the two natal colonies separately. A global test was then obtained by adding the individual χ^2 values and their respective degrees of freedom. Once a starting model is identified and an overdispersion factor is calculated (when needed), model selection can proceed (see Appendix S2 for more details).

For computational convenience, we followed a step-up approach; we started from a simple model and increased its complexity progressively. Backward controls were also done by dropping off the factors incorporated in any of the three parameters of interest in order to assess their importance. Model fit was achieved by maximizing the likelihood with program M-SURGE (Choquet *et al.* 2004). Model selection relied on the modified version of the Akaike Information Criterion (QAICc; Burnham & Anderson 2002). Models developed following this approach are presented in Table 1 (Appendices S5 and S6 for M-SURGE notations).

ENCOUNTER PROBABILITIES

Previous studies of the Camargue colony showed strong time variations of encounter probabilities (Cézilly *et al.* 1996; Pradel *et al.* 1997a; Tavecchia *et al.* 2001). We thus first considered a time effect on this parameter. Also, in the absence of reproduction at Fuente de Piedra (years 1983, 1989, 1992, 1993 and 1995) and at Molentargius (2001), we constrained the encounter probabilities to equal 1. This forces the model to recognize that an individual was certainly absent from this site in these years; thus, movements towards this site as well as from this site are automatically ruled out. Similarly, in the absence of field surveys (2002 at the Camargue, 1984 and 1985 at Fuente de Piedra and 1999 at Molentargius), the encounter probabilities were forced to equal 0. Moreover, to reflect the presumed differences of observation effort, we allowed encounter probabilities to differ among colonies in all models. Encounter probabilities have also been shown to increase with the age of flamingos (see Pradel *et al.* 1997a). Age may act on its own but may also be a surrogate of breeding experience. Here, because our study deals with breeding adults, we concentrated on the second interpretation by distinguishing two pseudo-age classes. The first age-class corresponds to the encounter probability 1 year after the first observed breeding, as it is the first estimable encounter probability in the models (i.e. the encounter probability of newly-experienced breeders) and the second one, of individuals observed later, i.e. already-experienced breeders.

SURVIVAL PROBABILITIES

To test the effect of breeding experience on dispersal and given that in this species the first reproduction is costly for early breeders (Tavecchia *et al.* 2001), we distinguished two pseudo age-classes for survival and movements. For these parameters, the two experience classes are first-time breeders (short cut for first-time *observed* breeders) and experienced breeders (short cut for *confirmed* experienced breeders), respectively. We modelled apart the survival following the 1985 cold spell. Interbreeding survival in the other years was considered as constant. We then pursued by assessing the influence of the breeding site and the natal colony on survival.

MOVEMENT PROBABILITIES

We could not track yearly variations of movement probabilities due to the low amount of observations from Fuente de Piedra and Molentargius. On the other hand, because movements to and from some sites were impossible in some years, we distinguished four kinds of years: years when all colonies were occupied (1994, 1996–2000 and 2002), years when all but Fuente de Piedra were occupied (1993 and 1995), years when all but Molentargius were occupied (1984–1988, 1990–1991 and 2001) and years when only the Camargue colony was occupied (1989 and 1992). Movement probabilities were set equal within each of these groups of years. To explore if movements were influenced by breeding experience and natal colony, we allowed movement probabilities to differ between first-time and experienced breeders of Camargue and Fuente origin.

A critical issue in dispersal studies is that, most of the time, there will be inaccessible and even unknown sites where individuals cannot be tracked. Movements of individuals to unobservable sites and then back to observable sites are defined as temporary emigration (Burnham 1993; Kendall, Nichols & Hines 1997). Even though our system accounts for > 85% of breeding flamingos of the Western Mediterranean, it is not unlikely that flamingos could move outside our study area. Also, flamingos may skip reproduction in some years. To acknowledge the possibility of such temporary emigration, we incorporated an unobservable state as a catchall site for alternative non-monitored colonies and skipping episodes. Encounter probabilities in this unobservable state were constrained to 0 (Kendall & Nichols 2002; Schaub *et al.* 2004). A risk with models with an unobservable state (or more generally with temporary emigration) lies in the existence of a strong degree of capture heterogeneity among individuals. Then, individuals with low catchability would wrongly be considered as moving to the unobservable state too often. This may become problematic if catchability covaries with a factor of interest (e.g. breeding experience). Here we contrast dispersal probabilities of individuals observed breeding for the first time to the other birds in order to study the effect of breeding experience. While it is true that first observed breeders are globally less experienced, the oldest of them could be essentially made up of experienced breeders of low resighting probabilities. Then, results concerning the effect of experience on movements could be biased. To check this point, we separated the 2349 individuals (49·7%) first observed breeding before or at the peak of recruitment (8 years of age; Pradel *et al.* 1997a) from the 2461 first observed breeding older (50·3%) and ran an additional model in which resighting probabilities differed between these two categories.

