

To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo

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Summary

1. The balance between costs and benefits of migration under different environmental, density-dependent and individual conditions may promote a broad range of migratory behaviours. We studied the factors influencing first-year migration and subsequent fidelity or dispersal among wintering areas, and the survival costs of different wintering behaviours in the greater flamingo (*Phoenicopterus roseus*).

2. We analysed by multievent capture–recapture modelling among-site dispersal/fidelity and site-dependent survival probabilities from 22 671 flamingos ringed in the Camargue (France) between 1977 and 2010 and resighted subsequently in their wintering grounds classified as France, Iberian Peninsula, Italy and North Africa.

3. We found that first- and second-year birds either resident or wintering at medium distances from their birth place, survived better than those wintering further afield. However, under severe winter conditions (extremely cold winter 1984–1985), individuals with the sedentary strategy suffered the highest levels of mortality. From the third winter onwards, the pattern of survival reversed: the long-distance wintering individuals (i.e. North Africa) survived better.

4. The proportion of first-year birds migrating for wintering was highly variable among cohorts and increased with favourable environmental conditions (wet years). After the first winter, birds showed high fidelity (> 90%) to their previous wintering area and wintered preferably near their natal colony when they became adults (> 2 years).

5. Survival estimates suggest that long-distance migration was costly for young and inexperienced individuals. Nonetheless, for adults, the most southern wintering areas seem to offer the most favourable local conditions for overwinter survival.

6. The higher availability of intermediate stopover sites during wet years may facilitate first-year migration. Then, once they have some wintering experience, flamingos appear to favour the known wintering grounds. As they grow older, dispersing towards the vicinity of the natal colony may provide higher breeding prospects for individuals wintering closer to this high-quality and saturated breeding ground, as predicted by the arrival-time hypothesis.

Key-words: arrival-time hypothesis, capture–recapture, environmental conditions, *Phoenicopterus ruber*, wintering

Introduction

Migration, a common phenomenon among many animal taxa, plays a central role in the spatial dynamics of mobile populations (Dingle 1996; Gill *et al.* 2001; Dingle & Drake 2007). It is a highly flexible system that has responded historically (i.e. glacial and post-glacial periods) and continues

to respond nowadays to environmental changes (Berthold *et al.* 1992; Fiedler 2003; Pérez-Tris *et al.* 2004; Visser *et al.* 2009; Piersma 2011). Migration is widely recognized as an adaptation to spatiotemporal fluctuations of resources and a response to environmental adversity (Gauthreaux 1982; Dingle 1996; Dingle & Drake 2007). Using the most seasonally suitable habitats at each moment in their life cycle, individuals may improve their fitness by increasing future fecundity and/or survival (Gauthreaux 1982; Ketterson &

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Nolan 1982; Berthold 2001). However, the benefit of increased resource availability and avoidance of harsh climatic conditions may be balanced by costs associated with the migratory process such as an increased risk of predation, exposure to new parasites and of course the energetic cost of movement (Alerstam, Hendenström & Akesson 2003). The balance between costs and benefits may also change in some years because of environmental stochasticity and density-dependent factors (Chapman *et al.* 2011; Kokko 2011). Also the interindividual variation in the costs and benefits of migration linked to individual characteristics may promote a broad range of migratory strategies within a population (Kaitala, Kaitala & Lundberg 1993).

In many animal populations (including insects, fishes, mammals and birds), the seasonal migration between breeding sites and winter quarters involves only a fraction of the population; this is called partial migration (Dingle 1996). Several, nonexclusive hypotheses have been proposed to explain the individual differences in migratory tendency. Partially migratory populations may consist of genetically different sedentary and migratory individuals (Lack 1944). In this case, migratory behaviour will be fixed at the individual level determining sedentary and migratory morphs ('obligate partial migration'; Lack 1944; Berthold 2001). The partial migration strategy will be maintained, that is, be 'evolutionarily stable', if the pay-offs (lifetime reproductive success) of both morphs in the population are balanced (Gauthreaux 1982). Alternatively, partial migration may respond to a behavioural or a state-dependent mixed evolutionary strategy varying over an individual lifetime ('facultative partial migration'; Ketterson & Nolan 1983; Kaitala, Kaitala & Lundberg 1993). In this case, the migratory behaviour is expected to be conditional on trade-offs influenced by environment (i.e. density-dependent processes; Kaitala, Kaitala & Lundberg 1993) and individual competitive abilities (linked to body condition, age or sex, the dominance hypothesis) (Ketterson & Nolan 1983; Chapman *et al.* 2011). Under the conditional strategy, fitness balancing between different migratory strategies is not necessary: migratory and resident strategies can evolve as the 'best of a bad job' where individuals maximize their fitness considering their internal and external state (Lundberg 1987). For instance, competitively inferior individuals (e.g. young or individuals in poor body condition) could be forced to migrate to suboptimal areas where their chances of survival may be lower (Lok *et al.* 2011). The combination of environmental conditions at wintering quarters with the route and distance of migration, which ultimately influences fitness components (i.e. survival and reproductive output), will determine the suitability of a wintering site (Lok *et al.* 2011). Among dense populations, sexually mature individuals arriving early in the season to breeding areas could benefit from a higher breeding success because of intense intraspecific competition for high-quality breeding territories and/or for mates favouring the reduction in migration distances; that is the arrival-time hypothesis (Kokko 1999). Hence, competition for the best breeding sites could push

reproductive individuals to take higher mortality risks by wintering nearer the breeding area than they would have under the sole migration costs (Kokko 2011). In this case, residency is expected to increase with the probability of reproduction, that is when the individuals become sexually mature (Marques, Sowter & Jorge 2010). Although age-differential migration is a widespread phenomenon (Cristol, Baker & Carbone 1999), several studies have also found that individuals increase their fidelity to their previous wintering areas when they become older (Barbraud, Johnson & Bertault 2003; Lok *et al.* 2011). Familiarity with a known environment where conditions are relatively predictable from year to year may enhance wintering site fidelity (Greenwood 1980). Migratory behaviour is thus under the antagonistic influence of several ecological and endogenous factors; in this context, partially migratory species provide opportunities to understand the mechanisms, environmental or ecological factors causing some individuals to migrate when others remain resident year round, and the consequences of different migratory strategies (Chapman *et al.* 2011).

