Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition

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Summary

1. Factors influencing post-fledging movements before the first breeding attempt were studied in individually marked greater flamingos (*Phoenicopterus ruber roseus*) born in the Camargue, southern France, between their natal area and their principal wintering grounds (Spain, Sardinia, Tunisia and France) from 1995 to 1999.

2. We tested whether post-fledging dispersal was affected by sex, age, year, body condition, body mass and tarsus length using a multistate capture–recapture modelling approach. We focused particularly on the hypothesis that increased movement probabilities were associated with good and poor body condition. Because long-distance dispersal is energetically expensive and may involve a high risk of mortality, the acquisition of a robust physical condition prior to dispersal probably plays a critical role in determining the extent to which animals disperse. At the other extreme, birds in poor condition either leave their natal area or starve, which should result in relatively high dispersal rates.

3. Movement probabilities were not sex-dependent, but were age-dependent with high movement probabilities during the first year of life (above 0·6) and low probabilities after the first year (0·055). Movement probabilities also differed between years and localities.

4. Movement probability from the natal area was related to the body condition (and body mass) of the fledglings, with a high movement probability (0·873) when juveniles were in good body condition, and a relatively lower probability (from 0·629 to 0·724) when juveniles were in poorer condition. The proportion of variability in dispersal explained by body condition and body mass were 90·9% and 63·5%, respectively.

5. Results support the hypothesis that condition affects dispersal patterns from the natal area. They also suggest that body condition and local environmental conditions during the early growth play a role in dispersal.

Key-words: body condition, multistate capture–recapture models, greater flamingo, *Phoenicopterus ruber roseus*, post-fledging dispersal.

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Introduction

The study of dispersal has received increasing attention from evolutionary ecologists throughout the last two decades. Dispersal has important implications for population structure and dynamics and can affect reproduction and survival strongly (Greenwood 1980; Greenwood & Harvey 1982; Johnson & Gaines 1990; Clobert *et al.*

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2001), which are two major determinants of fitness. Although birth and death processes have a long and rich history of scientific investigation, the causes and consequences of the process of dispersal constitute one of the biggest gaps in our knowledge of ecological dynamics (Wiens 2001). Several factors have been found to influence dispersal, including individual (e.g. sex, age) and population specific characteristics such as population density, and environmental characteristics such as availability of food or good territories (for reviews, see Greenwood 1980; Greenwood & Harvey 1982; Johnson & Gaines 1990; Paradis *et al.* 1998; Dieckmann, O'Hara & Weisser 1999; Clobert *et al.* 2001).

Most of the studies on dispersal have investigated the causes and consequences of natal dispersal (the movement of individuals between birth place and the first breeding place) and breeding dispersal (the movements between successive breeding places) (Greenwood 1980). However, in many species juveniles of both sexes disperse from parental territories or from the birthplace during the post-fledging period, soon after they achieve independence. The movements of individuals from the birth place and before the first breeding attempt (post-fledging dispersal, Morton *et al.* 1991) and the factors affecting these movements have been poorly investigated (mammals: Holekamp 1986; Nunes & Holekamp 1996; birds: Nilsson & Smith 1985; Ferrer 1993; Belthoff & Dufty 1998), although they may affect future survival and/or reproduction. The proximate and ultimate factors that determine young to initiate dispersal are thus not well understood. Both exogenous (environmental) and endogenous factors have been suggested to drive post-fledging dispersal such as parental aggression towards young (Gonzalez *et al.* 1989; Wiggett & Boag 1993), aggression of young towards each other (de Laet 1985; Strickland 1991), declining food availability within the natal area (Veltman 1989; Kenward *et al.* 1993) and body condition (Nunes & Holekamp 1996; Belthoff & Dufty 1998). Young individuals may also prospect for potential future breeding/foraging sites, thereby increasing their knowledge of site availability within a geographical area (Bell 1991). Finally, some authors have proposed a genetic component of post-fledging dispersal based on similarities in dispersal behaviour between siblings and between parent and offspring (Dhondt 1979; Greenwood, Harvey & Perrins 1979; Newton & Marquiss 1983; Fleischer, Lowther & Johnston 1984).

Here, we present data on post-fledging dispersal of greater flamingos *Phoenicopterus ruber roseus* Pallas born in the Camargue, southern France. Data from a long-term capture–mark–recapture study indicate that juveniles disperse widely across the western Mediterranean and North Africa after fledging (Green, Hirons & Johnson 1989; Johnson 1989; Johnson 2000), but the factors influencing whether an animal stays or leaves a given site remain unknown. A previous study on greater flamingos has reported that breeding failure and environmental variability at breeding sites affected breeding dispersal, whereas natal dispersal was affected by breeding access to colonies, although the vast majority of individuals were highly philopatric (Nager *et al.* 1996). In this study we use recently developed models to estimate wintering site fidelity of young greater flamingos before their first breeding attempt and to examine the effects of age, year, sex, body size and body condition on post-fledging dispersal.

HYPOTHESES AND PREDICTIONS

Are there sex-specific differences in post-fledging dispersal behaviour? There are two main reasons to test for sex-dependence of post-fledging dispersal in greater flamingos. First, although this has not been reported for natal and breeding dispersal in flamingos (Nager *et al.* 1996), there is general evidence that sex is a potentially important source of variation in dispersal probability among birds (e.g. Greenwood 1980; Greenwood & Harvey 1982; Pärt & Gustafsson 1989; Clarke, Saether & Røskaft 1997; Serrano *et al.* 2001). Secondly, because male greater flamingos are on average 20% larger (tarsus length) and heavier than females (del Hoyo, Elliott & Sargatal 1992), body size and body condition cannot a priori be treated as the same trait (or at least not on the same scale) in both sexes.