Finally, we assessed the effect of the 1985 cold spell on the fidelity to the Camargue by implementing a model distinguishing movement probabilities of breeders starting from the Camargue in 1984 – the summer preceding the cold spell – from the remaining years.

Results

GOODNESS-OF-FIT TESTS

The JMV model applied separately to birds from Camargue and Fuente ($\psi^{sz}_{t*g}, F^{s}_{t*g}, P^{sz}_{t*g}$) was strongly rejected

Table 1. Model selection for the breeding dispersal of Greater flamingos in the Western Mediterranean. Movement probabilities (ψ), survival probabilities (F), encounter probabilities (P), model deviances, number of estimable parameters (k), Δ_i (QAIC differences between a given model and the best model) and model weights (w_i) are given. The best model (lowest QAICc) is in bold

Model	ψ	F	P	Deviance	k	QAIC	Δ_i	w_i
1	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	$P^{s}_{t+e(2,3)_{s(1)}}$	**37669·10**	**179**	**14572·75**	**0·00**	**0·998**
2	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	$P^{s}_{t.e(2,3)_{s(1)}}$	37618·08	195	14585·50	12·75	0·000
3	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	$P^{s}_{t.e(2,3)_{s(1\&3)}}$	37590·46	203	14591·08	18·32	0·000
4	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{g.s^{(1\&2\&3)}}_{CS.e(1,2)}$	$P^{s}_{t+e(2,3)_{s(1)}}$	37700·72	185	14596·41	23·66	0·000
5	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	P^{s}_{t}	37741·09	178	14597·92	25·17	0·000
6	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&3)}}_{CS.e(1,2)}$	P^{s}_{t}	37736·90	179	14598·34	25·59	0·000
7	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&2)}}_{CS.e(1,2)}$	P^{s}_{t}	37742·59	179	14600·49	27·73	0·000
8	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s}_{CS.e(1,2)}$	P^{s}_{t}	37738·61	180	14600·99	28·23	0·000
9	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	$P^{s}_{t.e(2,3)_{s(1\&2)}}$	37597·12	208	14603·59	30·84	0·000
10	$\psi^{sz''}_{4t.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	$P^{s}_{t.e(2,3)}$	37569·10	216	14609·02	36·27	0·000
11	$\psi^{sz''}_{4t.CS.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	P^{s}_{t}	37739·58	184	14609·35	36·59	0·000
12	$\psi^{sz}_{4t.e(1,2).g}$	$F^{s^{(1\&2\&3)}}_{CS.e(1,2)}$	$P^{s}_{t+e(2,3)_{s(1)}}$	38703·93	120	14845·26	272·50	0·000
13	$\psi^{sz}_{4t.e(1,2).g}$	$F^{s}_{CS.e(1,2)}$	P^{s}_{t}	38798·62	123	14886·99	314·23	0·000
14	$\psi^{sz}_{4t.e(1,2).g}$	$F^{s}_{CS.e(1,2)}$	$P^{s}_{t_{s(1\&2)}}$	38917·61	115	14915·89	343·14	0·000
15†	$\psi^{sz}_{t.g}$	$F^{s}_{t.e(1,2).g}$	$P^{sz}_{t.g}$	37402·52	401	14916·16	343·40	0·000
16	$\psi^{sz}_{4t.e(1,2).g}$	$F^{s}_{CS.e(1,2)}$	$P^{s}_{t_{s(1)}}$	39464·36	104	15100·21	527·46	0·000
17	$\psi^{sz}_{4t.e(1,2).g}$	$F^{s}_{CS.e(1,2)}$	$P^{s}_{t_{s(2)}}$	39724·42	98	15186·35	613·59	0·000
18	$\psi^{sz}_{4t.e(1,2).g}$	$F^{s}_{CS.e(1,2)}$	$P^{s}_{t_{s(3)}}$	40208·78	93	15359·12	786·37	0·000
19	$\psi^{sz}_{4t.e(1,2).g}$	$F^{s}_{CS.e(1,2)}$	P^{s}	40294·26	85	15375·38	802·63	0·000
20	ψ^{sz}_{4t}	$F^{s}_{CS.e(1,2)}$	P^{s}	40682·60	31	15413·92	841·17	0·000

s: site-dependence. *s'*: full site-dependence on first-time breeders and selectively on experienced breeders. *sz*: movements depend on both departure and arrival sites. *sz''*: idem with the unobservable state. $t_{s(i)}$: time-dependence at one site *i* or a combinations of sites. *e*(1,2): breeding experience for survival and movements (first-time and experienced breeders). *e*(2,3): breeding experience for resighting probabilities (newly-experienced and already-experienced breeders). *t* + *e*(2,3): breeding experience additive to time. *CS*: cold spell in the Camargue for Camargue-born birds. *4t*: 4 groups of years. *g*: natal colony.