The greater flamingo (*Phoenicopterus roseus*) is such a partially migratory long-lived species with a delayed reproduction (Pradel *et al.* 1997; Barbraud, Johnson & Bertault 2003; Balkız *et al.* 2007; Johnson & Cézilly 2007). Some individuals spend the winter near their breeding colonies such as the Camargue (southern France), whereas others migrate to distant wintering areas over the western Mediterranean and North Africa (Barbraud, Johnson & Bertault 2003; Johnson & Cézilly 2007). However, catastrophic mortalities linked to extremely low temperatures happen occasionally near the breeding grounds (Johnson & Cézilly 2007). For example, during winter 1984–1985, consecutive extremely cold days with temperatures down to -11°C caused the coastal lagoons in the south of France to freeze during 2 weeks causing the death of >3000 flamingos (Johnson, Green & Hirons 1991). These cold spell episodes may explain why many individuals spend the winter as far away as North Africa. On the other hand, wintering migration may be a costly process, especially for young inexperienced flamingos. Because flamingos use temporal and permanent wetlands as stopover sites (Amat *et al.* 2005), juvenile migration may in particular be limited during drought years. Also, the size of the colony may influence the probability of migration of juveniles through density-dependent processes. The balance between the benefits and costs of migration may vary with local environmental conditions and familiarity with the wintering site but may also depend on age. Indeed, in accordance with the arrival-time hypothesis, sexually mature individuals overwintering near their breeding colony may enhance their reproductive prospects.

Using a long-term (35 years) data set of more than 22 000 greater flamingos born in the Camargue (France) and resighted all over the Mediterranean we studied: (i) the age-related survival consequences of wintering in different areas (i.e. close to the natal area, at medium-distance areas or at long-distance areas); (ii) the impact of the extreme cold

winter 1984–1985 on survival of resident individuals; (iii) the influence of the winter NAO index, a proxy for precipitation and droughts over the Mediterranean (Sousa *et al.* 2011), on juvenile migration and survival; (iv) the influence of the annual number of breeding pairs on first-year migration and (v) the ontogeny of wintering site choice and fidelity (age-specific dispersal among wintering sites). We applied multievent capture–recapture models (Pradel 2005) to estimate simultaneously the probabilities of survival, first migration, fidelity and dispersal between wintering sites.

Materials and methods

SPECIES AND STUDY AREA

The greater flamingo can live up to 40 years in the wild and > 60 years in captivity (Johnson & Cézilly 2007). Flamingos inhabit temporary and permanent coastal brackish wetlands and salt lakes all over the world where they feed on aquatic invertebrates and seeds (Johnson & Cézilly 2007; Béchet *et al.* 2009). Flamingos breed intermittently in most of their natural breeding areas (Johnson & Cézilly 2007). Reproduction depends on the availability of undisturbed islands to avoid predation (Johnson & Cézilly 2007). Access to reproduction is progressive, the youngest age of reproduction ever observed being 3 year old (Pradel *et al.* 1997). Movement is important in this species, so that the breeding colonies of the Mediterranean basin function like a metapopulation *sensu lato* (Balkiz *et al.* 2007, 2010). Flamingos have bred intermittently in the saline lagoons of the Camargue (southern France) for centuries (Johnson & Cézilly 2007). Owing to human management of water levels, since 1969, flamingos have bred every year (except 2007) in the Fangassier lagoon (43°25'N, 4°37'E; Salin de Giraud, Camargue), with an average of 10 000 breeding pairs.

INDIVIDUAL DATA

Since 1977, with the exception of 2002 and 2007, 7–30% of the fledglings (of unknown sex) reared each year in the Camargue have been marked individually with plastic rings engraved with a three or four digit code. Ring codes can be read using a telescope and from a distance up to 300–400 m (Johnson & Cézilly 2007). After fledging, these birds are resighted throughout the year all around the Mediterranean basin. We considered the initial capture at fledging and the subsequent winter resightings of 22 671 flamingos ringed as chicks on the Fangassier lagoon during the period 1977–2010. First capture was coded differently from subsequent resightings in the different wintering areas. Four wintering areas, considered as the most important sites for the species in the Mediterranean, were identified (Fig. 1): southern France (FR), Iberian Peninsula (Spain and Portugal) (IB), Italy (IT) and North Africa (Guinea-Bissau, Mali, Mauritania, Senegal, Algeria, Egypt, Libya, Morocco and Tunisia) (AF). This latter region encompasses various sites where observation effort is low. Also, to avoid observations during migratory stopovers, we only considered sightings from November to January ($n = 793\,485$ observations). During this period, 162 individuals (0.71% of marked chicks) were observed in two different wintering areas the same winter. In this case, we retained the observation closest to the middle of the winter period (i.e. 15 December).

ENVIRONMENTAL DATA

We used the global indices of winter NAO available at <http://www.cgd.ucar.edu/cas/jhurrell/indices.html> as a covariate to investigate the possible association between demographical parameters and environmental conditions (i.e. rainfall levels). The NAO index measures differences in sea level and atmospheric pressure between the Azores and Iceland (Hurrell 1995). The winter NAO drives the precipitation variability during the wettest months in the Mediterranean



Fig. 1. Wintering areas of flamingos born in the Camargue (France) considered for the analyses: IB, Iberian Peninsula; FR, southern France; IT, Italy and AF, Northern Africa. Grey squares indicate the resighting locations of greater flamingos from 1977 to 2010 in the four wintering areas considered, and Black squares indicate the location of colonies where breeding occurred at least once between 2000 and 2010.

and has a direct impact on droughts (Sousa *et al.* 2011). During its negative phase, NAO steers the storm track towards southern Europe, thus increasing precipitation observed over the Mediterranean, and vice versa (Sousa *et al.* 2011).

The number of breeding pairs was determined using aerial photographs of the colony taken in May, when peak numbers were incubating (Descamps *et al.* 2011).