Prediction 1

Because long-distance dispersal is energetically expensive and may involve a high risk of mortality, the acquisition of a sufficiently robust physical condition prior to dispersal probably plays a critical role in determining the extent to which animals disperse (Dufty & Belthoff 2001). It seems appropriate for an animal to delay dispersal until it has attained sufficient size or stored sufficient energy to increase its probability of surviving to move. For example, a good body condition (i.e. a large amount of body reserves) would allow an individual to cover a greater distance without increasing its mortality probability. However, for individuals in very poor body condition the decision of whether to stay or leave a given site is influenced probably by proximate factors: a bird may either leave or starve. The fact that dispersal in birds generally results from individuals in poor condition being forced to disperse has support in the literature (e.g. Pyke 1984; Korpimäki 1993) and undernourished birds increase their activity levels and foraging activities (Astheimer *et al.* 1992; Piersma & Poot 1993), which may enhance dispersal. Therefore, we predicted high dispersal rates for individuals in good and poor condition, and low dispersal probability for individuals in intermediate condition.

Prediction 2

Alternatively, birds in good condition could benefit by remaining near their natal site until breeding, while less competitive individuals, i.e. those in poor condition, could be expelled from their natal sites or forced to disperse due to intraspecific competition for resources. The Camargue being recognized as a high-quality breeding site within the Mediterranean region (Nager *et al.* 1996), one could expect high-quality individuals (those in good condition) to remain in or close to the natal site until breeding. Under this hypothesis, we predicted lower dispersal rates for individuals in good condition than for those in poor condition.

Prediction 3

This prediction is based on previous results on flamingos and on prediction 1. First, Green *et al.* (1989) found

differences between cohorts in the proportion of individuals observed in two different wintering sites. Secondly, fledgling body condition is influenced by water levels in the Camargue, which are very variable from year to year (Cézilly *et al.* 1995). If prediction 1 is verified, we would then expect variation in dispersal rates between years. We thus predicted time- and region-dependent dispersal rates.

Prediction 4

A previous study has revealed that flamingos wintering in Tunisia and Spain are faithful to their first wintering site during subsequent winters (Green *et al.* 1989). Moreover, there is ample evidence in the literature that juveniles disperse widely from their natal site after their independence (Greenwood & Harvey 1982). We therefore predicted age-dependent dispersal rates with high dispersal immediately after fledging and low dispersal (i.e. high wintering site fidelity) during subsequent years.

Prediction 5

There is evidence that for some species tarsus length is influenced by environmental conditions (van Noordwijk 1988; Gebhardt-Henrich & van Noordwijk 1991). Because in greater flamingos fledgling body condition is affected by environmental conditions (water levels), and because tarsus length in fledglings is variable from year to year (Johnson, unpublished data and this study), we hypothesized that tarsus length may also partly reflect growth conditions. Following our first prediction we predicted higher dispersal rates for individuals with longer tarsus length.

Methods

STUDY AREA AND SPECIES

The study area includes the major saline and brackish lagoon complexes in the western Mediterranean and North Africa. Within this area, greater flamingos breed in one to nine colonies and all evidence suggests that they constitute a single population (Johnson 1989). For this analysis we rely on birds born in the Camargue, where 30–100% of the western Mediterranean population was breeding during the last 10 years. Studies on dispersal are often biased because they are based on small study areas and long-distance dispersers may be unnoticed (Koenig, Vuren & Hooge 1996). This bias was minimized in our study, as the study area was large and included almost the entire range of the western Mediterranean population.

The study area was divided into four regions (Fig. 1), chosen to represent the principal staging and wintering areas of flamingos born in the Camargue, and based on a previous study of movements of greater flamingos (Green *et al.* 1989). For convenience these regions will be referred to as southern France (SF), which includes all the coastal lagoons from the Etang de Berre (43°26′ N, 05°70′ E) to the Etang de Salses (42°50′ N, 03°00′ E); the Iberian peninsula (IB), which includes the coastal lagoons from the Ebro delta (40°40′ N, 00°40′ E) to the Guadalquivir and Odiel deltas (36°27′–37°12′ N, 05°59′–06°58′ W) and the inland lagoons of Pedro Munoz (39°23′ N, 02°57′ W) and Fuente de Piedra (37°60′ N, 04°46′ W); Sardinia (SA), which includes the coastal lagoons of Cagliari (39°13′ N, 09°20′ E); and Tunisia (TU), which includes the coastal lagoons of Sfax in Tunisia (34°20′–36°50′ N, 10°10′ E). Although the IB region included localities separated by ≈ 1000 km, we chose to group these localities within the same region as they are all part of the same flyway (Johnson 1989).

FIELD METHODS

From summer 1995 to summer 1999, a total of 1575 chicks have been sexed through DNA analysis (Bertault *et al.* 1999) and marked individually with PVC plastic rings engraved with a four-digit code (Johnson 1983), which can be read through a telescope. The present analysis has been restricted to resightings of live birds in any part of the four previously defined regions from
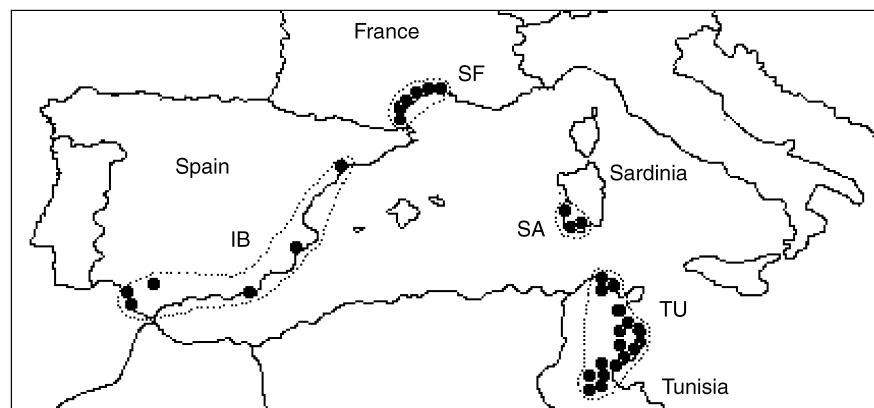
Fig. 1. Map showing the whole study area with the study sites used to model post-fledging dispersal of young greater flamingos born in the Camargue.

