

Comparing demographic parameters for philopatric and immigrant individuals in a long-lived bird adapted to unstable habitats

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Abstract Theoretical models about the benefits of philopatry predict that immigrant fitness can be higher, lower or similar to that of philopatrics depending on habitat heterogeneity, dispersal costs, distance between patches or population densities. In this study, we compared transience rates, local survival and recruitment among philopatric and immigrant individuals of Audouin's gull *Larus audouinii*, a long-lived bird with high dispersal capacities. Several previous studies have shown that these capacities were probably the result of adaptation to unstable and highly discrete habitats; hence, we tested the hypothesis that fitness components for philopatrics and immigrants were similar. During 1988–2006, ca. 27,800 chicks were marked in 31 colonies in the western Mediterranean metapopulation, and more than 52,000 resightings were made in a single, high-quality colony, to estimate local demographic parameters by capture–recapture analyses. Results suggest that, even though parameters related to site-tenacity (e.g. recapture rates) were higher for philopatrics than for immigrants, survival and recruitment were fundamentally similar. Small differences between philopatrics and immigrants were probably influenced by a highly suitable habitat at the study site, which reduced dispersal costs for immigrants; furthermore, the similarities in most fitness components were also probably the result of a life-history strategy of a species living in unpredictable, unstable habitats with high emigration rates among local populations, and with a relatively low cost of dispersal.

Keywords Gull · Fitness · Immigration · Philopatry · Recruitment · Survival · Transient

Introduction

While survival and fecundity have long attracted the interest of population ecologists, the importance of dispersal and its measurement has only been considered over recent decades. Several theoretical models such as island biogeography and metapopulations have been developed in recent times, in which dispersal was considered one of the most important life history traits involved in both species population dynamics and evolution. Movements of individuals in open or metapopulation systems are crucial for their stability, their genetic properties and for local dynamics (Dieckmann et al. 1999; Clobert et al. 2001; Hanski and Gaggiotti 2004). From an evolutionary point of view, being philopatric or emigrant has its own benefits and costs. For instance, philopatry has a potential cost in terms of kin competition, as well as inbreeding, while dispersal implies facing new sites and consequently a number of potential risks such as predation or higher competition (Forbes and Kaiser 1994; Clobert et al. 2001; Bullock et al. 2002). On the other hand, philopatric birds can take advantage of the knowledge they acquire about their environment (Greenwood and Harvey 1982). Theoretical models predict that immigrant fitness should be lower than that of philopatrics because of the costs of dispersal (Forbes and Kaiser 1994; Murren et al. 2001), although those models also consider that immigrants can increase their fitness by dispersing. In fact, all three possible hypotheses about the fitness of philopatrics and immigrants have been already stated: being higher for philopatrics (due to their knowledge about the social and biotic environment, the so-called “resident fitness” hypothesis; e.g. Anderson

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1989), being lower for philopatrics (when immigrants move to a higher quality site, called the “cost of philopatry” hypothesis; e.g. Morris 1992) and being similar between the two groups (when dispersal and philopatry are components of a mixed, evolutionarily stable strategy; e.g. Maynard-Smith 1982; Doncaster et al. 1997).

Although comparisons between philopatric and immigrant fitness are constrained by technical issues (such as the difficulties at monitoring animals during the dispersal phase; see Bélichon et al. 1996; Doligez and Pärt 2008), a number of empirical studies now exist for testing theoretical predictions, with an overall trend of a lower fitness for immigrants (e.g. Julliard et al. 1996; Orell 1999; Doligez et al. 2002, Lin and Batzli 2004; Doligez and Pärt 2008). However, Doligez and Pärt (2008) showed that immigrant fitness may have been underestimated in many of those studies (for instance, the small size of the study area compared to the range of dispersal), and that one possible solution is to reduce the effects of a spatially limited study area. There is in fact a logistic limitation to marking individuals and monitoring them at large spatial scales (e.g. Reid et al. 2006; van de Pol et al. 2006); empirical results at such scales are scarce and show contradictory results (Bélichon et al. 1996; Doligez and Pärt 2008). Such contrasting results have seldom been considered in terms of habitat stability and temporal autocorrelation in habitat quality (Doncaster et al. 1997; Dieckmann et al. 1999), which should influence the rates of dispersal and their associated costs (e.g. Parejo et al. 2006). In temporal and unpredictable habitats, sites remains suitable for breeding during a short period, and these habitats are likely to show a greater variance in the length of unfavourable periods (e.g. Southwood 1977). In fact, theoretical models predict that mean dispersal rates within populations are bound to be lower given longer habitat persistence (Travis and Dytham 1999; Keymer et al. 2000). Empirical studies suggest that, in stable habitats, philopatry will be preferred over immigration, which is not the case in environments in which habitats are temporary (Denno et al. 1991; Wissinger 1997). Nevertheless, most examples come from insects and short-lived species, because for many systems, such as host-parasitoids, flooded pastures, tide pool fishes and amphibians or infectious diseases with fast turnover rates, environments are highly dynamic. In contrast, it is assumed that most vertebrates (particularly mammals and birds) live in stable systems and thus the influence of habitat stability and predictability on dispersal is much less known, though the hypothesis of the use of public information on dispersal decisions in birds requires a corollary of temporal autocorrelation in habitat quality (e.g. Danchin et al. 2004). Thus, if habitat predictability and stability are low, dispersal in birds and mammals should also be selectively advantageous.

In the present study, we compare survival, recruitment and transience of philopatric and immigrant individuals of Audouin’s gull (*Larus audouinii*) at a large spatio-temporal scale. Previous studies on this species have shown that there is a high spatial heterogeneity in habitat quality and that the largest colony exhibits higher quality in its metapopulation, with higher availability of breeding sites and of food and lower predator densities (Oro et al. 1996, 2000; Cam et al. 2004). Previous monitoring of marked birds at a large spatio-temporal scale showed that colonies are well connected through dispersal of individuals (Oro and Pradel 1999; Tavecchia et al. 2007), with a higher level of exchange between neighbouring colonies and with the largest colony attracting most immigration (Oro and Ruxton 2001; Oro 2003; Cam et al. 2004). Oro and Ruxton (2001) illustrated that the growth rate of local populations was mainly explained by high immigration rates from abroad, even beyond the exponential growth phase. Audouin’s gulls have a life-history strategy that has evolved in unstable, ephemeral habitats resulting in high rates of dispersal among local populations compared with close, phylogenetically related species (Martínez-Abraín et al. 2003; Cam et al. 2004; Parejo et al. 2006; Tavecchia et al. 2007). For instance, an average 20 and 12% of local populations in this metapopulation are colonized and extinct, respectively, each year (unpublished results); consequently, we predict that immigrants and philopatric individuals will have similar survival and fitness.