MULTI-EVENT CAPTURE-RECAPTURE ANALYSES

Goodness-of-fit

The goodness-of-fit of a general multistate model assuming a full-time variation of recapture, survival and transition parameters (the Jolly Movement model, Brownie *et al.* 1993) was assessed using program U-CARE 2.2.2 (Pradel, Wintrebert & Gimenez 2003; Choquet *et al.* 2009). This test was statistically significant ($\chi^2 = 4963.67$, d.f. = 1830, $P < 0.001$, see Data S1, Table S1.3, Supporting information). This is because of changes in survival with age but also possibly to other unknown cohort-dependent factors. Indeed, a goodness-of-fit test that accounts for full cohort dependence showed no lack of fit (see Data S1, Table S1.4, Supporting information). Because a full-cohort-dependent model would be overparameterized, we decided to focus on the cohort differences early in life where cohort effects are likely to be the strongest. To remain on the safe side, we calculated a variance inflation factor based on the lack of fit of the model without cohort effect as the ratio of the goodness-of-fit statistic to its degrees of freedom (Lebreton *et al.* 1992) ($\hat{c} = 2.71$). This factor was used to scale down model deviances and account for any remaining lack of fit.

Multievent model design

We evaluated the influence of age, wintering area and environmental conditions on the probabilities of survival and of presence in the different wintering areas. To do this, observations were encoded in multievent encounter histories and analysed using multievent capture-recapture models (Pradel 2005; Data S1, Supporting information). The multievent framework distinguishes what can be observed in the field (the events coded in the capture histories), from the underlying biological states of the individuals, which must be inferred. Here, the events were as follows: '0' – bird not resighted, '1' – fledgling marked in France, '2' – bird resighted in the Iberian Peninsula, '3' – bird resighted in France, '4' – bird resighted in Africa and '5' – bird resighted in Italy. The underlying biological states considered were as follows: 'Fled' – fledgling in France, 'IB' – bird wintering in the Iberian Peninsula, 'FR' – bird wintering in France, 'AF' – bird wintering in Africa, 'IT' – bird wintering in Italy and 'D' – dead bird.

Multievent models use three kinds of parameters: the initial state probabilities, the probabilities of transition between the states, and the probabilities of the events conditional on the underlying states. As every individual in our data set was ringed as a chick in France (state 'Fled' with certainty), the initial state probabilities were not used in our analyses. The transition probabilities corresponded to survival, the probabilities of the first migration for fledglings and the probabilities of fidelity or of dispersal among the wintering areas. The event probabilities corresponded to the probabilities of resighting in the different areas.

Transition probabilities can be decomposed to distinguish several steps, each potentially affected by different effects. Traditionally, one separates survival (Φ_t^r), specific to the state of departure r and to the time interval t to $t + 1$, from the probability of dispersal conditional

on survival. Matrix representations with departure states in rows and arrival states in columns are commonly used. For the survival step, we have:

$$\Phi_t^r = \begin{matrix} & \begin{matrix} Fled & IB & FR & AF & IT & D \end{matrix} \\ \begin{matrix} Fled \\ IB \\ FR \\ AF \\ IT \\ D \end{matrix} & \begin{pmatrix} \phi & 0 & 0 & 0 & 0 & 1 - \phi \\ 0 & \phi & 0 & 0 & 0 & 1 - \phi \\ 0 & 0 & \phi & 0 & 0 & 1 - \phi \\ 0 & 0 & 0 & \phi & 0 & 1 - \phi \\ 0 & 0 & 0 & 0 & \phi & 1 - \phi \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{matrix}.$$

By convention in the traditional approach, transitions are described after survival (Hestbeck, Nichols & Malecki 1991; Schwarz, Schweigert & Arnason 1993). Thus, at the end of the survival step, a fledgling that survives (first row) is still considered a fledgling (first column), and a bird wintering in Iberia (second row) that survives is still considered 'in Iberia' (second column). The next step describes the transitions Ψ_t^{rs} of survivors between live state r at time t and live state s at $t + 1$. In our analyses, the first row corresponds to the possible first migrations of fledglings and the subsequent rows to fidelity/dispersal between wintering areas.

$$\Psi_t^{rs} = \begin{matrix} & \begin{matrix} Fled & IB & FR & AF & IT & D \end{matrix} \\ \begin{matrix} Fled \\ IB \\ FR \\ AF \\ IT \\ D \end{matrix} & \begin{pmatrix} 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{matrix}.$$

This classical decomposition was used to perform most of the models. However, to study in details the first migration of fledglings and in particular to test the effect of temporal covariates on the decision to leave, irrespective of the direction of migration, we further decomposed the second step in two. A first matrix, in which the covariate was tested, describes on the first row whether a fledgling departs (first column) or remains in France (third column, probability ' γ '). The second to fifth rows describe the dispersal among the wintering areas and remain unchanged.

$$\Upsilon_t / \Psi_t^{rs} = \begin{matrix} & \begin{matrix} FledM & IB & FR & AF & IT & D \end{matrix} \\ \begin{matrix} Fled \\ IB \\ FR \\ AF \\ IT \\ D \end{matrix} & \begin{pmatrix} 1 - \gamma & 0 & \gamma & 0 & 0 & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & \psi & \psi & \psi & \psi & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{matrix}.$$

A second matrix corresponds to the destination of migrating fledglings (*FledM*): Iberian, Italian or African wintering areas (ε_t^s).

$$\varepsilon_t^s = \begin{matrix} & \begin{matrix} Fled & IB & FR & AF & IT & D \end{matrix} \\ \begin{matrix} FledM \\ IB \\ FR \\ AF \\ IT \\ D \end{matrix} & \begin{pmatrix} 0 & \varepsilon & 0 & \varepsilon & \varepsilon & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \end{matrix}.$$

The event probabilities relating the observations coded in the capture histories to the underlying biological states contain site- and time-specific resighting probabilities (p_i). For instance, a bird wintering in Iberia (second row) will have a code 2 in its capture history if it is resighted (third column, probability p) and a code 0 if it is not resighted (first column, probability $1 - p$).

$$P_i^r = \begin{matrix} & '0' & '1' & '2' & '3' & '4' & '5' \\ \begin{matrix} Fled \\ IB \\ FR \\ AF \\ IT \\ D \end{matrix} & \begin{pmatrix} 0 & 1 & 0 & 0 & 0 & 0 \\ 1-p & 0 & p & 0 & 0 & 0 \\ 1-p & 0 & 0 & p & 0 & 0 \\ 1-p & 0 & 0 & 0 & p & 0 \\ 1-p & 0 & 0 & 0 & 0 & p \\ 1 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \end{matrix}$$

These parameters were estimated simultaneously from the whole set of encounter histories by maximum likelihood procedure. Models used do not distinguish mortality from permanent emigration, and survival should be considered as local (Lebreton *et al.* 1992). However, given that the most important wintering areas of greater flamingos were considered (with the exception of Turkish and Greek sites, where only 54 marked birds (0.2%) have been resighted over the study period), estimates obtained should be close to true survival.