Table 1. Numbers of greater flamingo chicks ringed and sexed (1995–99) and resighted (1995–2000) within the study area

Year	Number of chicks ringed and sexed		Number resighted	
	Males	Females	Males	Females
1995	108	68	23	53
1996	67	64	37	32
1997	223	189	82	86
1998	268	162	44	51
1999	255	171	21	33

1995 to 2000, which can be treated as recapture data (Lebreton *et al*. 1992). Because one of our primary interests was to estimate wintering site fidelity and to satisfy the basic assumptions of the Cormack–Jolly–Seber model, i.e. that interoccasion time intervals are regular and longer than the capture sessions (Lebreton *et al*. 1992), only resightings made from November to January were retained. Resightings come from a network of amateur ornithologists spread across the Mediterranean basin that send their observations to us regularly, supplemented by expeditions by the Tour du Valat. Table 1 shows the number of birds resighted at least once during the study period. Our analysis deals with the capture histories of those individuals.

To estimate the effect of morphological characteristics on post-fledging dispersal we chose the following individual traits: tarsus length, body mass and body condition at ringing. Tarsus length was measured (±1 mm) as the distance from the distal end of tarsometatarsus to the outer edge of the midtarsal joint (thus including the thickness of the tibia). The date of the ringing operation in the Camargue is determined using the date of the first hatched chick, so that ringing takes place every year when the oldest chick is *c*. 75 days old, i.e. just before fledging (Johnson 2000). Breeding is usually highly synchronous in flamingos (Ogilvie & Ogilvie 1986), and the age of chicks varies from *c*. 1 month to 2·5 months at ringing. Because sex was determined at ringing we could control for a sex effect on tarsus length. The body condition index (BCI) was calculated as the residuals from the model II (reduced major axis) regression of body mass (measured to the

nearest 50 g using a 0–5000 g Pesola spring balance) on the tarsus length (Green 2000). Body mass was related to tarsus length (body mass = $-1776·87$ (SE = 95·86) + 19·01 (SE = 0·435) × tarsus, r = 0·852, $P < 0·001$ for males and body mass = $-1475·69$ (SE = 83·54) + 17·55 (SE = 0·408) × tarsus, $r = 0·811$, $P < 0·001$ for females). We tested for non-linear relationships between body mass and tarsus length for each year of the study, and the relationships were linear for each year (lowest *P*-value for tarsus^2 was 0·304). Table 2 shows the body size traits for chicks included in the analysis.

DISPERSAL ANALYSIS

To estimate dispersal probabilities we rely on the multisite modelling approach developed by Arnason (1973) and extended by Hestbeck, Nichols & Malecki (1991), Brownie *et al*. (1993) and Schwarz, Schweigert & Arnason (1993). Multisite models yield estimates of probabilities of movement between all pairs of locations, location-specific survival probabilities, and permit location-specific differences in capture probabilities. Movement probabilities can be modelled directly as a function of external covariates (Spendelow *et al*. 1995).

A common problem with multistratum models is that the number of parameters can become large very quickly, particularly if a general transition matrix allowing for arbitrary movements among states is allowed. Thus, because there is a fixed amount of information in our data, diluting the information over many parameters would lead to poor inference on any one parameter. Because our primary interest was to test several a priori hypotheses about factors affecting dispersal from the natal area to wintering areas between fledging and the first breeding attempt, our most general model assumes that survival and re-encounter probabilities were constant over time. None the less, it is reasonable to suppose that recapture effort may differ among sites and sexes (for example, as males have longer tarsi than females, males' rings have a higher probability of being seen above water level) and therefore, recapture probability was assumed to be sex- and site-specific in our initial model. In addition, to test for eventual differential mortality or permanent emigration between sexes the survival probability was set sex-specific.

Table 2. Mean (± SD) values of body mass and tarsus length for male and female juvenile greater flamingos ringed and sexed in 1995–99 in the Camargue colony, and included in the analysis of post-fledging dispersal. Numbers in parentheses are sample sizes

Year	Females		Males	
	Body mass	Tarsus length	Body mass	Tarsus length
1995	1850·7 ± 361·6 (108)	198·5 ± 22·3 (108)	2075·0 ± 491·8 (68)	212·9 ± 23·4 (68)
1996	2661·3 ± 358·2 (67)	226·8 ± 12·4 (67)	2855·9 ± 374·3 (64)	243·4 ± 17·4 (64)
1997	2280·0 ± 319·6 (223)	207·8 ± 14·9 (223)	2603·8 ± 383·4 (189)	222·3 ± 17·2 (189)
1998	2007·0 ± 416·4 (268)	196·6 ± 21·3 (268)	2270·3 ± 483·9 (162)	212·2 ± 24·6 (162)
1999	2095·6 ± 394·6 (255)	205·9 ± 19·6 (255)	2480·9 ± 435·4 (171)	225·2 ± 21·5 (171)

Previous studies in the Camargue indicate that greater flamingos are faithful to wintering areas used in the first and second winters of life (Green *et al*. 1989). In our case, this implies that movement probabilities from the wintering sites are probably relatively small and that very few individuals changed wintering locality during their first years of life, which was confirmed by individual resighting histories included in the data set. We thus started with a model allowing for sex-, age-, time- and region-dependent movements from SF and assuming that movement probabilities were constant over time and were neither sex-, age- nor region-specific for IB, SA and TU [model (ϕ_s,p_{s*re},$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$) where ϕ, p and ψ, respectively, indicate survival, resighting and movement probability, and *i*, *s*, *a1*, *a2* and *re*, respectively, indicate the time, sex, age with two age-classes, and region effects]. A model with two age-classes was chosen to take into account the fact that movement probability from the first to subsequent wintering sites is low and can be assumed to be constant with age. This model permits estimates of movement probabilities between fledging and first winter (age class 1) and between subsequent winters (age class 2) for each cohort. The ability of model (ϕ_s,p_{s*re},$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$) to describe the data was assessed by repeating for each cohort and each sex the goodness-of-fit (GOF) test implemented in program MSSURVIV (the χ^2 statistic calculated after pooling of cells within rows of the data array with degrees of freedom reduced accordingly, Brownie *et al*. 1993), and then adding the individual χ^2 values and degrees of freedom to build a global test.