Materials and methods

Study area and species

Audouin’s gulls are vulnerable and endemic to the Mediterranean region (total world estimate of 21,000 breeding pairs), where the species is mostly confined to the western area of the basin, ranging from Italy and southern France to Gibraltar. The population is spatially structured in one large colony—holding more than 60% of total world population—located in the delta of the Ebro river (Punta de la Banya, Catalonia, Spain), and several smaller colonies scattered on islands and salt marshes mainly on Spanish and Italian archipelagos (see Fig. 1). Data on individually marked birds have shown that the Ebro Delta colony is a population source that also attracts immigrants due to its higher habitat quality (e.g. lower predator densities, higher availability of main and secondary food resources, higher availability of suitable breeding habitat) than that of other local populations (Cam et al. 2004; Oro et al. 2006). During 1988–2006, ca. 27,800 chicks were individually marked in most Spanish local populations (31 colonies) of the western Mediterranean metapopulation; this metapopulation occupies a surface of

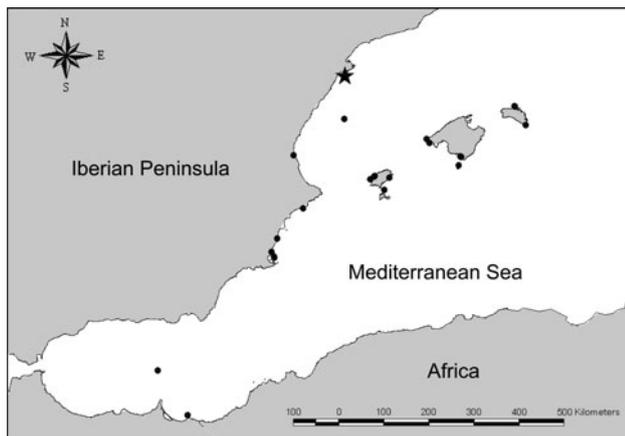


Fig. 1 The western Mediterranean showing the main local populations of Audouin's gulls (*Larus audouinii*) where most marking and resighting efforts were carried out during 1988–2006. The *star* shows the focal local population (the Ebro Delta), where parameters from philopatric individuals and immigrants were compared. This geographical area holds ca. 92% of the total world population of the species

more than 10^5 km² (Fig. 1). The median distance of those 31 colonies to the Ebro Delta colony is 235 km (range 75–656 km). Resightings of marked birds (with known age) were carried out in the focal study colony (the Ebro Delta) to estimate local demographic parameters by capture–recapture analyses (see details in Tavecchia et al. 2007). Only birds resighted at least once in the study colony were considered. The breeding status of resighted birds was not always recorded because in ground-nesting gulls this is difficult to monitor; to reduce the resulting potential bias, we excluded all resightings from non-sexually mature ages (birds younger than 3 years old), those made at non-breeding clubs, on beaches or at the beginning of the breeding season. The sex of the individual was seldom recorded because the species is not highly dimorphic (Oro 1998); thus, and even though sex is a strong driver of dispersal (e.g. Greenwood and Harvey 1982), we could not test for this effect. We used resightings made at the other 31 colonies of the metapopulation (using the same restrictions to at least partially avoid the inclusion of resightings of non-breeding birds) to assess whether breeders at the Ebro Delta had been seen before in those colonies. These resightings were also used to assess whether a bird seen at the Ebro Delta was observed later in the same season breeding at the other colonies; this occurred in only four cases during the study and these resightings were excluded from the analysis. We compiled this information for birds resighted only in one breeding season at the Ebro Delta (transients) and for those seen over multiple years (residents). Birds born in the Ebro colony are considered ‘philopatric’, while those born in any of the other colonies are referred to as ‘immigrants’ (see model notation below).

The capture–recapture framework

We individually marked fledglings using a darvic ring with a unique alphanumeric code, and resighted from a distance using a spotting scope at the Ebro Delta colony between April and July during 1992–2006. Marking birds as chicks allowed us to test for the effect of age on demographic parameters (see below). We estimated our local demographic parameters of main interest, namely survival, transience (individuals that were only seen once at the Ebro Delta) and recruitment using standard capture–mark–recapture methods described elsewhere (Lebreton et al. 1992; Pradel 1996). Individuals were considered as marked when they were encountered as breeders for the first time, although we could test for an age effect. We analyzed survival and recruitment separately by defining:

p_i = probability of resighting an individual known to be alive at time i , recapture probability hereafter.

ϕ_i = probability of being alive at $i + 1$ for an individual known to be alive at time i , survival probability hereafter.

γ_i = probability of being present in the population at $i - 1$ for an individual known to be alive at time i , seniority probability hereafter (see Pradel 1996). This is a capture–recapture procedure to estimate recruitment in a population (see also Pradel et al. 1997).

The probabilities above can be estimated from the encounter histories by maximum likelihood procedures. Since the goodness-of-fit tests to assess the fit of the more general capture–recapture model showed a transient effect (see below), this was taken into account in all the modelling procedure. Transients are individuals seen only once in the Ebro Delta study colony and never seen again here, while resident birds are birds breeding more than once at the Ebro Delta. In our analysis, the proportion of such birds was higher than expected. Tavecchia et al. (2007) showed that most of these birds did not die but rather dispersed to other colonies. From a methodological point of view, these transients are treated by differentiating the first survival from survival in subsequent years (Pradel et al. 1997). Pradel et al. (1997) have shown that, at population level, initial survival probability is related to the proportion of transients, τ , as:

$$\tau = 1 - \frac{\phi^*}{\phi}$$

where ϕ^* is survival the year after the first resighting and ϕ the year thereafter (see also Oro et al. 1999).

To test the adequacy of the most general model, the fully time-dependent model on survival and recapture within each group—philopatric and immigrants—(e.g. Tavecchia et al. 2001), we carried out a goodness-of-fit test (GOF) on

this model. This can be tested by contingency tables that compare the fate of individuals known to be alive at time i according to their past and future capture-recapture history or determine whether they were observed at time i or not. The sum of all χ^2 components provides a general test for the adequacy of time-dependent models. The hypothesis of homogeneity is rarely confirmed for large datasets and this heterogeneity can be partially taken into account by adding extra parameters to the general model. When the source of heterogeneity was not identified, we used a variance inflation factor, \hat{c} , to scale model deviances, calculated as the ratio between the χ^2 value from the GOF test and its degrees of freedom (Lebreton et al. 1992). The analyses of survival and recruitment were based on the same dataset, and hence the GOF test and the corresponding \hat{c} were unique for both analyses; this test was performed using U-CARE software (Choquet et al. 2005).