Parameters aggregation follows model definition language of M-SURGE (Choquet *et al.* 2004), with ',' to estimate category-dependent parameters, '.' for interaction and '+' for additive effects on a logit scale and '&' to constrain 2 parameters to be the same (i.e. 1&3 forces the estimation of a single categorical value for 1 and 3). Breeding sites are identified by their codes, 1 for the Camargue, 2 for Fuente de Piedra and 3 for Molentargius.

†JMV model with two groups of natal colony on all parameters (g) and two age-classes on survival.

($\chi^2 = 1070{\cdot}313$, d.f. = 372, $p < 0{\cdot}0001$). Four out of five components, especially the memory test (WBWA) and the transience test (3G.SR) were significant (Appendix S2). Our data were too sparse to allow treatment of the memory effect, so that this effect could not be taken into account. On the other hand, transience can be treated exactly by considering an artificial first age-class on survival (Pradel *et al.* 1997b; Pradel, Gimenez & Lebreton 2005).

Discounting the transience component, an overdispersion factor $\hat{c}$ was calculated to account for the remaining lack of fit as 2·65 (Appendix S2). The resulting model (ψ^{sz}_{t*g}, $F^{s}_{t*a(1,2)*g}$, P^{sz}_{t*g}) allows movements to occur to all sites every year. However in our models, in some years, we prevented the movements to occur to the sites where there was no reproduction. To check if, because of this additional constraint $\hat{c}$ was not underestimated, the GOF tests were recalculated on a restricted time period when all breeding sites were continuously occupied: 1996–2000. Results were all significant in the same order of importance as with the complete dataset, and the starting JMV model was rejected again ($\chi^2 = 90{\cdot}3$, d.f. = 54, $p = 0{\cdot}0014$). When removing the transience component we obtain a $\hat{c}$ of 1·26. Because this $\hat{c}$ value was much lower than that from the complete dataset (2·65), we concluded that overdispersion was not underestimated and we proceeded along with the $\hat{c}$ derived from the complete dataset.

ENCOUNTER PROBABILITIES

Based on the time-independent model (Model 19; Table 1), encounter probabilities appear to be higher at the Camargue (95% CI: 0·386–0·416), than at Fuente de Piedra (95% CI: 0·247–0·336) and at Molentargius (95% CI: 0·026–0·054). However, strong variation occurs over years at all colonies (ΔQAIC = 488 between Model 19 and Model 13; Table 1). In the Camargue, encounter probabilities increased from newly-experienced breeders to already-experienced ones and varied over time (Model 2 compared to Models 10, 9 and 3). The QAIC further decreased when we dropped the interac-

Table 2. Survival estimates from the best model (Model 1) with lower (CI−) and upper (CI +) confidence intervals and standard error (SE). The cold spell effect in the Camargue is given separately for the first-time and experienced breeders (only Camargue-born breeders were available at that time)

	Estimate	CI−	CI +	SE
First-time breeders				
Camargue				
Cold spell	0·663	0·396	0·855	0·125
Other years	0·951	0·911	0·974	0·015
Fuente de Piedra	0·940	0·812	0·983	0·037
Molentargius	0·717	0·386	0·911	0·144
Experienced breeders				
Camargue				
Cold spell	0·843	0·476	0·969	0·120
All colonies	0·983	0·975	0·988	0·003

tion and modelled breeding experience additively with time (ΔQAIC = 12 between Models 2 and 1).

SURVIVAL PROBABILITIES

As expected, the cold spell sharply decreased survival probabilities in the Camargue (Table 2). Among the different models run (Models 5–8; Table 1), the model with site-specific survival only on first-time breeders was selected (ΔQAIC = 3 between Model 5 and 8). The survival probabilities of first-time breeders in the Camargue (0·951 ± 0·015) and in Fuente de Piedra (0·940 ± 0·037) are close and much higher than in Molentargius (0·717 ± 0·144). This effect disappears once birds gain experience, their survival being similar whatever the colony (0·983 ± 0·003; Model 1; Table 1). Finally, flamingo survival at a breeding site is independent of its natal colony (Model 4, ΔQAIC = 23·6).

MOVEMENT PROBABILITIES

Breeding dispersal differs according to birds' natal colony and breeding experience: the model incorporating these two factors (Model 19) was supported with a ΔQAIC of 38·5 (in comparison with Model 20; Table 1). Contrary to our prediction (iv), the cold spell did not affect the level of fidelity of first-time breeders to the Camargue as the model distinguishing movement probabilities of breeders departing from the Camargue in 1984 from the remaining years was rejected, with an increase of 11 points of the QAIC (from Models 11 to 5).