Multievent model selection

Models were built and fitted to the data using program E-SURGE 1.7.1 (Choquet, Rouan & Pradel 2009) (see details on modelling procedure and model selection in Data S1, Supporting information).

We used informed models based on previous knowledge of the species (Johnson, Green & Hirons 1991; Cézilly *et al.* 1996; Nager *et al.* 1996; Barbraud, Johnson & Bertault 2003):

- Variation in survival probabilities limited to 4 age classes: from fledging to first winter, first to second winter, second to third winter, and between any following successive winters.
- Probability of first migration (from fledging to the first wintering area) varying by year and destination site.
- Probabilities of fidelity and dispersal between successive wintering areas depending on the sites of departure and of destination.
- Temporal and spatial variations in resighting probabilities.

Additionally, each model considered one or more effects of interest (See Table S1.1, Data S1, Supporting information). We tested potential differences in survival of individuals wintering at different distances from the natal area in different ways (see below), and we addressed the effect of cold spell on survival of birds wintering in France. In particular, we evaluated differences in survival between (i) individuals wintering in France (i.e. nonmigrants) vs. elsewhere (i.e. migrants); (ii) individuals wintering in France, wintering in Iberian Peninsula or Italy (i.e. medium-distance migrants) and wintering in Africa (i.e. long-distance migrants); (iii) individuals wintering along the northern shore of the Mediterranean (i.e. nonmigrants and medium-distance migrants) vs. those in the southern parts (i.e. long-distance migrants). For the probabilities of transition between wintering areas (i.e. fidelity and dispersal), we tested the influence of age. We contrasted models with and without differences in fidelity and movement between wintering sites for the first, the second and the third winter onwards.

As several effects on both probabilities of survival and movement (i.e. fidelity and dispersal) were possible, models including different combinations were tested (see details in Data S1, Supporting infor-

mation). Model selection was based on the Akaike's Information Criterion corrected for overdispersion (Q) (QAIC, Burnham & Anderson 2002). Additionally for each model j , we calculated the Akaike weight, w_j , as an index of its relative plausibility (Burnham & Anderson 2002).

Once selected the structure of survival and fidelity/dispersal probabilities that minimized QAIC, we ran specific models considering the influence of environmental covariates on young survival (first to second winter survival) and first migration probabilities. We studied the influence of the winter NAO index (as a proxy of precipitation in the Mediterranean) on survival probabilities of young birds and on the probability of migration out of France after fledging. We also evaluated the influence of the annual number of breeding pairs at the French colony (as a proxy for density-dependence) on postfledging dispersal. The effect of the environmental covariates was tested using the analysis of deviance with a Fisher-Snedecor distribution (ANO-DEV; Skalski, Hoffmann & Smith 1993) that compares deviances of the constant model, of the time-dependent model and of the model including the temporal covariate. This method allows testing whether the part of variability in the parameter under study explained by the covariate is significant. It is calculated as:

$$F_{(1,np(M_t)-np(M_{cnt}))} = \frac{Dev(M_{cnt}) - Dev(M_{cov})}{(Dev(M_{cov}) - Dev(M_t)) / (np(M_t) - np(M_{cov}))}$$

where Dev is the deviance estimated for the constant model (M_{cnt}), the model with climatic covariate (M_{cov}) and the time-dependent model (M_t), and np is the number of estimable parameters of the constant, temporal or covariate models. The percentage of variation that was explained by a covariate (r^2) was estimated as:

$$r^2 = \frac{Dev(M_{cnt}) - Dev(M_{cov})}{Dev(M_{cnt}) - Dev(M_t)}$$

Results

SURVIVAL PROBABILITIES

Model selection showed an important effect of both the wintering area and of the cold spell occurred in France on survival probabilities, model 9 vs. model 11 (Table 1, Δ QAIC = 47.36) and model 12 vs. model 9 (Table 1, Δ QAIC = 81.08). A model assuming differences in survival probabilities between birds wintering in the natal area (FR) vs. birds wintering elsewhere (IB, IT and AF) was strongly rejected, model 12 vs. model 13 (Table 1, Δ QAIC = 36.97). Finally, three models were tied in terms of QAIC: model 7, model 14 and model 12 (Table 1, Δ QAIC = 3.20). Model 7, the best model, considered differences in survival between individuals wintering in the northern Mediterranean (FR, IB and IT) and individuals wintering in Africa (AF). Model 14 considered additional differences between flamingos wintering in France and flamingos wintering at medium distance (IB and IT). And model 12 considered full spatial variation on survival. Model averaged estimates from the best models (models 7, 14 and 12, Table 1) showed an increase in survival probabilities with flamingo age (Fig. 2). Young flamingos (1st and 2nd year) wintering in Africa had a lower survival than those wintering in the northern Mediterranean (i.e. FR, IB and IT) that had similar survival (Fig. 2). Survival probabilities in African winter quarters became higher than in

Table 1. Multievent capture–recapture modelling of Camargue greater flamingo probabilities of survival

Model	Site specificity in survival	<i>np</i>	Dev	QAIC	Δ QAIC	w_i
7	CS_{FR}, resident = medium-distance \neq long-distance wintering (FR = IB = IT \neq AF)	266	195 352.94	72 617.95	0	0.51
14	CS _{FR} , resident \neq medium-distance \neq long-distance (FR \neq IB = IT \neq AF)	269	195 338.08	72 618.47	0.52	0.39
12	CS _{FR} , wintering area (FR \neq IB \neq IT \neq AF)	272	195 329.10	72 621.16	3.20	0.10
13	CS _{FR} , resident \neq medium-distance = long-distance (FR \neq IB = IT = AF)	266	195 461.80	72 658.12	40.17	0.00
9	Wintering area (FR \neq IB \neq IT \neq AF)	269	195 565.08	72 702.24	84.28	0.00
11	No effect of wintering area (FR = IB = IT = AF)	260	195 742.21	72 749.60	131.64	0.00

Model notation: CS_{FR}, cold spell occurred in France; FR, French wintering areas; IB, Spanish and Portuguese wintering areas; IT, Italian wintering areas; AF, African wintering areas; ‘=’ means no differences; ‘ \neq ’ means differences. Notation: *np*, number of estimable parameters; Dev, relative deviance; QAIC, Akaike information criterion corrected for overdispersion; Δ QAIC, the QAIC difference between the current model and the one with the lowest QAIC value; w_i , Akaike’s weight. It should be noted that all models considered annual and wintering site variation in resighting and first migration probabilities, a constant survival probability from fledgling to the first winter, and differences in fidelity/dispersal from wintering areas between first and second winters. The model with the lowest QAIC is in bold.