Effects, model notation and model selection

After confirming the presence of transients from GOF tests, our analyses estimated five parameters: first-year survival probability (ϕ^*), survival probability of resident birds (ϕ), seniority probability (γ' and γ , for transient and residents gulls, respectively), and recapture probability (p). We tested the influence of several potential factors on these parameters: time (14 levels, noted t in model notation), age (15 levels from 3—the first age of reproduction—to 17, noted a , or A when used as a covariate or linear trend) and the group (2 levels: philopatric and immigrants, noted P and I , respectively). Considering the number of effects and parameters modelled, model notation was complex. To guide the reader through the modelling procedure, in our notation each parameter was separated by a “/” and followed by the letter P or I to indicate philopatric or immigrant birds, respectively. For a model in which all survival parameters vary over time, an extension of the known Cormack-Jolly-Seber model was denoted $\phi^*P(t)/\phi P(t)/\phi^*I(t)/\phi I(t)/pP(t)/pI(t)$. For example, when a model assumed the same survival for philopatric and immigrant residents was noted $\phi^*P(t)/\phi P(t) = \phi I(t)/\phi^*I(t)/pP(t)/pI(t)$ where the symbol “/” was changed by the symbol “=”. The symbol “+” was used when parameters were assumed to vary in parallel, i.e. without statistical interactions between effects. For example, a model as above, but assuming p to vary in parallel over time according to the group (philopatric vs. immigrants), was noted $\phi^*P(t)/\phi P(t) = \phi I(t)/\phi^*I(t)/pP(t) + pI(t)$; we used the same notation in modelling the seniority probability, γ . In both analyses we began with the same general model assuming the effect of the group, of the year, the bird age and their statistical interaction, noted $\phi^*P(t^*a)/\phi P(t^*a)/\phi^*I(t^*a)/\phi I(t^*a)/pP(a^*t)/pI(a^*t)$ and $\gamma^*P(t^*a)/\gamma P(t^*a)/\gamma^*I(t^*a)/\gamma I(t^*a)/pP(a^*t)/pI(a^*t)$. This model

was clearly overparameterized, but was the one for which a GOF test was available. We used the MSURGE1.5 program (Choquet et al. 2004) to obtain parameter estimates. We progressively eliminated the effects on each parameter separately and kept the structure of the others as general as possible. Model selection was based on the Akaike's Information Criterion (QAICc; see Williams et al. 2001).

We modelled seniority probability, γ , by reversing the encounter histories used to estimate survival: seniority probability was the probability that an individual was present before the date of the first resighting (Pradel et al. 1997). The complement of γ is the probability of recruitment, i.e. the probability that an individual was ‘new’ when first seen. The GOF of the general model $\gamma^*P(t^*a)/\gamma P(t^*a)/\gamma^*I(t^*a)/\gamma I(t^*a)/pP(t^*a)/pI(t^*a)$ was taken as the starting model (Pradel et al. 1997); hence, we corrected the deviance with the same scale parameter.

Results

Demographic parameters were estimated from 52,671 resightings made at the colony from 1992 to 2006, corresponding to 6,133 sexually mature gulls (≥ 3 years old) marked between 1988 and 2003. Among the total resighted individuals, 407 (ca. 7%) were immigrants, i.e. individuals born in other colonies. Despite an average recapture probability of ca. 0.70 (see also Oro et al. 1999; Cam et al. 2004), about a third of the individuals were seen only once over the entire study period, which denoted a high proportion of transient birds (Tavecchia et al. 2007). Using more than 8,500 resightings of sexually mature birds made at the other colonies of the metapopulation (for which we assumed that most were breeders), we found that for philopatric transients (i.e. born in the Ebro Delta and only seen once), more first sightings occurred at the colony than expected (99% of 1,008 individuals; Table 1), whereas a significantly higher proportion of immigrant transients were seen at other colonies before they were sighted at the Ebro Delta ($\chi_1^2 = 83.6$, $P < 0.0001$; Table 1). Those results suggested that at least 31 transient immigrants (15%) had some previous reproductive experience before settling at the Ebro Delta, and thus were likely breeding dispersers. Among resident birds (birds breeding more than once at the Ebro Delta), this trend was higher: 20% of immigrants were seen breeding at other colonies before dispersing to the Ebro Delta ($\chi_1^2 = 322.5$, $P < 0.0001$, Table 1). Resightings at other colonies also allowed us to assess whether transients actually dispersed to other colonies: at least 11% of the 1,218 transients seen at the Ebro Delta were resighted again at other colonies in subsequent years.

Table 1 Contingency table of resighting frequencies for Audouin’s gull (*Larus audouinii*) at the Ebro Delta and elsewhere—at other colonies of the metapopulation—depending on status (transients vs residents) and separated according to philopatrics and immigrants

Status	First sighted at the Ebro Delta	
	Yes	No
Transients		
Philopatrics	994 (971) 98.6%	14 (37) 1.4%
Immigrants	179 (202) 85.2%	31 (8) 14.8%
Residents		
Philopatrics	4,038 (4,007) 98.9%	44 (75) 1.1%
Immigrants	132 (163) 79.5%	34 (3) 20.5%

Altogether, 63,500 resightings made in the entire metapopulation during 1992–2006 were used. Expected frequencies depending on whether the individuals were seen first at the Ebro Delta or elsewhere are shown in parentheses. The two comparisons between philopatrics and immigrants depending on whether they were first seen at the Ebro Delta or not for transients and residents were statistically different (see “Results”)