FIDELITY AND BREEDING DISPERSAL

Adding the possibility that flamingos move to an unobservable state resulted in a sharp decrease of QAIC (ΔQAIC = 286 from Model 8 to Model 13, Table 1), indicating non-random temporary emigration. Among the models tested, the model having the lowest QAIC had overwhelming support (Model 1, $w_i = 0{\cdot}998$, Table 1 &Appendix S3). To ascertain that estimates from this best model were not biased by a potential heterogeneity in resighting probabilities, we ran an additional model considering an additive effect on resighting probability of the age category at first observed breeding (individuals first observed breeding before or at 8 versus individuals first observed breeding after this age). Resighting probabilities estimated by this model were almost identical for the two groups, yet the differences were consistent with a low level of capture heterogeneity between these two groups. For instance, in Molentargius in 1998, a year with high observation effort, resighting probability was 0·18 ± 0·07 for birds having been first observed breeding the previous year at age ≤8 and 0·17 ± 0·07 for those having been first observed breeding the previous year at age > 8. Most important, estimates of movements from this additional model did not differ significantly from those of our best model. This additional model was not as supported as our initial best model by the data (Likelihood Ratio Test, $\chi^2 = 1{\cdot}24$, d.f. = 1, $p = 0{\cdot}27$) so that resighting heterogeneity is unlikely to have caused bias in movement estimates. Finally, another bias could follow from the low encounter rate at Molentargius and the importance of movements to the unobservable state. The model might have erroneously assigned a bird to one of these two sites given the low information provided by the data. To evaluate this potential bias, we removed observations at Molentargius and ran Model 1 again on the new dataset. Movement estimates between the Camargue and Fuente de Piedra were almost identical as those obtained for the full dataset with again a strong positive effect of the natal colony (see Appendix S4).

Hereafter, we present the estimates from our best model only (i.e. Model 1; Appendix S3). Estimates are from the period when all colonies were occupied because when some colonies were not available due to unfavourable conditions, dispersal to these colonies could obviously not be calculated: at the same time, dispersal rates to the other colonies were inflated when compared with years with all colonies available, because movements are estimated as the percentage of birds reaching each colony.

Raw data show that more flamingos originating from Fuente de Piedra (807) than from the Camargue (298) were observed breeding for the first time at Fuente de Piedra. Conversely, more flamingos from the Camargue (910) than from Fuente de Piedra (63) were observed breeding for the first time in the Camargue. This imbalance remains true even when correcting for the numbers ringed at the two colonies and is consistent with natal philopatry. As regards breeding fidelity, whatever the experience and the origin, fidelity is higher at the natal colony (97–98% fidelity for first-time and experienced breeders from Fuente at Fuente and 84–97% fidelity for first-time and experienced breeders from Camargue at Camargue; Fig. 2), thus supporting our first prediction. Fidelity is relatively low when flamingos first breed at the other major colony (38% at Camargue for Fuente-born birds and 53% at Fuente for Camargue-born ones; Fig. 2a). It is generally intermediate at the smaller-sized Molentargius colony, the exception being the experienced Fuente-born flamingos at Molentargius (Fig. 2b).

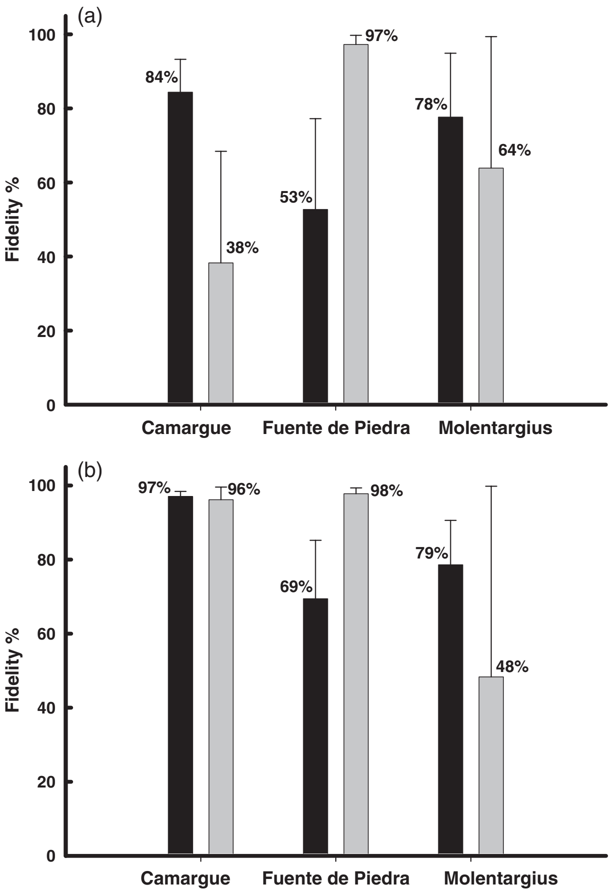

Fig. 2. Breeding fidelity probabilities (+95%CI) of (a) first-time breeders and (b) experienced breeders greater flamingos depending of their natal colony (black bars – Camargue-born breeders, grey bars – Fuente-born breeders).