European wintering areas from the third winter onward (Fig. 2). The 1984–1985 cold spell reduced mean survival probabilities for first-year, second-year and older flamingos wintering in France by 77%, 55% and 35%, respectively (Fig. 2).

FIDELITY TO WINTERING AREAS AND DISPERSAL PROBABILITIES

Model selection showed a substantial effect of age on the probabilities of fidelity and dispersal from the previous wintering area, model 7 vs. model 6 (Table 2, Δ QAIC = 54.52). Model 7 considered differences between the probabilities of fidelity/dispersal from the first to the second winter than afterwards. Additional fidelity/dispersal differences among older birds were not retained, model 7 vs. model 8 (Table 2, Δ QAIC = 5.18).

Estimates from model 7 (Table 2) showed that fidelity to wintering areas was very high and increased from the second winter onwards (with the exception of birds wintering in

Africa that showed similar fidelity whatever their age) (Fig. 3). No substantial differences in the future wintering location of individuals leaving their first wintering area were detected (Data S2, Table S2, Supporting information). From their second winter, individuals that did not return to their Iberian, Italian or African wintering areas wintered preferably in France (Fig. 4). At this time, fidelity to French areas was higher than fidelity to any other wintering areas (Fig. 3).

THE EFFECT OF ENVIRONMENTAL VARIATION ON SURVIVAL AND FIRST WINTERING MIGRATION

None of the models including the effects of the environmental covariates tested improved QAIC (Tables 3 and 4).

No significant relationship between first winter survival and the winter NAO index was detected ($F_{1,60} = 0.45$, $P = 0.500$), the NAO covariate only explained 1% of the temporal variability of survival (Table 3).

There was a substantial temporal variation in the selection of the first wintering area after fledging (Fig. 5)

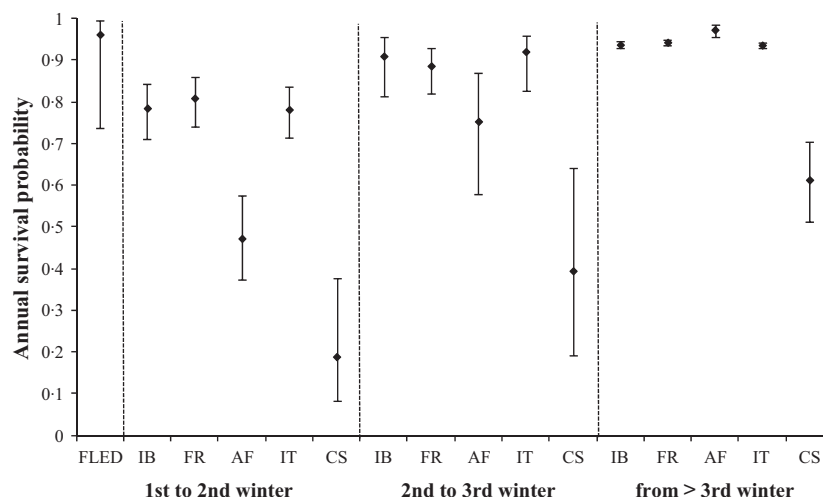


Fig. 2. Model averaged estimates of survival (95% confidence intervals) of flamingos wintering in Africa (AF), Iberian Peninsula (IB), Italy (IT) and France (FR) during normal winters and in France during the exceptionally cold winter 1984–1985 (CS). Estimates were calculated by model averaging from models 7, 14 and 12 (Table 1). The first estimate is from fledging to first winter (FLED) (c. 4 months), all subsequent estimates are annual estimates from one winter to the next.

Table 2. Multievent capture–recapture modelling of Camargue greater flamingo probabilities of fidelity/dispersal from wintering areas

Model	Age specificity in fidelity/dispersal	<i>np</i>	Dev	QAIC	ΔQAIC	<i>w_i</i>
7	2 ages (1st to 2nd winter ≠ from ≥2nd winter)	266	195 352.94	72 617.95	0	0.93
8	3 ages (1st to 2nd winter ≠ 2nd to 3rd winter ≠ from ≥3rd winter)	278	195 301.93	72 623.13	5.18	0.07
6	No age effect	254	195 565.74	72 672.48	54.52	0.00

Model notation '=' means no differences; '≠' means differences. Notation: *np*, number of estimable parameters; Dev, relative deviance; QAIC, Akaike information criterion corrected for overdispersion; ΔQAIC, the QAIC difference between the current model and the one with the lowest QAIC value; *w_i*, Akaike's weight. It should be noted that all models considered annual and wintering site variation in resighting and first migration probabilities, a constant survival probability from fledgling to the first winter, an effect of the cold spell on survival of flamingos wintering in France and survival differences between flamingos wintering in European and African wintering areas (FR = IB = IT ≠ AF). The model with the lowest QAIC is in bold.

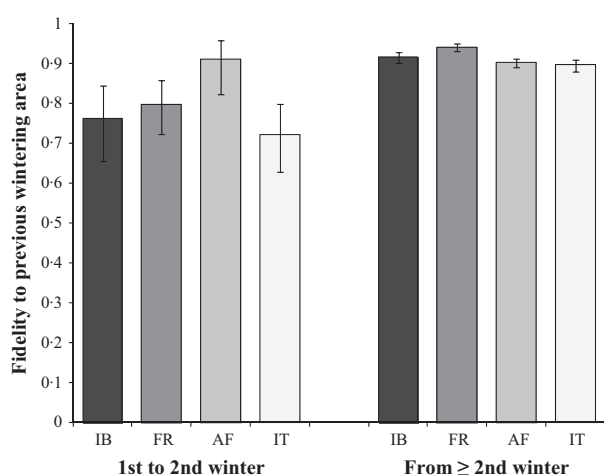


Fig. 3. Age-related fidelity to the different wintering areas (IB, Iberian Peninsula, FR, France; IT, Italy; AF, Africa) used by greater flamingos born in France. Estimates were extracted from model 7 (Table 2).