Using this initial model one can estimate the wintering site fidelity ($1 - \psi^{IB,SA,TU}$), and test the hypothesis of an effect of sex on post-fledging dispersal by investigating models that did and did not include sex-specific movement probabilities. To test the hypothesis that dispersal probabilities were phenotype-specific we developed models in which movement probability is a function of body condition, body mass and tarsus length. We included models in which movement probability was modelled as a linear-logistic function of a phenotypic trait:

$$\text{logit}(\psi) = \log\left(\frac{\psi}{1 - \psi}\right) = \alpha + \beta \times trait, \tag{1}$$

where α and β are the intercept and slope parameters, respectively, and *trait* is the phenotypic trait (i.e. body condition, body mass or tarsus length). The sign of the slope parameter indicates whether dispersal probability from SF increases ($\beta > 0$) or decreases ($\beta < 0$) with the studied trait. To test for our a priori predictions on the effect of body condition on the probability of movement we included a model in which movement probability was modelled as a quadratic-logistic function of body condition:

$$\text{logit}(\psi) = \alpha + \beta \times \text{BCI} + \gamma \times \text{BCI}^2 \tag{2}.$$

Our selection of models for estimation was based on model GOF tests and a modified Akaike's information criterion that takes into account sample sizes (AICc, see Akaike 1973; Burnham & Anderson 1998). The GOF test of a general model was performed to determine whether or not this general model provided an adequate description of the data. AICc values were used to select which model provided an adequate description of the data with the smallest number of model parameters, i.e. the most parsimonious model. The model where AICc is minimized is selected as best for describing the data. The evidence for each of the alternative models was evaluated using Δ_iAICc (Δ_i) values defined as the difference between the AICc of a model and the AICc for the current minimum AICc model (Anderson, Burnham & Thompson 2000). The larger the Δ_i, the less plausible is the fitted model *i* as being the best approximating model in the candidate set. As a general guideline, Δ_i values > 2 are a good indication that the model with the lower AICc is preferable, whereas Δ_i values < 2 indicate that models are fairly similar in abilities to describe the data in a parsimonious manner (Lebreton *et al*. 1992). The likelihood of a model, given the data, was estimated with a likelihood-based inference approach with AICc weights (w_i) following Anderson *et al*. (2000). The w_i can be interpreted as approximate probabilities that model *i* is the best model in the set of models considered. The relative likelihood of model *i* vs. model *j* is just w_i/w_j. All estimates and AICc values were computed using program MARK (White & Burnham 1999). GOF tests (see next paragraph) led to the incorporation of an overdispersion factor and the use, accordingly, of a modified AICc (noted thereafter QAICc) following Lebreton *et al*. (1992).

The proportion of variation in dispersal rates explained by a covariate, which is akin to r^2, was estimated based on the ratio of differences in relative deviance (QDev) of constant, covariate- and time-dependent models (Schemper 1990):

$$r^2_{\text{QDdev}} = \frac{\text{QDev}(covariate) - \text{QDev}(constant)}{\text{QDev}(t) - \text{QDev}(constant)}$$

where *covariate* is the covariate-dependent dispersal rate, *t* time-dependent dispersal rate, and *constant* is constant dispersal rate, other things being equal.

Results

GOODNESS-OF-FIT TESTS

Results shown in Table 3 indicate a lack of fit for the starting model (ϕ_s,p_{s*re},$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$), although none of the cohort-sex groups showed lack of fit. Lack of fit may result from either structural deficiencies or overdispersion. Structural deficiency results from omitting an important source of variation in the model. Overdispersion means that the variance is greater than expected under the assumption of a multinomial distribution due to some interdependence among individuals, or heterogeneity among individuals. In order to identify the origin of the observed lack of fit we examined

Table 3. Goodness-of-fit tests of the dispersal model by cohort and sex applied to the resighting data of Camargue young greater flamingos. Test of model (ϕ_s,p$_{s*re}$,$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$); $\hat{c}$ denotes the overall overdispersion factor estimate. F = female; M = male

Sex	Cohort	χ^2	d.f.	P
F	1995	22·939	14	0·0613
F	1996	11·024	9	0·2741
F	1997	18·563	10	0·0462
F	1998	1·420	1	0·2334
F	1999	– no valid test –		
Total F		53·946	34	0·0162
M	1995	32·939	22	0·0627
M	1996	14·005	9	0·1221
M	1997	17·837	11	0·0854
M	1998	2·191	1	0·1388
M	1999	– no valid test –		
Total M		66·972	43	0·0111
Total		120·918	77	0·0007 $\hat{c}$ = 1·570

the value of c, the ratio of the overall χ^2 value to its number of degrees of freedom. On average c = 1 when the model fits. The c-value was greater than 1 (1·570), implying overdispersion of the data or a mild structural

problem (see Burnham *et al.* 1987: 246–252). However, the c-value was less than 3, as recommended by Lebreton *et al.* (1992), and well below 10, suggesting that the model structure was satisfying. Thus, subsequent analyses started from model (ϕ_s,p$_{s*re}$,$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$) and made use of the overall overdispersion estimate $\hat{c}$ = 1·570.