Testing the adequacy of capture–recapture hypotheses

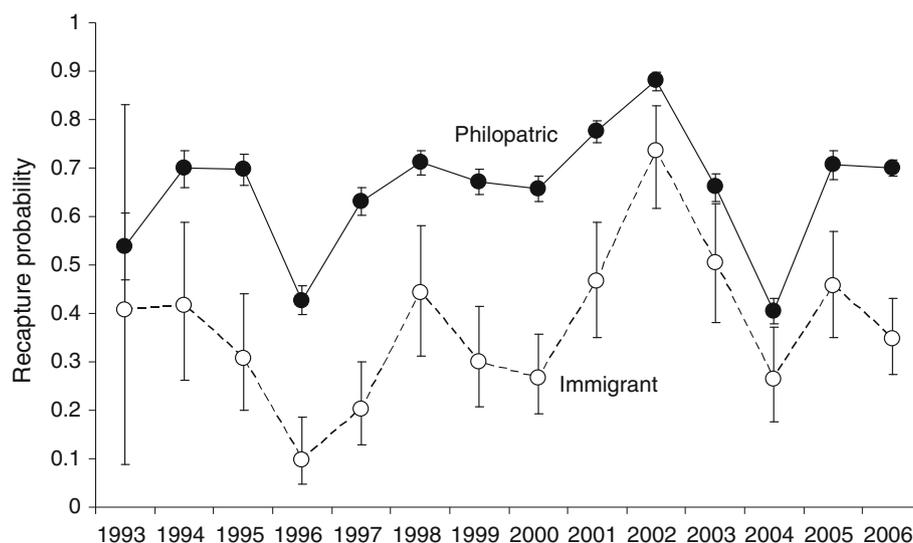
The GOF test of the model including age, time and their interactions, noted $\phi P(t^*a)/\phi I(t^*a)/pP(a^*t)/pI(a^*t)$, indicated that a significantly large part of the deviance remained unexplained ($\chi^2_{517} = 1160.45, P < 0.001$). The specific components of the GOF test pointed out the presence of transient individuals, a consistent result with previous analyses of the same population (Oro et al. 1999, 2004; Tavecchia et al. 2007). This lack of fit can be corrected including extra parameters for newly observed birds or transients (Pradel et al. 1997), a model noted $\phi^*P(t^*a)/\phi P(t^*a)/\phi^*I(t^*a)/\phi I(t^*a)/pP(a^*t)/pI(a^*t)$ (Model 1, Table 2). However, there was evidence of a large residual deviance ($\chi^2_{377} = 572.59, P < 0.01$), partly due to the fact that a subset of individuals were systematically observed more than others, a phenomenon known as trap-dependence. Again, this effect can be controlled by increasing model complexity (Pradel 1993), but in this case we preferred to scale model deviances because adding further parameters would have complicated the analysis unnecessarily. Hence we estimated the variance inflation factor as the ratio between the χ^2 and its degrees of freedom ($\hat{c} = 572.59/377 = 1.52$) and used it to scale all model deviances.

Table 2 Modelling survival (ϕ' and ϕ , for ‘first-seen’ and resident gulls, respectively), seniority (γ' and γ , for ‘first-seen’ and resident gulls, respectively), and recapture (p) probabilities

Model	Dev	Np	QAICc	Δ QAICc	
Survival probability					
1	$\phi^*P(t^*a)/\phi P(t^*a)/\phi^*I(t^*a)/\phi I(t^*a)/pP(t^*a)/pI(t^*a)$	34,989.818	393	23,823.805	560.443
2	$\phi^*P(t^*a)/\phi P(t^*a)/\phi^*I(t^*a)/\phi I(t^*a)/pP(t) + pI(t)$	35,031.281	234	23,730.629	467.267
3	$\phi^*P(t)/\phi P(t)/\phi^*I(t)/\phi I(t)/pP(t)/pI(t)$	35,354.490	68	23,413.910	150.548
4	$\phi^*P(t + a)/\phi P(t)/\phi^*I(t)/\phi I(t)/pP(t) + pI(t)$	35,109.787	81	23,278.794	15.432
5	$\phi^*P(t)/\phi P(t)/\phi^*I(t)/\phi I(t)/pP(t) + pI(t)$	35,354.490	68	23,413.910	150.548
6	$\phi^*P(t) = \phi P(t) = \phi^*I(t) = \phi I(t)/pP(t) = pI(t)$	36,096.008	27	23,820.136	556.774
7	$\phi^*P(\cdot)/\phi P(\cdot)/\phi^*I(\cdot)/\phi I(\cdot)/pP(t) + pI(t)$	36,716.658	19	23,554.367	291.005
8	$\phi^*P(A + t)/\phi P(t)/\phi^*I(t)/\phi I(t)/pP(t) + pI(t)$	35,124.690	70	23,266.606	3.244
9	$\phi^*P(A + t)/\phi P(t) = \phi I(t)/\phi^*I(t)/pP(t) + pI(t)$	35,159.251	57	23,263.362	0
Seniority probability					
10	$\gamma^*P(a + t)/\gamma P(a + t)/\gamma^*I(a + t)/\gamma I(a + t)/pP(t) + pI(t)$	28,572.535	131	19,074.572	21.093
11	$\gamma^*P(A + t)/\gamma P(a + t)/\gamma^*I(a + t)/\gamma I(a + t)/pP(t) + pI(t)$	28,596.162	118	19,064.129	10.650
12	$\gamma^*P(a + t)/\gamma P(a6 + t) = \gamma I(a6 + t)/\gamma^*I(a + t)/pP(t) + pI(t)$	28,756.653	80	19,093.798	40.319
13	$\gamma^*P(a + t)/\gamma P(a10 + t) = \gamma I(a10 + t)/\gamma^*I(a + t)/pP(t) + pI(t)$	28,752.700	83	19,097.221	43.742
14	$\gamma^*P(A + t)/\gamma P(a6 + t)/\gamma^*I(a + t)/\gamma I(a + t)/pP(t) + pI(t)$	28,690.434	108	19,106.718	53.239
15	$\gamma^*P(A + t)/\gamma P(a10 + t)/\gamma^*I(a + t)/\gamma I(a + t)/pP(t) + pI(t)$	28,687.993	112	19,112.592	59.113
16	$\gamma^*P(A + t)/\gamma P(a + t)/\gamma^*I(a + t)/\gamma I(a6 + t)/pP(t) + pI(t)$	28,621.967	109	19,063.119	9.640
17	$\gamma^*P(A + t)/\gamma P(a + t)/\gamma^*I(a + t)/\gamma I(a10 + t)/pP(t) + pI(t)$	28,618.210	112	19,066.640	13.161
18	$\gamma^*P(A + t)/\gamma P(a + t) = \gamma I(a + t)/\gamma^*I(a + t)/pP(t) + pI(t)$	28,668.078	89	19,053.479	0

Dev model deviance, Np number of estimable model parameters, QAICc corrected Akaike’s Information criterion. Notation of potential factors was: T time, I and P philopatric and immigrants, respectively, A linear trend of age up to age 17, aj age up to age j (3 < j < 15)

Fig. 2 Variation of recapture probability according to time and group (philopatrics vs immigrants), from the best model including these two effects (Model 18; Table 2). Bars indicate a 95% confidence interval