First-time breeders show lower fidelity to their breeding site than experienced breeders in all cases except Fuente-born flamingos at Molentargius (Fig. 2a vs. 2b), thus supporting only partially our second prediction.

Again with the exception of the Fuente-born experienced breeders from Molentargius, dispersers move preferentially either to the unobservable state (Camargue-born first-time breeders from Fuente de Piedra (Fig. 3a), Fuente-born first-time breeders from the Camargue (Fig. 3b) and Camargue-born experienced breeders from Fuente de Piedra (Fig. 3c)) or to their natal site (Fuente-born experienced breeders from the Camargue (Fig. 3d), Camargue-born first-time breeders from Molentargius (Fig. 3e), Fuente-born first-time breeders from Molentargius (Fig. 3f) and Camargue-born experienced breeders from Molentargius (Fig. 3g)). The preferential dispersal to the unobservable state is marked only for first-time breeders on a large colony. The categories that move preferentially to the unobservable state have in all cases their natal colony as second choice (Fig. 3a–c). Hence our third prediction is partially supported: the natal colony is the first dispersal destination (sometimes after the unobservable state) except for Fuente-born experienced flamingos breeding at Molentargius; Fig. 3h).

Discussion

NON-RANDOM BREEDING DISPERSAL PATTERN

Our results largely support our first three predictions. Breeding site fidelity generally increases with experience and breeding dispersal is enhanced towards the natal colony. Indeed, breeding site fidelity is always higher at the natal colony than elsewhere and, with the exception of Fuente-born experienced breeders at Molentargius, an important proportion of emigrants comes back to the natal colony the next year (Fig. 3). The atypical behavior of Fuente-born experienced breeders at Molentargius, which disperse only to the Camargue and not back to their natal colony, may be due to a preferential flyway connecting Molentargius to the Camargue. Dominant winds likely explain preferential long distance winter movements from Camargue to Tunisia with Sardinia being used as a stop-over site between the two (Green, Hirons & Johnson 1989). Dispersal back to the natal colony from the two large colonies is delayed by substantial temporary emigration to an unobservable state (Fig. 3a–c). This may result from either reproductive skipping caused by a cost of first reproduction, or from breeding outside the study area which would not be surprising as Camargue- and Fuente-born flamingos have been found to breed regularly in Turkey and in Mauritania (Balkız *et al.* 2007; Diawara *et al.* 2007). The overall pattern that takes shape is that of flamingos vying against adversity (likely in the form of intraspecific competition) to come back to their natal colony and eventually succeeding when they have gained enough experience. Dispersal rates are experience-dependent, decreasing from high to moderate with increasing experience (2–61% and 2–52% for first-time and experienced breeders, respectively). Local colony dynamics is thus significantly affected by immigration, and contrary to other long-lived colonial species such as the wandering albatross *Diomedea exulans* (Inchausti & Weimerskirch 2002), Greater flamingo dispersal lasts long into adulthood.

The importance of transience detected in our dataset may result from two phenomena. As suggested by Perret *et al.* (2003), transience can reveal nomadic dispersal, i.e. in our case, the presence of birds that would permanently emigrate outside the study area after their first-breeding attempt (e.g. to Turkey and Mauritania; Balkız *et al.* 2007; Diawara *et al.* 2007). Another explanation could be that because of an important cost of first reproduction on the survival of birds breeding before the age of 7 (Tavecchia *et al.* 2001), these birds die and appear as transients in our analysis.

Our estimates are robust to temporary emigration, permanent emigration, capture heterogeneity and low resighting rates in Molentargius, four potential sources of bias. They provide the first reliable dispersal estimates for this species at the scale of the western Mediterranean by extending previous works to Fuente-born birds (Nager