MODEL TESTS AND SELECTION

Modelling variation in recapture, survival and movement probabilities

Starting with the general model (ϕ_s,p$_{s*re}$, $\psi^{SF}_{a1[i*s*re],a2[s*re]}$, $\psi^{IB,SA,TU}$), we examined whether there was an effect of region on recapture probability. A model with recapture probability equal over regions was preferred over the general model (Table 4: model 14). Models with survival probability and recapture probability equal over sexes (models 13 and 12) were preferred to model 14, suggesting that survival and recapture probabilities did not differ between males and females. Note that estimates of model (ϕ_s,p$_{s*re}$,$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$) suggest slightly higher recapture probabilities for

Table 4. Description of constraints, modified deviance (QDev = rDev/$\hat{c}$, where rDev is the relative deviance), number of estimated parameters (np), QAICc, Δ_i values, and QAICc weights (w_i) for various models of post-fledging dispersal of young greater flamingos born in the Camargue between 1995 and 1999. Models are ranked according to Δ_i

Model[1]	Description of constraints	QDev	np	QAICc	Δ_i	w_i
1 (ϕ,p,$\psi^{SF}_{a1[(bci2+bci)*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal as a quadratic function of body condition with interaction	2418·12	14	2446·34	0	0·4948
2 (ϕ,p,$\psi^{SF}_{a1[bci*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal function of body condition with interaction	2424·24	11	2446·37	0·04	0·4854
3 (ϕ,p,$\psi^{SF}_{a1[bci2+bci+re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal as a quadratic function of body condition without interaction	2426·02	14	2454·24	7·91	0·0095
4 (ϕ,p,$\psi^{SF}_{a1[(mass2+mass)*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal as a quadratic function of body mass with interaction	2426·40	14	2454·62	8·28	0·0079
5 (ϕ,p,$\psi^{SF}_{a1[i*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal equal over sex	2415·39	21	2457·86	11·53	0·0016
6 (ϕ,p,$\psi^{SF}_{a1[i*re],a2}$,$\psi^{IB,SA,TU}$)	Dispersal equal over region for age class 2	2422·06	19	2460·45	14·12	0·0004
7 (ϕ,p,$\psi^{SF}_{a1[(i+s)*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Additive effect of sex on dispersal	2414·72	23	2461·29	14·96	0·0003
8 (ϕ,p,$\psi^{SF}_{a1[re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal constant over time and equal over sex	2445·57	9	2463·67	17·33	< 0·0001
9 (ϕ,p,$\psi^{SF}_{a1[tars*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal equal over sex and function of tarsus length	2441·92	11	2464·05	17·72	< 0·0001
10 (ϕ,p,$\psi^{SF}_{a1[mass*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Dispersal equal over sex and function of body mass	2443·93	11	2466·07	19·73	< 0·0001
11 (ϕ,p,$\psi^{SF}_{a1[i*s*re],a2[re]}$,$\psi^{IB,SA,TU}$)	Absence of an effect of sex on dispersal for age class 2	2410·90	36	2484·29	37·96	< 0·0001
12 (ϕ,p,$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$)	Absence of a sex effect on recapture	2408·93	39	2488·57	42·23	< 0·0001
13 (ϕ_s,p,$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$)	Absence of a sex effect on survival	2407·58	40	2489·30	42·97	< 0·0001
14 (ϕ_s,p$_s$,$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$)	Absence of a region effect on recapture	2405·95	41	2489·76	43·42	< 0·0001
15 (ϕ_s,p$_{s*re}$,$\psi^{SF}_{a1[i*s*re],a2[s*re]}$,$\psi^{IB,SA,TU}$)	Constant survival and recapture over time (starting model)	2398·02	47	2494·39	48·06	< 0·0001

[1]See Methods section and Lebreton *et al.* (1992) for model nomenclature.

Table 5. Year- and region-specific estimates of greater flamingo movement probabilities between fledging to first winter (age class 1) and between subsequent winters (age class 2) and their standard errors in brackets from model ($\phi_s, p_{s*re}, \psi^{SF}_{a1[i*re],a2[re]}, \psi^{IB,SA,TU}$)

Year	Transition ψ^{SF}	Movement probability age class 1	Movement probability age class 2	Transition $\psi^{IB,IT,AF}$
1995	SF-IB	0·267 (0·080)		
	SF-IT		0·134 (0·068)	
	SF-AF		0·315 (0·090)	
Total		0·716 (0·138)		
1996	SF-IB	0·204 (0·075)		
	SF-IT		0·325 (0·088)	
	SF-AF		0·144 (0·077)	
Total		0·673 (0·139)		
1997	SF-IB	0·069 (0·029)		
	SF-IT		0·231 (0·049)	
	SF-AF		0·573 (0·057)	
Total		0·873 (0·081)		
1998	SF-IB	0·069 (0·054)		
	SF-IT		0·299 (0·096)	
	SF-AF		0·314 (0·096)	
Total		0·682 (0·146)		
1999	SF-IB	0·120 (0·081)		
	SF-IT		0·200 (0·100)	
	SF-AF		0·280 (0·113)	
Total			0·600 (0·171)	
All years	SF-IB		0·000 (0·000)	
All years	SF-IT		0·122 (0·051)	
All years	SF-AF		0·060 (0·048)	
All years				0·055 (0·016)

males (0·241, SE = 0·034) than for females (0·173, SE = 0·023), and lower survival probabilities for males (0·696, SE = 0·054) than for females (0·793, SE = 0·054). A model with dispersal rates for age class 2 equal over sexes (model 11) was preferred over model 12, and a model with an additive effect of sex on dispersal rates for age class 1 (model 7) was preferred over model 11, suggesting that dispersal rates of males and females followed the same pattern. However, the sex effect on dispersal was not obvious because a model without an effect of sex (model 5) was preferred by a wide margin in QAICc (3·43) over model 7. Thus, there was no evidence of an effect of sex on the dispersal probability.