Survival and transience probabilities

Model selection began by fitting the general model $\phi^*P(t^*a)/\phi P(t^*a)/\phi^*I(t^*a)/\phi I(t^*a)/pP(t^*a)/pI(t^*a)$ (Model 1, hereafter). Model 1 assumed the effect of age (15 levels), time (14 levels) and their interaction for philopatric and immigrant birds, and distinguished between newly and previously captured birds. Model 1 was highly parameterized (393 parameters) but not all parameters were estimable, as data were missing for some age-by-time interactions, especially for older birds. We quickly simplified this model by eliminating irrelevant effects and/or their interactions. An unexpected result was that recapture probability was statistically higher for philopatrics than for immigrants, and this difference was constant over time (i.e. there was an additive effect of the group over time, see Fig. 2). A model without the statistical interaction between time and the group (philopatrics vs. immigrants) had a lower QAICc value. Time had a significant effect on all parameters, whereas age negatively influenced *P but had no effect on the other parameters. These results were confirmed by the lower QAICc value of the simpler model $\phi^*P(t + a)/\phi P(t)/\phi^*I(t)/\phi I(t)/pP(t) + pI(t)$ (Model 4, Table 2). A further reduction in QAICc value was obtained by modelling age as a continuous variable (Model 8, Table 2). At this point, we tested a model in which immigrant and philopatric birds showed the same survival (Model 9, Table 2). This model, noted $\phi^*P(t + A)/\phi P(t) = \phi I(t)/\phi^*I(t)/pP(t) + pI(t)$ had the lowest QAICc and no further reductions were made. According to this model, resident birds showed a similar mortality regardless of the group (philopatrics and immigrants) (Fig. 3). In contrast, philopatric birds were more likely to become residents than immigrant birds; however, this probability decreased according to the age at which the bird was seen for the first

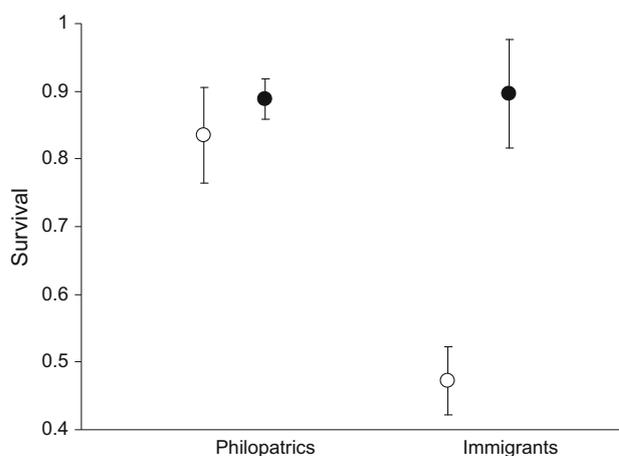


Fig. 3 Survival probability estimates for Audouin's gull at the Ebro Delta according to state (transient vs resident, shown by open and black dots, respectively) and group (philopatrics vs immigrants); values were drawn from the model in which survival parameters were assumed to be constant (model 7; Table 2) to stress the differences. Bars show the 95% confidence intervals

time, a phenomenon that was not observed among immigrant birds (Figs. 3, 4).

Seniority probability

Model selection began from the model $\gamma^*P(a + t)/\gamma P(a + t)/\gamma^*I(a + t)/\gamma I(a + t)/pP(t) + pI(t)$, which assumes for p the same structure retained as in the survival analysis (Model 10, Table 2). As we did for survival, we tested the significance of interaction terms first and then modelled the effect of age. Unlike survival, age was important in all seniority parameters modelled. However, we found some differences in transient versus resident birds and in philopatric versus immigrant individuals. A model in

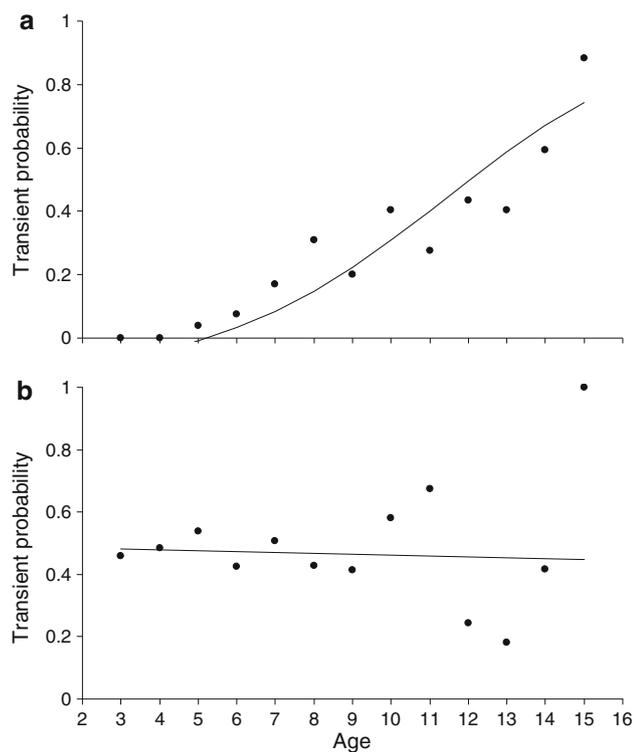


Fig. 4 Probability of transience (i.e. of leaving the study colony after being there only once) according to age (values for 2003): for philopatrics (a) such probabilities increased with age, yet remained constant for immigrants (b). Dots show the ML estimates from the full-age model effect, while lines show the ML estimated from the retained model. The average value was higher for immigrants than for philopatrics

which the seniority probability of transient birds born at the colony was assumed to vary linearly with bird age was preferred (Model 11; Table 2), as in the survival analysis. In contrast, we were not able to eliminate the age effect in the parameter for newly seen immigrants, but this parameter does not have clear biological significance in the reverse approach (Pradel et al. 1997).

Although we found that most recruitment also occurred before birds reached the age of 6 years, a model assuming constant recruitment probability after this age was not retained (Table 2; Fig. 5). Finally, a model assuming the same seniority parameters for immigrants and philopatrics (Model 18) showed the lowest QAICc value (Table 2).

Discussion

Limitations of the study

The results found in the present analysis are based on the comparison of survival, transience and recruitment between gulls born locally and gulls born in other colonies. There are some obvious limitations to comparing fitness components

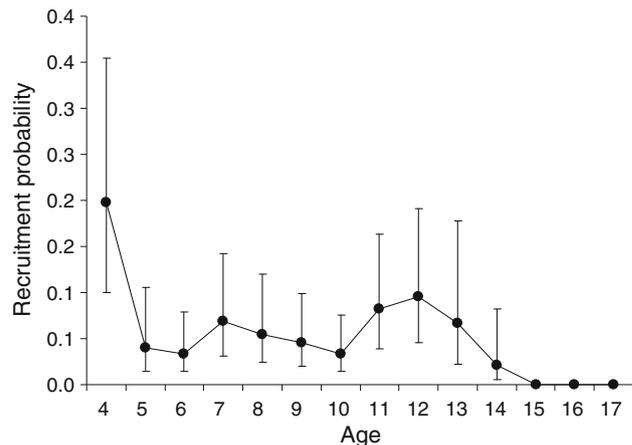


Fig. 5 Variation of recruitment according to age for Audouin's gull breeding at the Ebro Delta in 2006, with all ages represented. Estimates were from the retained model (Model 18, Table 2) and were the same regardless of the group (philopatrics vs immigrants). By definition, 3-year old birds had a recruitment probability of 1, i.e. the earliest age of reproduction ever recorded for the species (not shown in the figure). Bars show 95% confidence intervals