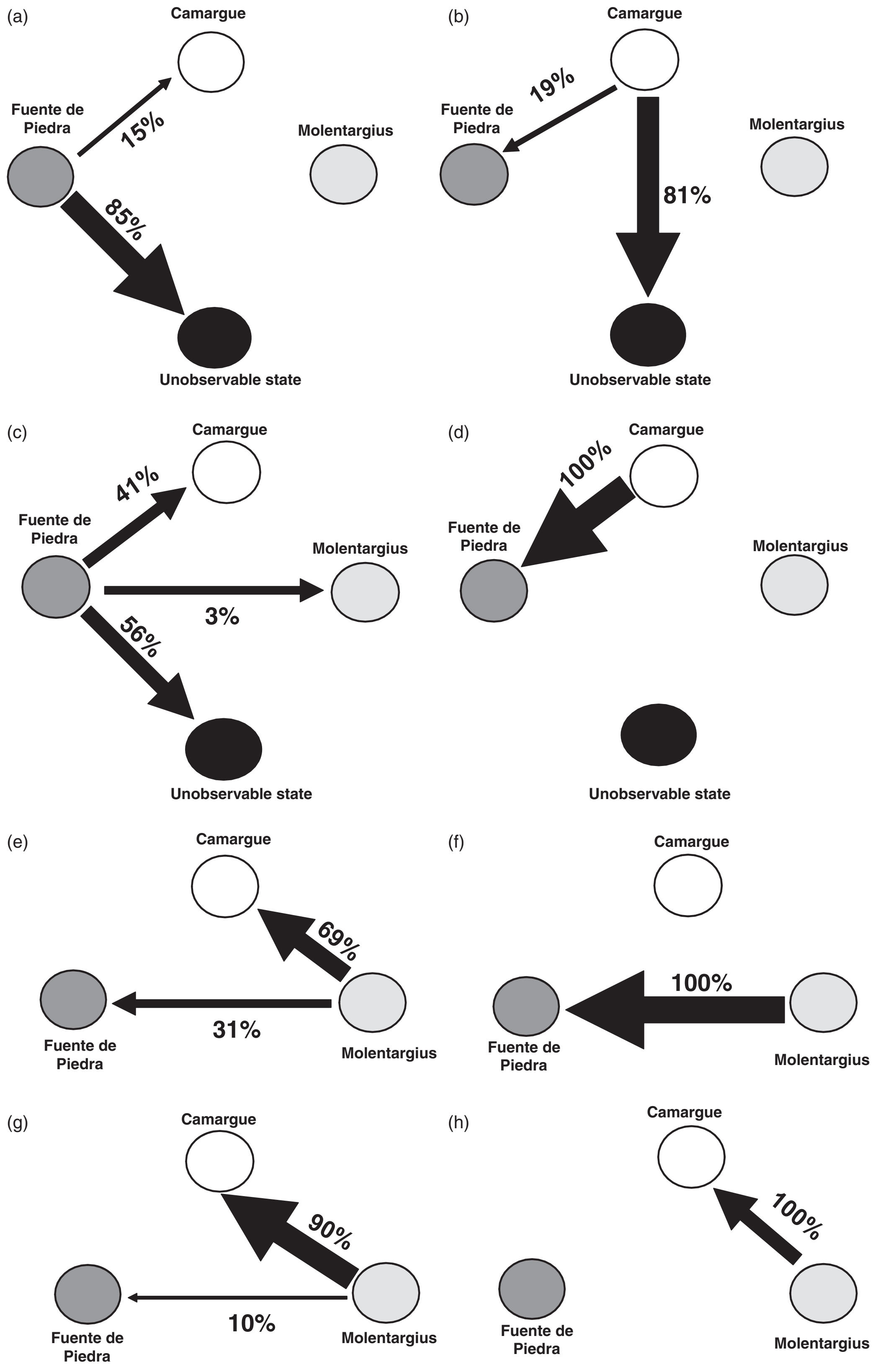

Fig. 3. Destinations of (a) Camargue-born first-time breeders leaving Fuente, (b) Fuente-born first-time breeders leaving the Camargue, (c) Camargue-born experienced breeders leaving Fuente, (d) Fuente-born experienced breeders leaving the Camargue, (e) Camargue-born first-time breeders leaving Molentargius, (f) Fuente-born first-time breeders leaving Molentargius, (g) Camargue-born experienced breeders leaving from Molentargius and (h) Fuente-born experienced breeders leaving from Molentargius. The width of the arrow is proportional to dispersal probabilities.

et al. 1996). Understanding the processes that generates the large-scale dynamics observed requires evaluating how costs and benefits of natal philopatry may vary with experience.

POTENTIAL FITNESS ADVANTAGES OF LONG-TERM NATAL PHILOPATRY

If for immature birds natal philopatry can be passive, resulting from the imperfect sampling of available breeding sites by young animals (they certainly know the existence of their site of birth before any alternatives), other hypotheses must be put forward to explain the long-term persistence of breeding movements back to the natal site. Environmental conditions may differ consistently among natal sites in terms of foraging resources, parasites or predators, so that it results in the selection of local adaptations. Hence, an individual may be advantaged at its natal site because its genotype/phenotype is favoured at this site in terms of parasite resistance as it has been shown in Great tits (*Parus major*) infested by hen fleas (Heeb *et al.* 1999). In turn, breeding at the natal site may avoid the risk of outbreeding and favour mating with genetically similar individuals, thus preserving genes co-adapted to the environmental constraints at the natal site (Shields 1982; Pusey & Wolf 1996). Indeed, it has been shown that philopatric birds could present higher fitness than dispersers (e.g. Bensch *et al.* 1998). It would thus be the familiarity with the distribution of food resources, with predators and parasites and with other individuals which could increase the fitness of philopatric birds and drive long lasting movements back to the natal site (Forero, Donazar & Hiraldo 2002; Péron, Lebreton & Crochet 2010).