The probability of dispersal for age class 1 was year-specific, as suggested by the Δ_i between model 5 and model 8 (Table 4). Year- and region-specific dispersal probabilities for young flamingos between fledging and first winter (age class 1) obtained from model 5 are shown in Table 5. Model 5 estimates of capture and survival probabilities were 0·200 (SE = 0·018) and 0·749 (SE = 0·035), respectively. After the first winter, the dispersal probability from SF to IB and TU were low, although slightly higher from SF to SA (Table 5). However, the a posteriori hypothesis of equality of dispersal probabilities over regions of destination at age 2 was rejected, as suggested by the Δ_i value (2·59) between model 5 and model 6. From the preferred model (model 5), the wintering site fidelity was high (0·945, SE = 0·014), indicating very high faithfulness to the first wintering region.

Modelling factors affecting movement probabilities

We next tested predictions 1 and 2, and examined movement probabilities by first modelling dispersal probability of first year birds as a linear function of body condition. We did the same for body mass and tarsus length. The QAICc indicates a preference for model ($\phi, p, \psi^{SF}_{a1[bci*re],a2[re]}, \psi^{IB,SA,TU}$) (Table 4), with a large Δ_i value relative to model 5 (11·49). We next tested for a non-linear effect of body condition on dispersal (model 1) and tried to eliminate the interaction term between region and condition (model 3). The QAICc indicates a preference for model 1, suggesting an interaction between region and condition. However, models 1 and 2 had similar QAICc values. The evidence that a model with a non-linear effect of condition on dispersal is better than a model with a linear effect of condition can be judged by the ratio of Akaike weights of model 1 and model 2 (Anderson *et al.* 2000). The relative likelihood of model 1 vs. model 2 was 1·02 (0·406/0·398), i.e. model 1 was nearly as likely as model 2. In total, the evidence for a condition effect on dispersal probability was very strong, as suggested by QAICc values of models 1, 2 and 3 compared to model 5, and by the fact that the sum of the Akaike weights for models including condition as a covariate was 0·992 (i.e. models with condition as a covariate were 781 times more likely than model 5).

The slope estimates for model 1 and 2 are shown in Table 6, and suggest that the dispersal probabilities

Table 6. Slope and intercept parameter values with their standard errors (SE) and lower (lower) and upper (upper) 95% confidence intervals for the linear-logistic model ($\phi,p,\psi^{SF}_{a1[bci*re],a2[re]},\psi^{IB,SA,TU}$), for the quadratic–logistic model with interaction ($\phi,p,\psi^{SF}_{a1[(bci2+bci)*re],a2[re]},\psi^{IB,SA,TU}$), and for the quadratic model without interaction ($\phi,p,\psi^{SF}_{a1[bci2+bci+re],a2[re]},\psi^{IB,SA,TU}$). Parameter slope ($\beta$) refers to the linear component in eqns 1 and 2, and parameter slope (γ) refers to the quadratic component in eqn 2

| Movement	Intercept (α)	SE	Lower	Upper	Slope (β)	SE	Lower	Upper	Slope (γ)	SE	Lower	Upper
Model ($\phi,p,\psi^{SF}_{a1[bci*re],a2[re]},\psi^{IB,SA,TU}$)												
SF–IB	−2·000	0·251	−2·492	−1·509	−0·591	0·208	−0·999	−0·184				
SF–SA	−1·172	0·182	−1·529	−0·815	0·098	0·164	−0·223	0·419				
SF–TU	−0·546	0·180	−0·900	−0·193	0·551	0·162	0·233	0·869				
Model ($\phi,p,\psi^{SF}_{a1[(bci2+bci)*re],a2[re]},\psi^{IB,SA,TU}$)												
SF–IB	−2·075	0·391	−2·842	−1·309	−0·528	0·227	−0·974	−0·083	0·060	0·224	−0·380	0·500
SF–SA	−0·829	0·300	−1·417	−0·242	0·042	0·169	−0·289	0·372	−0·269	0·197	−0·656	0·117
SF–TU	−1·187	0·324	−1·822	−0·553	0·604	0·155	0·299	0·908	0·452	0·182	0·096	0·808
Model ($\phi,p,\psi^{SF}_{a1[bci2+bci+re],a2[re]},\psi^{IB,SA,TU}$)												
From SF	−1·261	0·122	−1·499	−1·022	0·140	0·050	0·042	0·238	0·117	0·068	−0·016	0·250
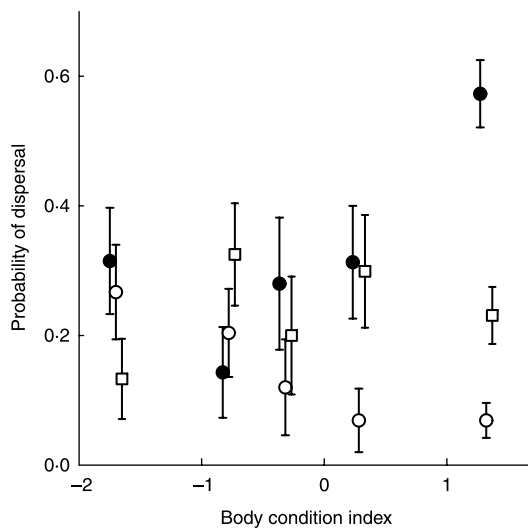
Fig. 2. Estimated movement probabilities (±1 SE) between southern France and Tunisia (full circles), Spain (open circles) and Sardinia (open squares) plotted against the mean annual body condition index of juvenile greater flamingos from 1995 to 1999 in the Camargue. The probabilities were estimated from model 5, where movement probabilities for the first age class are time-dependent.