(model 7, Table 4). No significant effect of the number of breeding pairs on the probability that fledglings emigrate from France for their first winter was detected ($F_{1,31} = 0.68$, $P = 0.410$), this covariate explaining only 2% of the temporal migration variability. The NAO covariate, which explained 12% of the temporal variability, was close to significance at the 5% level ($F_{1,31} = 3.96$, $P = 0.055$) (model 18, Table 4). The NAO index was negatively correlated with the probability of migration. Migration probabilities ranged from 0.88 in years of low winter NAO values to 0.76 in years of high winter NAO values. To estimate the mean probabilities of spending the first winter in French, Iberian, Italian and African sites over the study period, an additional model with parameters constant over years was run. First-year flamingos showed a mean probability of wintering in France of 18% (IC: 17–20%), and a mean probability of migrating to Iberian, Italian or African wintering

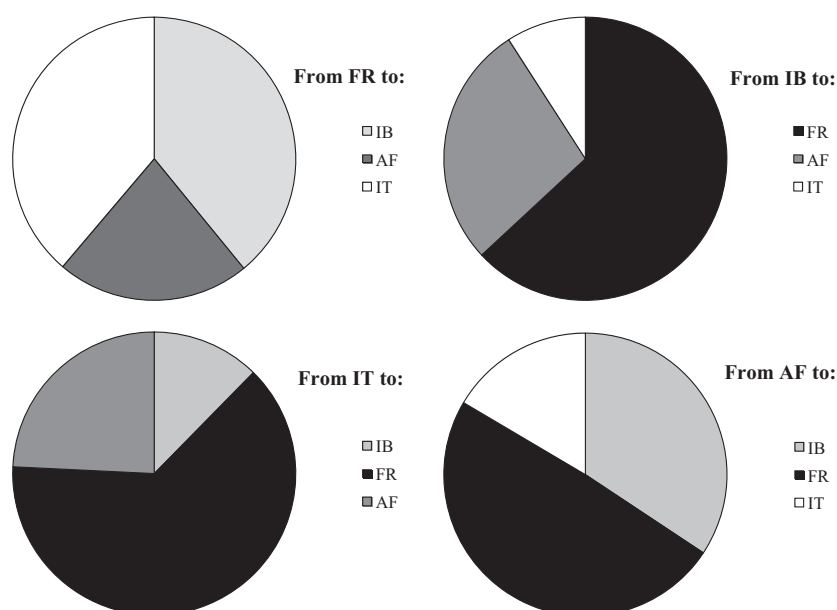


Fig. 4. Destination of dispersal from each wintering area by greater flamingos from the second winter onward. Estimates were extracted from model 7 (Table 2).

Table 3. Multievent capture–recapture modelling of Camargue greater flamingo probabilities of first wintering survival related to environmental covariates

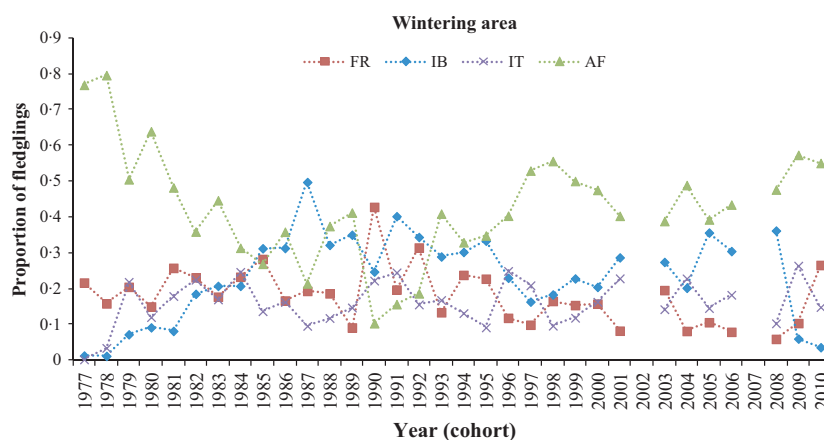
Model	Survival from 1st to 2nd winter	<i>np</i>	Dev	QAIC	ΔQAIC	<i>w_i</i>	<i>F</i> _{1,60}	<i>P</i> -value	<i>R</i> ²
7	Constant in time	266	195 352.94	72 617.95	0	0.83			
16	Winter NAO	268	195 350.79	72 621.16	3.21	0.17	0.45	0.500	0.01
15	Temporal variation	326	195 071.50	72 634.10	16.15	0.00			

Notation: *np*, number of estimable parameters; Dev, relative deviance; QAIC, Akaike information criterion corrected for overdispersion; ΔQAIC, the QAIC difference between the current model and the one with the lowest QAIC value; *w_i*, Akaike's weight. It should be noted that all models considered annual and wintering site variation in resighting and first migration probabilities, a constant survival probability from fledgling to the first winter, an effect of the cold spell on survival of flamingos wintering in France, survival differences between flamingos wintering in European and African wintering areas (FR = IB = IT ≠ AF) and differences in fidelity/dispersal from wintering areas between first and second winters. The model with the lowest QAIC is in bold.

Table 4. Multievent capture–recapture modelling of Camargue greater flamingo probabilities of fledgling winter migration related to environmental covariates

Model	1st wintering migration from France	<i>np</i>	Dev	QAIC	ΔQAIC	<i>w_i</i>	<i>F</i> _{1,31}	<i>P</i> -value	<i>R</i> ²
7	Temporal variation	266	195 352.94	72 617.95	0	1			
18	Winter NAO	236	195 643.45	72 665.16	47.20	0.00	3.96	0.055	0.12
19	Breeding pairs	236	195 674.55	72 676.63	58.68	0.00	0.68	0.410	0.02
17	Constant in time	235	195 681.82	72 677.31	59.36	0.00			

Notation: *np*, number of estimable parameters; Dev, relative deviance; QAIC, Akaike information criterion corrected for overdispersion; ΔQAIC, the QAIC difference between the current model and the one with the lowest QAIC value; *w_i*, Akaike's weight. It should be noted that all models considered annual and wintering site variation in resighting and first migration probabilities, a constant survival probability from fledgling to the first winter, an effect of the cold spell on survival of flamingos wintering in France, survival differences between flamingos wintering in European and African wintering areas (FR = IB = IT ≠ AF) and differences in fidelity/dispersal from wintering areas between first and second winters. The model with the lowest QAIC is in bold.