between philopatrics and immigrants in a single site, pointed out by B elichon et al. (1996): first, we only analysed the phase after settlement, when selection could have already taken place filtering the low-quality individuals during dispersal (e.g. Bowler and Benton 2005; Doligez and P art 2008; Devillard and Bray 2009); secondly, we did not have complete information on the breeding experience of immigrants and we could not separate the effects of natal dispersal from those of breeding dispersal, nor the time elapsed since first breeding in the study colony, which precluded the analysis of experience (i.e. breeding events at the study colony); finally, sex (dispersal can affect each sex differently; e.g. Ronce 2007) could not be included in the analysis. However, some of those limitations were partially countered by the large spatial scale covered in our study, i.e. that immigrants had to move large distances to disperse (see B elichon et al. 1996; Hixon et al. 2002; Doligez and P art 2008); in some previous studies, dispersal was considered at an intra-colony level and the distances covered were small (e.g. Osorio-Beristain and Drummond 1993). Furthermore, fitness differences between philopatrics and immigrants are still recorded after settlement in many studies (B elichon et al. 1996; Lemel et al. 1997; Reid et al. 2006). Finally, reliability of the comparisons on demographic parameters between philopatrics and immigrants was high due to the large sample sizes and also the high number of resightings out of the study colony.

The influence of immigrants on local population dynamics

At the level of local population dynamics, Audouin's gull immigrants not only result in an increase in the population

density, but also in an increase of local recruitment from breeding output (similar to that of philopatric individuals), with important consequences for metapopulation dynamics. Some theoretical models have shown that dispersal can influence the size and stability of populations (e.g. McPeck and Holt 1992). Using the proportion of Audouin's gulls resighted at the Ebro Delta born in other colonies over the years, and correcting this number by the proportion of birds ringed at each site and a different recapture probability (Fig. 2), we can estimate that ca. 16% of breeders were immigrants. Such numbers (compared with an average immigration proportion of 3% in southern fulmars *Fulmarus glacialis*, 40% in lesser snow goose *Chen caerulescens* or 50% in black guillemots *Cephus grylle*; see Jenouvrier et al. 2003; Johnson 1995; Frederiksen and Petersen 2000, respectively) should have an influence on the metapopulation dynamics (see also Oro and Ruxton 2001): in 2006, 5,428 females bred out of the Ebro Delta in the other colonies of the metapopulation (own data), while in that year ca. 2,452 of the females breeding at the Ebro Delta were immigrants. In fact, recent studies on several long-lived animals, identified as highly philopatric, show that the importance of dispersal for their population dynamics is greater than previously considered (e.g. Bullock et al. 2002; Inchausti and Weimerskirch 2002; Oro et al. 2004; Serrano et al. 2004; Gerber et al. 2005).

Are there differences in demographic parameters between philopatrics and immigrants?

According to our study, some demographic parameters were lower for immigrants, in agreement with the resident fitness hypothesis (Anderson 1989). For instance, immigrants were less likely to become residents in the Ebro Delta colony than philopatrics, probably because they were more likely to return to their natal colonies (Table 1; see also Prévot-Julliard 1996; Tavecchia et al. 2007). Also, an interesting difference was that the probability of becoming resident was negatively associated with age in philopatric birds, but not in immigrants. This also suggests that immigrants had a greater tendency to return to their natal colonies, regardless of the recruiting age at the Ebro Delta. The oldest philopatrics would disperse to other breeding patches at higher rates after their first reproductive attempts at the natal site (see also Serrano et al. 2003; Dittmann et al. 2005). Furthermore, the striking differences in resighting probability could not be explained by higher skipping of reproduction in immigrants (this is a rare behaviour in Audouin's gulls; see Oro 1998), but rather suggested some type of despotic behaviour of philopatrics against immigrants (Oro 2008), or once again a stronger tendency among the latter to be absent from the study colony due to breeding alternatively in other colonies (Table 1; see also Tavecchia et al. 2007). Nevertheless, and

despite the abovementioned differences in site-tenacity and dispersal, philopatric and immigrant Audouin's gulls shared most of the demographic parameters. For a long-lived species such as Audouin's gulls, the most sensitive parameters for their population dynamics are adult survival and recruitment, and these components were very similar between philopatrics and immigrants. In our study, dispersal and philopatry could be components of a mixed, evolutionarily stable strategy, in which fitness of immigrants would be similar to that of philopatrics (e.g. Gaines et al. 1979; Johannesen and Andreassen 1998; Gillis and Krebs 2000). The question is, what could influence such low differences between philopatric and immigrants? A potential factor is the high environmental quality of the Ebro Delta, with higher food availability per capita and higher breeding success than the rest of the colonies (see Oro et al. 1996; Oro and Ruxton 2001; Oro 2003). That factor probably allowed immigrants to exhibit a relatively successful performance; in fact, the benefits of dispersal to suitable patches in heterogeneous habitats have been pointed out previously, and in extreme cases of habitat quality, immigrants can perform even better than philopatrics (McPeck and Holt 1992; Stenseth and Lidicker 1992; Lin and Batzli 2004; Clobert et al. 2009). Nevertheless, differences in breeding success between philopatric and immigrants are unknown in our study; yet, the differences in the probability of recapture and that of becoming resident may suggest that immigrants could be breeding worst and having a higher probability of emigrating (temporally or not, respectively) from the Ebro Delta colony. In fact, the idea that vertebrates have a higher probability of dispersal after a bad breeding experience is highly accepted and proved elsewhere (e.g. Serrano et al. 2003).

The influence of habitat stability on philopatric and immigrant fitness

Audouin's gulls have a life-history strategy that evolved in unstable habitats—such as salt marshes and river deltas—with low temporal autocorrelation in habitat quality (see Martínez-Abraín et al. 2001 and 2003; Parejo et al. 2006; Valdemoro et al. 2007). In such dynamic systems and particularly for long-lived birds, i.e. with no predators and with no important geographical barriers, and thus the ability to fly easily among local populations, the costs of dispersal should be rather low (e.g. Serrano et al. 2003). The temporal unpredictability of ephemeral habitats is known to affect dispersal in dynamic systems typical of r-type organisms (e.g. insects, parasites), and this pattern has been shown in studies on pest control, life histories and biodiversity (Palmer and Strathmann 1981; Wissinger 1997). In contrast, the influence of habitat stability on dispersal and metapopulation dynamics in vertebrates has seldom been addressed

despite the frequency of ecosystems with high unpredictability (e.g. Magoulick and Kobza 2003). Together with Audouin's gulls, several other avian species have been identified occupying ephemeral habitats, such as some gulls *Larus* spp., terns *Sterna* spp., skimmers *Rynchops* spp., flamingos *Phoenicopterus roseus* and snail kites *Rostrhamus sociabilis* (McNicholl 1975; Crawford et al. 1994; Erwin et al. 1998; Valentine-Darby et al. 1998; Oro 2002; Balkız et al. 2009), although the influence of habitat predictability on dispersal processes has received scarce attention (with exceptions such as Oro and Ruxton 2001).