Fig. 3. Estimated overall movement probabilities (±1 SE) from the natal area (SF) plotted against the mean annual body condition index of juvenile greater flamingos from 1995 to 1999 in the Camargue (full circles). The probabilities were estimated from the time-dependent model (model 5). Plain line indicates movement probabilities as predicted by model 1 (quadratic model with interaction); dashed line indicates movement probabilities as predicted by model 3 (quadratic model without interaction); dotted line indicates movement probabilities as predicted by model 2 (linear model).

between SF and IB and between SF and TU were, respectively, negatively and positively related to body condition (Fig. 2). The slope parameter of the relationship between condition and dispersal probability between SF and SA did not differ from zero, suggesting a weak but positive effect of condition on dispersal probability. Thus, when fledglings were in good body condition in the Camargue the probability of dispersal from SF was high (0·873 from model 1; Fig. 3), but differed between regions of dispersal. When body condition decreased to intermediate levels the dispersal probability decreased to its lowest values (0·629 from model 1). When fledglings were in poor condition, the probability of dispersal increased (0·663 from model 2; 0·724 from model 1). Based on the ratio of differences in relative deviance (QDev) of models with time-dependent, constant and condition-dependent
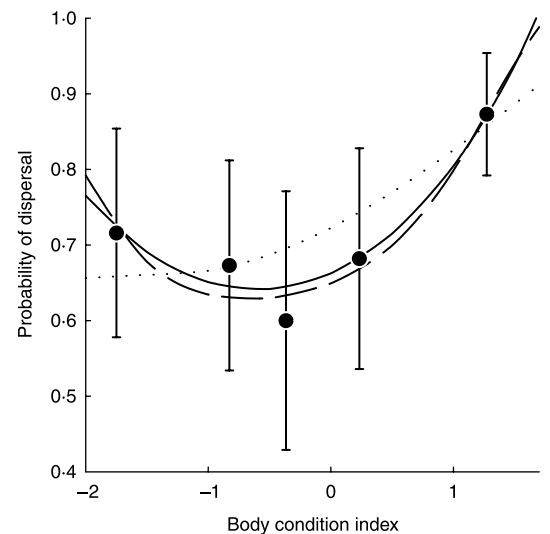
dispersal, the proportion of the variability in dispersal explained by the body condition was $r^2_{QDev}= 0\cdot706$ for model 2 and was $r^2_{QDev} = 0\cdot909$ for model 1.

Finally, model ($\phi,p,\psi^{SF}_{a1[(mass2+mass)*re],a2[re]},\psi^{IB,SA,TU}$) was not preferred to model 1 but was preferred to model 5 ($\Delta_i = 3\cdot24$) and to model ($\phi,p,\psi^{SF}_{a1[mass*re],a2[re]},\psi^{IB,SA,TU}$), reinforcing our finding that post-fledging dispersal was partly determined by fledgling physical body condition. Model 3 explained 63·5% of the variability in dispersal.

Discussion

The patterns of movement we observed were consistent with the hypothesis that body condition was part of the

mechanism involved in initiating movements from the birth place to the first wintering site. Body condition was also a determinant of the target localities. When young flamingos are in good condition at fledging, overall dispersal probabilities are high, and movements to Tunisia are high compared to movements to other wintering sites. When condition decreases to intermediate levels, dispersal probabilities decrease. The pattern of dispersal is less clear when condition is poor. Either dispersal stabilizes and remains relatively low (linear model) or dispersal increases (convex model). We could not distinguish between these two models given our data. Thus, our results were consistent with the prediction that individuals in good condition should disperse at higher rates than other individuals, but there was only little evidence for higher dispersal rates for individuals in poor condition. Although the Camargue is a high-quality breeding site and young birds in good condition could benefit remaining in their natal area until breeding, intraspecific competition may be high and younger individuals may be displaced to lower-quality wintering sites by adults, regardless of their condition, as shown by Rendón *et al.* (2001) during the breeding season.

An alternative explanation is that survival depends on body condition and that individuals that do decide to leave might die before reaching the wintering grounds in their first year depending on body condition. Although we cannot test this interaction specifically because individuals are only resighted after reaching the wintering grounds, i.e. after differential selection has occurred, we explored this possibility and ran an a posteriori model in which condition-dependent survival was added to model 1. This model had a smaller QAICc than model 1 (ΔQAICc = 1·72), although survival tended to increase with increasing condition (slope = 0·07 ± 0·142). This suggests that, in our data set, body condition had a stronger effect on the decision to leave than on survival.

Although we used recently developed methods based on capture–recapture data that yield strong inferences, a potential bias in our data is permanent emigration from our study area because (i) flamingos can move over long distances (Johnson 1989) and (ii) males were significantly less resighted than females in three out of the five cohorts studied (Table 1). This lower resighted proportion may suggest higher mortality and/or permanent emigration of young males. Our survival estimates from model 14 suggest a (apparent) survival difference between females and males of *c.* 8–10%, which can reflect true mortality and/or permanent emigration of males. There was no strong evidence for a sex effect on survival in our analysis, but sex-specific survival in adult greater flamingos was demonstrated only recently by Tavecchia *et al.* (2001), who used a much larger data set than in earlier studies, and found higher mortality rates among females at first reproduction. Although the network of observers outside the study area is loose, a long-term ringing programme on

greater flamingos has been conducted in Iran since 1970 (Mansouri & Sadeghi Zadegan, unpublished data) and only seven of 30 000 ringed birds have been observed in the western Mediterranean, indicating very low exchange between the eastern and western Mediterranean populations. Young males born in the Camargue may have emigrated to west Africa but of a total of 12 sexed individuals observed in west Africa between 1995 and 2000, six were males. Interestingly, the fledgling mass of these 12 individuals was 3–17% higher than their respective cohort mean body mass. This suggests that the lower proportion of males resighted in our study is due mainly to differential mortality during the immature stage, thereby minimizing the bias in our data.

As expected, post-fledging dispersal was age-dependent as our results indicate that the probability of leaving the birth area was high (above 0·6) between fledging and the first winter of life, but decreased dramatically after the first winter. The present study also confirms the previously reported faithfulness to wintering areas used in the first winter (Green *et al.* 1989). These results conform to a more general pattern of long-term site-faithfulness observed across several taxa (e.g. Hestbeck *et al.* 1991; Nichols 1996; Blums *et al.* 2002). As found in a previous study (Nager *et al.* 1996), no sex difference in post-fledging dispersal probability was found. Although there was a tendency for fledglings with longer tarsus length to disperse more (positive slopes for model 9), tarsus length was not a good indicator of movement probability.