**Fig. 5.** Estimated proportions of Camargue greater flamingo fledglings wintering in the Iberian Peninsula (IB), French (FR), Italian (IT) and African (AF) areas by year. Estimates were extracted from model 7 (Table 4).

areas of 29% (IC: 26–33%), 18% (IC: 16–20%) and 34% (IC: 16–40%), respectively.

Discussion

The identification of demographical consequences associated with different wintering or migratory behaviours has important implications for evolutionary ecology and population dynamics (Gill *et al.* 2001; Dingle & Drake 2007; Chapman *et al.* 2011). Here, we found complex relationships between

migratory behaviour and birds survival; the best strategy in terms of survival chances varied depending on flamingo's age and winter environmental conditions.

SURVIVAL CONSEQUENCES OF DIFFERENT WINTERING BEHAVIOURS

Owing to benevolent climatic conditions and/or greater amounts of food available, migrants, in their more southern

wintering area, should, in general, have a higher overwinter survival rate than do residents in the northern wintering area (Ketterson & Nolan 1982; Hestbeck, Nichols & Hines 1992). For example, higher costs (lower survival) of wintering for young and inexperienced individuals at northern latitudes compared with migrants have been found in merlins (*Falco columbarius*) (Warkentin, James & Oliphant 1990). However, long-distance migration is likely to be energetically costly and may only be performed successfully by individuals in better conditions (Alerstam, Hendenström & Åkesson 2003). In fact, Sillett & Holmes (2002) found that migration caused > 85% of the annual mortality in the black-throated blue warbler (*Dendroica caerulescens*), a long-distance migrant passerine. We found that young flamingos wintering in African sites presented lower survival probabilities than those wintering in Iberian, Italian or French sites, suggesting the existence of a survival cost of migration related to distance, at least for the first migration. After their first winter, if young flamingos remain during the next year near their wintering site, the observed differences in survival of individuals wintering in different sites may also be linked to differential local conditions and not to the migration process *per se*. In accordance with our results, Adriaenssen & Dhondt (1990) found with the European robin (*Erithacus rubecula*) that local survival of resident males during normal winters was higher than local survival of migrants, but during cold winters, survival of residents decreased by 50%. Similarly, a recent study has shown that spoonbills (*Platalea leucorodia leucorodia*) wintering in African sites present lower survival probabilities than those wintering in Europe, where the population breeds (Lok *et al.* 2011).

In contrast with the pattern of survival found for young birds, after their second winter, survival probabilities of individuals wintering in African sites were higher than that of individuals wintering in the northern parts of the Mediterranean. Two possible and nonexclusive hypotheses may explain this result. First, better local foraging conditions in southern areas may increase survival chances of wintering individuals (Ketterson & Nolan 1982); the lower survival of young wintering in Africa would be due to a mortality cost of migration (Lok *et al.* 2011) paid mainly by young and inexperienced birds. Second, the survival cost early in life by individuals wintering preferentially in Africa may be paid differentially depending on individual quality. In this case, trans-Mediterranean migration may filter for high-quality individuals with higher survival (Tavecchia *et al.* 2001).

We also found a survival cost of residence related to environmental conditions. Although flamingos are extremely long lived, catastrophic mortalities linked to cyanobacteria blooms or extremely low temperatures have been reported (Alonso-Andicoberry *et al.* 2002; Johnson & Cézilly 2007). In fact, the exceptional cold spell that occurred in southern France during winter 1984–1985 greatly reduced survival probabilities of resident flamingos wintering in this area. Juvenile flamingos were much more affected by the cold spell than adults, suggesting that some adults were more able to escape. Previous studies (Lebreton *et al.* 1992; Cézilly *et al.*

1996; Balkız *et al.* 2010) estimated the impact of the cold spell on flamingos breeding in France, which includes those wintering in areas not affected by the extremely low temperatures. In contrast, our study estimates its direct impact on individuals wintering in the affected area. The lower survival values that we obtained further stress the effect of this event for this population. Our results suggest that greater flamingos might tolerate climatic constraints up to certain threshold based on plasticity and physiological limits. In this case, substantial reductions in survival probability would only be expected under climatic events going beyond their physiological limits (e.g. the 1984–1985 cold spell). In fact, we did not find effect of rainfall levels (i.e. winter NAO) on first wintering survival of flamingos. Environmental conditions (i.e. rainfall levels) in wintering areas are known to affect the survival of several migratory bird species such as European sand martins *Riparia riparia* (Szep 1995), storks *Ciconia ciconia* (Nevoux, Barbraud & Barbraud 2008) or Egyptian vultures *Neophron percnopterus* (Grande *et al.* 2009). However, greater flamingos feed on brackish wetlands, including managed wetlands such as salt pans, hunting marshes, rice fields and fish farms where hydrological stochasticity is buffered (Johnson & Cézilly 2007; Rendón *et al.* 2008; Béchet *et al.* 2009, 2012).

THE FIRST WINTERING MIGRATION

Proportions of fledglings migrating to the different wintering quarters over the Mediterranean varied substantially during the last 35 years. In accordance with Lok *et al.* (2011), we detected that high proportions of birds migrated to the areas where their survival expectancy early at life was lower (i.e. Africa). However, while the number of greater flamingo wintering in southern France has increased during the last decades (Johnson & Cézilly 2007), we did not find any increasing tendency of fledglings to remain resident near their breeding colony (Fig. 3). Consequently, the increasing number of wintering individuals in France may simply reflect the overall growth of the population of this extremely long-lived species. In accordance with our prediction, we found that annual variability in the probability of migrating to spend the first winter away from the natal colony was negatively correlated with the winter NAO index, that is, higher levels of migration from the natal area were associated with wet years. During droughts, temporary Mediterranean wetlands are commonly dry. The higher availability of intermediate stopovers during wet years may facilitate long-distance migration in this species (Amat *et al.* 2005), especially for individuals in poorer body condition (Barbraud, Johnson & Bertault 2003). Long-distance migration is a costly process (Alerstam, Hendenström & Åkesson 2003; Lok *et al.* 2011). Green, Hirons & Johnson (1989) showed that dominant winds likely explain preferential juvenile winter movements from Camargue to Tunisia. Barbraud, Johnson & Bertault (2003) showed that migration probability from the natal area was correlated with individual body condition, with higher movement probabilities for juveniles in good body condition.