Results concerning the differences in fitness between dispersers and philopatrics across a series of studies on several species of birds and mammals (Bélichon et al. 1996; Doligez and Pärt 2008) did not show a consistent pattern: some organisms exhibited differences between philopatrics and immigrants, whereas others did not. It has been argued that such contradictory results were the consequence of different evolutionary strategies, different phenotypic or condition-dependent (based on external information) responses, or even due to the biases in some studies (see also Ronce 2007; Clobert et al. 2009). Among the evolutionary causes, however, little has been said about the stability of habitats and the low temporal autocorrelation in habitat quality (e.g. Andersson 1980; Crawford et al. 1994; Dieckmann et al. 1999), which should result in high dispersal rates for organisms living in such systems (an example of the opposite evolutionary strategy—extremely low dispersal rates—in a Procellariiform, is Cory's shearwater *Calonectris diomedea* occupying very stable breeding habitats; see Igual et al. 2007). Thus, in species with high dispersal capabilities resulting from a life-history strategy that has evolved in unstable habitats, we would expect differences in fitness components between philopatric and immigrants to be rather low.

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References

- Anderson PK (1989) Dispersal in rodents: a resident fitness hypothesis. *American Society of Mammalogists*, Lawrence
- Andersson M (1980) Nomadism and site tenacity as alternative reproductive tactics in birds. *J Anim Ecol* 49:175–184
- Balkız Ö, Béchet A, Rouan L, Choquet R, Germain C, Amat JA, Rendón-Martos M, Baccetti N, Özsesmi U, Pradel R (2009) Metapopulation dynamics of the greater flamingo *Phoenicopterus roseus* in the Mediterranean: implications for conservation. *Flamingo* 1:12–16
- Bélichon S, Clobert J, Massot M (1996) Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecol* 17:503–517
- Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80:205–225
- Bullock JM, Kenward RE, Hails RS (2002) *Dispersal ecology*. Cambridge University Press, Cambridge
- Cam E, Oro D, Pradel R, Jimenez J (2004) Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture-recapture models. *J Anim Ecol* 73:723–736
- Choquet R, Reboulet AM, Pradel R, Gimenez O, Lebreton JD (2004) M-SURGE: new software specifically designed for multistate capture recapture models. *Anim Biod Cons* 27:207–221
- Choquet R, Reboulet AM, Lebreton J-D, Gimenez O, Pradel R (2005) U-CARE 22 user manual mimeographed document CEFE/CNRS
- Clobert J, Danchin E, Dhondt AA, Nichols JD (2001) *Dispersal*. Oxford University Press, London
- Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett* 12:197–209
- Crawford RJ, Dyer BM, Brooke RK (1994) Breeding nomadism in southern African seabirds—constraints, causes and conservation. *Ostrich* 65:231–246
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491
- Denno RF, Roderick GK, Olmstead KL, Dobel HG (1991) Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. *Am Nat* 138:1513–1541
- Devillard S, Bray Y (2009) Assessing the effect on survival of natal dispersal using multistate capture-recapture models. *Ecology* 90:2902–2912
- Dieckmann U, O'Hara B, Weisser W (1999) The evolutionary ecology of dispersal. *Trends Ecol Evol* 14:88–90
- Dittmann T, Zinsmeister D, Becker PH (2005) Dispersal decisions: common terns, *Sterna hirundo*, choose between colonies during prospecting. *Anim Behav* 70:13–20
- Doligez B, Pärt T (2008) Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *J Anim Ecol* 77:1199–1211
- Doligez B, Danchin E, Clobert J (2002) Public information and breeding habitat selection in a wild bird population. *Science* 297:1168–1170
- Doncaster CP, Clobert J, Doligez B, Danchin E, Gustafsson L (1997) Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. *Am Nat* 150:425–445
- Erwin RM, Nichols JD, Eyley TB, Stotts DB, Truitt BR (1998) Modeling colony-site dynamics: a case study of gull-billed terns (*Sterna nilotica*) in coastal Virginia. *Auk* 115:970–978
- Forbes LS, Kaiser GW (1994) Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos* 70:377–384
- Frederiksen M, Petersen A (2000) The importance of natal dispersal in a colonial seabird, the black guillemot *Cepphus grylle*. *Ibis* 142:48–57
- Gaines MS, Vivas AM, Baker CL (1979) An experimental analysis of dispersal in fluctuating vole populations: demographic parameters. *Ecology* 60:814–828