Our results provide empirical evidence that body condition can affect dispersal patterns of young animals that disperse over long distances, and support the hypothesis of good body condition as a critical prerequisite to dispersal. Juvenile flamingos moving to Tunisia must fly 800–850 km over water to reach feeding areas. Although flamingos fly in formation (Johnson 1989), which may reduce energy expenditure (Weimerskirch *et al.* 2001) during sea-crossing, they seldomly rest on the sea, and they need greater energy reserves than birds dispersing to Spain, which have several stopover sites available along their route (Green *et al.* 1989). Individuals in relatively poor condition which attempt to cross the Mediterranean Sea are probably at greater risk, and may rather stay within the natal area, resulting in relatively low dispersal rates at intermediate or low levels of body condition.

Effects of body condition and mass on the patterns of dispersal have been observed in several species of sciurid rodents (see review in Nunes & Holekamp 1996). Nunes & Holekamp (1996) have shown that juvenile males of Belding's ground squirrels (*Spermophilus beldingi* Merriam) postpone dispersal until they have attained a threshold body mass, and that the percentage of body mass composed of fat (i.e. body condition) may influence the timing of dispersal. Among birds, a study of Spanish imperial eagles (*Aquila adalberti* Brehm) has shown that dispersal distance was longer

for juveniles with low blood urea levels used as a surrogate of nutritional condition (Ferrer 1993). More recently, Belthoff & Dufty (1998) have proposed a model for dispersal in screech-owls based on inter-actions among hormonal changes, body condition and social stimuli (*Otus kennicottii* Elliot and *O. asio* L.). It predicts that corticosterone, an adrenal glucocorticoid known to stimulate locomotor and foraging activity, increases in blood plasma prior to dispersal through a combination of endogenous and exogenous (such as a decrease in parental provisioning or an increase in sibling aggression) events. The model predicts that individuals in adequate condition will disperse when corticosterone levels increase, and that individuals in poorer condition will continue to forage on the natal area and initiate dispersal later. Although Belthoff & Dufty did not test directly the effects of body condition on the dispersal, our data are in line with this model, as good condition favoured dispersal in juvenile greater flamingos. There have been no direct tests of the effects of corticosterone levels on locomotor activity of flamingos, but the effects of corticosterone on activity levels and dispersal have been found in several species (e.g. Silverin, Viebke & Westin 1989; Wingfield 1994). Belthoff & Dufty (1998) developed their model for non-migratory species, but our results and those of Ferrer (1993) are consistent with their view, and we suggest that it may also apply to species undertaking long-distance dispersal. However, a very poor condition may also favour dispersal, because at such a low resource level the bird either leaves or starves. Several studies have demonstrated that activity levels increase in undernourished birds (e.g. Astheimer *et al.* 1992; Piersma & Poot 1993), a physiological state that stimulates glucocorticoid secretion (Cherel, Robin & Le Maho 1988).

We suggest that the probability of dispersal of juvenile greater flamingos can be viewed in relation to a body condition gradient. Because in greater flamingos chick body condition is related closely to water levels and food availability in the Camargue (Cézilly *et al.* 1995), this body condition gradient is similar to the food availability gradient proposed by Bennetts & Kitchens (2000) for another nomadic species. At one extreme, when body condition is poor, corticosterone secretion stimulates an increase in activity levels and movements from the natal area (although we could not demonstrate clearly this with our data set). At intermediate levels of body condition the probability of dispersal decreases, as the bird's body reserves are sufficient to avoid starving but insufficient for leaving and reaching other wintering sites. As body condition continues to increase, the probability of dispersal in-creases since the bird has sufficient body reserves to travel great distances and reach wintering sites. This relationship between the probability of dispersal and body condition may be particularly pronounced in spe-cies undertaking long-distance movements compared to species making short-distance movements.

Although we could identify some proximate factors to explain the relationship between body condition and dispersal in juvenile greater flamingos, what are the ultimate causes of juvenile dispersal? Because young flamingos are faithful to their first wintering site and because both natal and breeding dispersal rates are low in the studied population (Nager *et al.* 1996), it seems unlikely that the observed patterns of post-fledging dispersal help to familiarize young flamingos with potential food resources or future breeding sites within the western Mediterranean region (see Bell 1991). Two hypotheses may be proposed as ultimate causes. First, birds may disperse in order to spend the winter in safer wintering grounds so as to avoid unfavourable climatic conditions. For example, the extreme severity of the 1984–85 winter in southern France reduced normal juvenile winter survival by 41·7% (Lebreton *et al.* 1992), which is considerable for such a long-lived species. Although cold winters are infrequent in southern France, natural selection may favour individuals that disperse to warmer areas given the important longevity of flamingos. In this case good condition may allow birds to reach these wintering grounds without increasing their mort-ality probability. Secondly, intraspecific competition may be an ultimate cause of dispersal, with age-related behavioural dominance as part of the mechanism re-sponsible for dispersal of juveniles. Significant num-bers of flamingos remain in southern France during winter (*c*. 25 000; Johnson 1997), suggesting that food resources are not a limiting factor, but only 10–40% of juveniles remain (Table 5). A despotic distribution of flamingos has been shown to occur in breeding colonies, with younger individuals displaced to lower-quality nesting colonies (Rendón *et al.* 2001). A similar pattern of settlement of individuals may also occur after the breeding season and during winter and would explain the dispersal of juveniles. In the closely related Amer-ican flamingo *P. ruber ruber* L., Schmitz & Baldassare (1992) found that juveniles lost more encounters than adults in aggressive interactions during foraging among non-breeders.

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