In accordance with these results, we also found higher migration probabilities when environmental conditions were more favourable (Amat *et al.* 2005). Nevertheless, in contrast with results found by Barbraud, Johnson & Bertault (2003) at the individual level, we did not detect a correlation between the number of breeding pairs, which is negatively correlated with the mean fledgling body condition at the population level (Béchet & Johnson 2008), and the migration probabilities. Individual body condition may explain intracohort variation in juvenile migration probabilities (Barbraud, Johnson & Bertault 2003), but other factors such as genetic propensity to exploratory behaviours (Mueller, Pulido & Kempenaers 2011), environmental conditions (Green, Hirons & Johnson 1989), changes in wintering habitats (Rendón *et al.* 2008) or density-dependent processes (Kaitala, Kaitala & Lundberg 1993) may also influence the observed intercohort differences.

FIDELITY TO WINTERING AREAS

Fidelity to natal, breeding and wintering sites is a common phenomenon among many bird species (Greenwood 1980; Berthold 2001). The benefits of familiarity with the environment may outweigh the potential benefits of dispersal when conditions are relatively predictable from year to year (Greenwood 1980). Breeding philopatry to natal colonies is rather high in the western Mediterranean flamingo metapopulation (> 84%, Balkız *et al.* 2010), and breeding fidelity also increases with individual breeding experience in the largest colonies (Balkız *et al.* 2010). Similarly, we found a very high individual fidelity to the wintering areas used during their first winter, as found previously by Green, Hirons & Johnson (1989), and Barbraud, Johnson & Bertault (2003). Similarly to Eurasian Spoonbill (Lok *et al.* 2011), wintering site fidelity was lower in first-winter flamingos than in older birds, with the exception of African wintering regions (Fig. 4). Additionally, individuals aged more than 2 years that changed their previous wintering area dispersed preferably to French wintering sites. Average breeding success in the Camargue is higher than in the other important Mediterranean colonies such as Fuente de Piedra (Spain) or Molentargius (Italy) (Balkız *et al.* 2010). Consequently, competition for settling at the Camargue colony is very intense (Rendón *et al.* 2002; Johnson & Cézilly 2007). Individuals wintering in French sites may benefit from arriving early, acquiring high-quality mate, establishing a nest within the colony and having a potentially higher reproductive success than do those arriving later from more distant wintering areas, the arrival-time hypothesis (Ketterson & Nolan 1983; Kokko 1999; Marques, Sowter & Jorge 2010). In fact, fidelity to French wintering areas from the second winter was extremely high (94%).

POPULATION CONSEQUENCES OF DIFFERENT MIGRATORY BEHAVIOURS

Survival rates of long-distance wintering individuals differed markedly from those of short- to medium-distance wintering

individuals: originally lower early in life, they become higher from the third winter on. However, only resident individuals are exposed to cold spells. Several cold spells occurred in southern France during the last centuries (Johnson & Cézilly 2007), the last occurring at intervals of around 25 years (i.e. 1962, 1984–1985 and 2012; Johnson & Cézilly 2007; own unpublished data). Based on our estimates, if individuals wintering in the different areas have a similar breeding success and cold spells occur every 25 years, the resident wintering strategy will generally be the worst (Data S3, Supporting information, Fig. 6). For high levels of breeding success (> 0.4), the medium-distance wintering strategy is the best (Fig. 6). For breeding success < 0.35, the long-distance wintering strategy is the most advantageous, but when breeding success drops below 0.17, the expected population growth rate is negative (Fig. 6). Data on specific breeding success for resident and migrant individuals are missing; however, it is more plausible that reproductive rates of flamingos lie at intermediate values. With the mean breeding success estimated at the Camargue colony (0.46; Béchet & Johnson 2008) and our estimates of survival rates for long-, medium- and short-distance wintering individuals, all the expected population growth rates are positive (Fig. 6), which is in agreement with the observed increase in numbers of greater flamingos in the western Mediterranean during the last decades (Johnson & Cézilly 2007). For the range of breeding success values estimated in the Camargue during the study period (Béchet & Johnson 2008), the long- and medium-distance wintering strategies are equivalent and better than the resident strategy (Fig. 6). However, this is assuming that residents share the same reproductive expectancy as migrants. If, in agreement with the arrival-time hypothesis, they have a higher reproductive expectancy (Ketterson & Nolan 1983; Kokko 1999), all the observed wintering strategies may be balanced in terms of fitness. The complex interactions

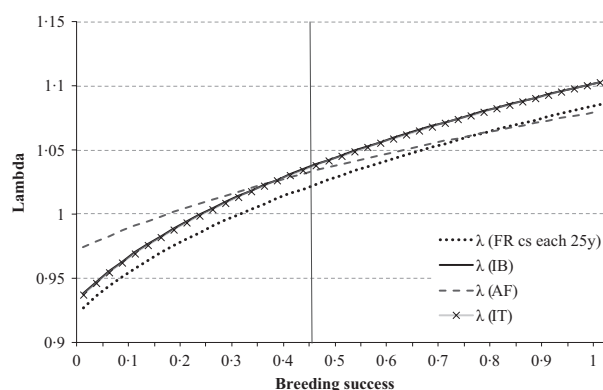


Fig. 6. Population growth rates (lambda) estimated for four types of hypothetical individuals exhibiting respectively the survival rates of Iberian, French, African and Italian wintering individuals as a function of breeding success. For French individuals, the occurrence of a cold spell reducing bird survival each 25 years was considered. Model averaged survival estimates were taken from models 7, 12 and 14 (Table 1). Vertical line represents the mean breeding success of flamingos at Camargue (0.46, Béchet & Johnson 2008).

between migratory behaviour, individual survival and environmental conditions found in this study may thus be compatible with the existence and maintenance of partial migration in this species (Chapman *et al.* 2011).

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Supporting information

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

Data S1. Multievent modeling of the probabilities of survival, recapture, first migration and fidelity/dispersal between wintering areas in the greater flamingo.

Data S2. Age-dependent fidelity/dispersal between wintering areas probabilities.

Data S3. Population matrix modeling.

Data S4. Flamingo reduced dataset.

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