- Gerber LR, Hyrenbach KD, Zacharias MA (2005) Do the largest protected areas conserve whales or whalers? *Science* 307:525–526
- Gillis EA, Krebs CJ (2000) Survival of dispersing versus philopatric juvenile snowshoe hares: do dispersers die? *Oikos* 90:343–346
- Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annu Rev Ecol Syst* 13:1–21
- Hanski IA, Gaggiotti OE (2004) *Ecology, genetics and evolution of metapopulations*. Elsevier, Amsterdam
- Hixon MA, Pacala SW, Sandin SA (2002) Population regulation: historical context and contemporary challenges of open vs closed systems. *Ecology* 83:1490–1508
- Igual JM, Forero MG, Gomez T, Oro D (2007) Do introduced predators trigger an evolutionary trap in a colonial seabird? *Biol Conserv* 137:189–196
- Inchausti P, Weimerskirch H (2002) Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *J Anim Ecol* 71:765–770
- Jenouvrier S, Barbraud C, Weimerskirch H (2003) Effects of climate variability on the temporal population dynamics of southern fulmars. *J Anim Ecol* 72:576–587
- Johannesen E, Andreassen HP (1998) Survival and reproduction of resident and immigrant female root voles. *Can J Zool* 76:763–766
- Johnson SR (1995) Immigration in a small population of snow geese. *Auk* 112:731–736
- Julliard R, Perret P, Blondel J (1996) Reproductive strategies of philopatric and immigrant blue tits. *Acta Oecol* 17:487–501
- Keymer JE, Marquet PA, Velasco-Hernández JX, Levin SA (2000) Extinction thresholds and metapopulation persistence in dynamic landscapes. *Am Nat* 156:478–494
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Lemel J-Y, Belichon S, Clobert J, Hochberg ME (1997) The evolution of dispersal in a two-patch system: some consequences of differences between migrants and residents. *Evol Ecol* 11:613–629
- Lin YK, Batzli GO (2004) Emigration to new habitats by voles: the cost of dispersal paradox. *Anim Behav* 68:367–372
- Magoulick DD, Kobza RM (2003) The role of refugia for fishes during drought: a review and synthesis. *Freshw Biol* 48:1186–1198
- Martinez-Abraín A, Viedma C, Ramón N, Oro D (2001) On the potential role of philopatry and conspecific attraction as conservation tools in Audouin's gull. *Bird Conserv Int* 11:143–147
- Martínez-Abraín A, Oro D, Forero MG, Conesa D (2003) Modeling temporal and spatial colony-site dynamics in a long-lived seabird. *Popul Ecol* 45:133–139
- Maynard-Smith J (1982) *Evolution and the theory of games*. Cambridge University Press, Cambridge
- McNicholl MK (1975) Larid site tenacity and group adherence in relation to habitat. *Auk* 92:98–104
- McPeck MA, Holt RD (1992) The evolution of dispersal in spatially and temporally varying environments. *Am Nat* 140:1010–1027
- Morris DW (1992) Scales and costs of habitat selection in heterogeneous landscapes. *Evol Ecol* 6:412–432
- Murren CJ, Julliard R, Schlichting CD, Clobert J (2001) Dispersal, individual phenotype, and phenotypic plasticity. In: Clobert J et al (eds) *Dispersal*. Oxford University Press, London, pp 261–272
- Orell M (1999) Immigration and gene flow in a northern willow tit (*Parus montanus*) population. *J Evol Biol* 12:283–295
- Oro D (1998) Audouin's gull account. *BWP Update* 4:47–61
- Oro D (2002) Breeding biology and population dynamics of slender-billed gulls *Larus genei* at the Ebro Delta (western Mediterranean). *Waterbirds* 25:67–77
- Oro D (2003) Managing seabird metapopulations in the Mediterranean: constraints and challenges. *Sci Mar* 67:13–22
- Oro D (2008) Living in a ghetto within a local population: an empirical example of an ideal despotic distribution. *Ecology* 89:838–846
- Oro D, Pradel R (1999) Recruitment of Audouin's gull to the Ebro Delta colony at metapopulation level in the western Mediterranean. *Mar Ecol Progr Ser* 180:267–273
- Oro D, Ruxton GD (2001) The formation and growth of seabird colonies: Audouin's gull as a case study. *J Anim Ecol* 70:527–535
- Oro D, Genovart X, Ruiz X, Jimenez J, Garcia-Gans J (1996) Differences in diet, population size and reproductive performance between two colonies of Audouin's gull *Larus audouinii* affected by a trawling moratorium. *J Avian Biol* 27:245–251
- Oro D, Pradel R, Lebreton J-D (1999) Food availability and nest predation influence life history traits in Audouin's gull, *Larus audouinii*. *Oecologia* 118:438–445
- Oro D, Baccetti N, Boukhalfa D, Eken G, El Hili A, Goutner V, Karauz S, Papaconstantinou C, Recorbet B, Ruiz X (2000) Current breeding distribution and status of Audouin's gulls *Larus audouinii* in the Mediterranean. In: Sultana J, Yésou P (eds) *Monitoring and conservation of birds, mammals and sea turtles of the Mediterranean and Black Seas*. BirdLife Malta, Malta, pp 69–80
- Oro D, Cam E, Pradel R, Martínez-Abraín A (2004) Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proc R Soc Lond B* 271:387–396
- Oro D, Martínez-Abraín A, Paracuellos M, Nevado JC, Genovart M (2006) Influence of density-dependence on predator-prey seabird interactions at large spatio-temporal scales. *Proc R Soc Lond B* 273:379–383
- Osorio-Beristain M, Drummond H (1993) Natal dispersal and deferred breeding in the Blue-footed booby. *Auk* 110:234–239
- Palmer AR, Strathmann RR (1981) Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia* 48:308–318
- Parejo D, Oro D, Danchin E (2006) Is “Habitat copying” used by a species adapted to variable environments? The importance of the spatial scale. *Ibis* 148:146–154
- Pradel R (1993) Flexibility in survival analysis from recapture data: handling trap-dependence. In: Lebreton J-D, North PM (eds) *Marked individuals in the study of bird populations*. Birkhäuser, Basel, pp 29–38
- Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709
- Pradel R, Johnson AR, Viallefont A, Nager RG, Cézilly F (1997) Local recruitment in the greater flamingo: a new approach using capture-mark-recapture data. *Ecology* 78:1431–1445
- Prévot-Julliard A-C (1996) *Rôle de la dispersion dans la dynamique d'une population de mouette rieuse *Larus ridibundus**. PhD thesis, Université de Montpellier II
- Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P (2006) Spatial variation in demography and population growth rate: the importance of natal location. *J Anim Ecol* 75:1201–1211
- Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu Rev Ecol Syst* 38:231–253
- Serrano D, Tella JL, Forero MG, Donázar JA (2003) Social and individual features affecting natal dispersal in the colonial lesser kestrel. *Ecology* 84:3044–3054

- Serrano D, Forero MG, Donázar JA, Tella JL (2004) Dispersal and social attraction affect colony selection and dynamics of Lesser Kestrels. *Ecology* 85:3438–3447
- Southwood TRE (1977) Habitat, the templet for ecological strategies? *J Anim Ecol* 46:337–365
- Stenseth NC, Lidicker WZ Jr (1992) Animal dispersal: small mammals as a model. Chapman & Hall, London
- Tavecchia G, Pradel R, Boy V, Johnson AR, Cézilly F (2001) Sex- and age-related variation in survival and the cost of first reproduction in Greater Flamingos. *Ecology* 82:165–174
- Tavecchia G, Pradel R, Genovart M, Oro D (2007) Density-dependent parameters and demographic equilibrium in open populations. *Oikos* 116:1481–1492
- Travis MJJ, Dytham C (1999) Habitat persistence, habitat availability and the evolution of dispersal. *Proc R Soc Lond B* 266:723–728
- Valdemoro H, Sánchez-Arcilla A, Jiménez JA (2007) Coastal dynamics and wetlands stability. The Ebro delta case. *Hydrobiologia* 577:17–29
- Valentine-Darby PL, Bennetts RE, Kitchens WM (1998) Seasonal patterns of habitat use by Snail Kites in Florida. *J Raptor Res* 32:98–103
- van de Pol M, Bruinzeel LW, Heg D, Van Der Jeugd HP, Verhulst S (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers *Haematopus ostralegus*. *J Anim Ecol* 75:616–626
- Williams BK, Conroy MJ, Nichols JD (2001) Analysis and management of animal populations. Academic, New York
- Wissinger SA (1997) Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biol Control* 10:4–15