Following this hypothesis, philopatric birds should ultimately present a better fitness than dispersers. The survival of first-time breeders was lower at Molentargius than at the two large colonies. First-time breeders may thus pay a cost by dispersing to this smaller colony. However, this cost disappears after the first-breeding occasion as survival becomes independent of the natal colony. In other words, Fuente-born breeders in the Camargue (respectively Camargue-born breeders in Fuente) do not appear to pay a cost in term of survival compared with Fuente-born breeders in Fuente (respectively Camargue-born breeders in the Camargue). The advantage of breeding at the natal colony is thus not detectable in terms of survival. This may be because adult survival is expected to be a canalized life-history trait in long-lived species such as flamingos (Gaillard, Festa-Bianchet & Yoccoz 1998) and in our case, this trait would be canalized at a regional scale (the western Mediterranean). Hence, costs of dispersal may rather be expected in term of breeding success.

In the Camargue, newly-experienced breeders (i.e. those 1 year after their first observed breeding) had lower resighting probabilities than experienced breeders. Previous studies suggested that young flamingos skipped breeding more often than adults (Cézilly *et al.* 1996; Pradel *et al.* 1997a; Tavecchia *et al.* 2001). However, these studies were restrained to the Camargue so that newly-experienced and younger birds were possibly breeding elsewhere. While in our case we could detect birds breeding at two other closely-related colonies, newly-experienced breeders still presented a lower encounter probability in the Camargue. Hence, this might rather be due to early failures during the breeding season or skipping reproduction following a previous successful breeding attempt, as first suggested by Cézilly *et al.* (1996). The lower proportion of younger breeders observed feeding their chicks (> 60 days old) than that expected based on the proportion incubating (A. Béchet, unpublished data) suggests that early failures are more common among young and inexperienced flamingos. As a consequence, they may desert the colony earlier, which in turn decrease their probability of being observed and confirmed as breeders. These results suggest that inexperienced flamingos encounter competitive conditions at the Camargue and have a low breeding success. In kittiwakes *Rissa tridactyla*, dispersers were shown to have lower breeding probabilities than faithful ones (Danchin & Cam 2002). For flamingos, dispersal caused movements to the unobservable state, corresponding either to non-breeding or to breeding outside the study area, for emigrants to the large colonies but not for emigrants to the smaller Molentargius colony. Hence, our results suggest that inexperienced birds may improve their breeding probability and success at Molentargius compared with the two large colonies, this effect disappearing after they have gained experience.

Settlement decisions are likely to be controlled by both individual and patch breeding success (Danchin & Cam 2002). In order to optimize their settlement decisions, individuals may cue on public information such as colony size (conspecific attraction hypothesis) or the breeding success of conspecifics (Danchin, Boulinier & Massot 1998; Doligez, Danchin & Clobert 2002; Valone & Templeton 2002; Cam *et al.* 2004). Except for Camargue-born first-time breeders from the Camargue who moved preferentially to Molentargius, all other dispersal movements were higher to the large colonies (Fuente and the Camargue) than to Molentargius (Appendix S4). This result thus globally supports the conspecific attraction hypothesis.

In flamingos, individual and colony breeding failure have been shown to increase dispersal rate from the Camargue (Nager *et al.* 1996). Over our study period, the average breeding success at Fuente and in the Camargue were similar (0·50 ± 0·03 and 0·61 ± 0·07, $p = 0{\cdot}14$) and lower than in Molentargius (0·79 ± 0·08, $p = 0{\cdot}02$). Therefore, in terms of instantaneous breeding success, flamingos did not move from the least productive colony to the better ones. However, by weighting breeding success by the frequency of colony availability over the study period, breeding success expectation at Molentargius drops to the lowest position (0·31 ± 0·08) followed by Fuente de Piedra and Camargue (0·46 ± 0·07 and 0·50 ± 0·03, respectively). For long-lived species which individuals probably prospect breeding sites (Frederiksen & Bregnballe 2000), the relative unpredictability of Molentargius availability may decrease its perceived quality. This concurs to explain the lower fidelity rates at this colony and provides support for the hypothesis that birds cue on the long-term expectation of colony breeding success to decide where to settle.

In summary, we could not detect direct benefits of natal philopatry in terms of survival, or of breeding success expectation, two surrogates of fitness accessible by our data. Survival was lower in Molentargius for first-time breeders but breeding attempts at Molentargius provides a better probability of successful outcome in the last years of the study, and this may be enhanced for inexperienced birds. Over the study period, the two large colonies have been more frequently available and globally more productive than Molentargius, which may explain their continuous attractiveness despite intraspecific competition. It would thus be important to study more precisely variations of lifetime reproductive success at the individual level to evaluate the possible payoffs of dispersal, natal philopatry and of an experience-dependent strategy of dispersal to the natal colony (Doligez & Pärt 2008).

LARGE-SCALE IDEAL DESPOTIC DISTRIBUTION?

At a local scale, flamingos distribution on nearby colonies is structured according to an age-related despotic pattern resulting from strong competition to acquire a nesting place, a phenomenon observed in several bird species (Waser 1985; Rendón *et al.* 2001; Serrano *et al.* 2003; Oro 2008). This pattern could remain true at the larger scale of the Western Mediterranean with the Camargue and Fuente de Piedra, two long-established and saturated colonies, being primarily occupied by experienced breeders, and Molentargius more easily accessible to first-time breeders. Several of our results support this hypothesis: (i) first-time breeders present a lower fidelity than experienced ones at the two major colonies but not at Molentargius; (ii) first-time breeders move to the unobservable state, from the two large colonies but not from Molentargius. This suggests that flamingos breeding for the first time at the two large colonies are forced to either skip breeding or to move to another presumably less competitive site the next year. Having managed to breed once at competitive site does not necessarily help breeding there the next year as a bird must compete again to secure a nest on the colony. Also, inexperienced bird may pay an additional cost when breeding at the two large colonies which may increase skipping rate afterward. The Ideal Despotic Distribution predicts that subordinates are constrained by the territoriality of dominant individuals to settle in low quality patches (review in Oro 2008). Two surrogates of fitness are in agreement with the assumption of the Ideal Despotic Distribution that animals should move to low quality patches: survival is lower at Molentargius for first-time breeders and the long-term expectation of breeding success is also lower. However at the individual level, breeding at Molentargius may be an advantageous strategy in the short term by avoiding queuing (and non-breeding) at the competitive colonies while gaining competitive ability for future attempts.

Contrary to our fourth prediction, the cold spell did not affect the fidelity of first-time breeders to the Camargue. This suggests that even though recruitment probabilities were generally higher this year, they did not make it easier for first-time breeders confirming previous analyses that did not detect changes in the age structure of recruits this year (Pradel *et al.* 1997a). Several years of low survival may be needed to significantly affect the pool of individuals queuing for breeding and reduce intraspecific competition.

Regarding the forces driving large-scale breeding dispersal of the greater flamingo, we must add natal philopatry and experience to previously documented drivers of movements, i.e. intraspecific competition (Rendón *et al.* 2001) and preferential flyways (Nager *et al.* 1996). The most original is probably the long lasting effect of natal philopatry on the breeding dispersal of a bird over a large geographic range. This phenomenon may be more common than generally thought, in particular for long-lived species. But at present, the relevance of this phenomenon for other vertebrates remains largely unexplored. Future studies aiming at assessing possible fitness benefits and costs of natal philopatry are likely to bring new insights into our understanding of dispersal strategies.

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Supporting information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Matrices of survival (F_t^s), movements (ψ_t^{sz}) and resighting probabilities (P_t^s) for the multistate model of flamingo breeding dispersal between the Camargue (superscript 1), Fuente de Piedra (2), Molentargius (3) colonies and an unobservable state combining skipping episodes and breeding outside the study area (temporary emigration; 4).

Appendix S2. Goodness-of-fit test calculated by adding the individual χ^2 values and degree of freedom (d.f.) for each natal colony (individuals born in the Camargue and Fuente de Piedra). Incorporating the transience effect (3G.SR) on the structure of the JMV model is presented at the last line of the table (as two age-classes on survival). The overdispersion factor ($\hat{c}$), computed as the ratio of the GOF test value to its number of degrees of freedom, is given for each test component and for the global GOF test.

Appendix S3. Fidelity and dispersal, given separately for Camargue- and Fuente-born first-time and experienced breeders. Estimates are derived from Model 1.

Appendix S4. Fidelity and dispersal, given separately for Camargue- and Fuente-born first-time and experienced breeders for Model 1 run on a dataset without the reobservations from Molentargius, i.e. here, Molentargius is included in the unobservable state.

Appendix S5. Model formulations developed using the model definition language of M-SURGE (Choquet *et al.* 2004).

Appendix S6. Open formulas of the shortcuts used in the model definitions.