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Hatching date influences age at first reproduction in the black-headed gull

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Abstract In long-lived colonial birds, age at recruitment is an important life-history character. Variation in this parameter may reflect differences in several factors, including competitive ability and breeding strategies. Further, these differences may be due to timing of hatching (for instance through differences in competitive ability). We investigated the age of first-time breeders in relation to hatching date in a black-headed gull *Larus ridibundus* colony situated in central France, from 1979 to 1993. Age at first breeding was estimated for four groups of individuals (total $n=550$) according to their hatching date, using a recent capture-recapture methodology which allowed us to estimate recruitment rate without the limiting assumptions of methods relying on simple return rates. The age at first breeding was negatively correlated with the hatching date of individuals: individuals hatched earlier in the season started breeding at a younger age than individuals born later. Proportionally more 2-year-old late-hatched individuals were seen breeding on small peripheral colonies than young early-hatched individuals. This difference disappeared after age 3 years. These results strongly suggest that individuals hatched late in the season start to breed on peripheral colonies before recruiting to their natal colony. A difference of few weeks in hatching date has consequences which can last for several years.

Keywords Capture-recapture · *Larus ridibundus* · Local recruitment · Hatching date · Metapopulation

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Introduction

For many species, when to start to reproduce is the most important life-history decision an individual has to take (Roff 1992; Stearns 1992). Age at first reproduction has been studied in many vertebrates species, especially small mammals (Prévot-Julliard et al. 1999) and large mammals (review in Gaillard et al. 1998). In birds, empirical studies of long-lived species have detected wide variation among individuals in this trait (Bradley and Wooller 1991; Danchin et al. 1991). Whether these differences are due to constraints (e.g. limitation of breeding sites or mates: Coulson 1968; Klomp and Furness 1991; Spear et al. 1995; constraint hypothesis, from Curio 1983) or reflect a variety of individual strategies (Cam et al. 1998) is open to debate. Indeed, by delaying reproduction, some individuals may avoid paying the high cost of early reproduction until their potential reproductive performance has sufficiently increased with age (Forslund and Pärt 1995; Cézilly and Nager 1996; Pyle et al. 1997; restraint hypothesis, Curio 1983). Furthermore, delaying reproduction may provide an opportunity to assess the quality of potential breeding patches through prospecting (Boulinier and Danchin 1997). In addition, if sites are heterogeneous in quality, competition is likely to be tougher at better sites. Thus, age at first reproduction may represent a compromise between the delay in reaching reproduction and the breeding site quality (Ens et al. 1995).

Individual ontogenic traits, such as relative birth date, have been reported to be correlated with variation in recruitment probability and/or age at first breeding (e.g. kestrel *Falco tinnunculus*, Daan et al. 1990; pied flycatcher *Ficedula hypoleuca*, Potti and Montalvo 1991; western gulls *Larus occidentalis*, Spear and Nur 1994). In short-lived birds, the return rate of late-hatched individuals has been reported to be lower than that of early-hatched individuals. This could result from either lower survival or lower recruitment probabilities. In addition, as early-hatched individuals are likely to be dominant over late-hatched ones (Eden 1987), late-hatched indi-

viduals may be constrained to start reproducing at an older age or to disperse out of the study site. Most previous studies of recruitment have been based on the distribution of age at first (observed) breeding attempt (Harrington 1974; Wooller and Coulson 1977; Serventy and Curry 1984; Gratto et al. 1985; Rattiste and Lilleleht 1986; Gaston et al. 1994; Thompson et al. 1994; Spear et al. 1995). However, in such cases, the accuracy of the estimates of age at recruitment strongly relies on resighting probability of individuals in the field being high: an individual which has apparently delayed its reproduction may have reproduced at an earlier age without being observed (Clobert 1995). When resighting probability is below 1, age at first reproduction may be strongly overestimated. New statistical capture-recapture methods to estimate recruitment probability that allow resighting probabilities to be below 1 have been developed recently (Clobert et al. 1994; Pradel 1996). The method of Pradel (1996) allows one to estimate the proportion of individuals that have been recruited into the breeding population between two censuses. As in standard studies of survival rates (Lebreton et al. 1992), this method also enables investigation of the influence of external factors (e.g. weather variables, density) and differences between groups (e.g. males vs. females, immigrants vs. residents, see Pradel et al. 1997).

We examined the influence of hatching date on age at first breeding in black-headed gull (*Larus ridibundus*) colonies. The age at first breeding on this species was first said to be between 1 and 3 years (Patterson 1965, in Cramp 1983), and capture-recapture analyses concluded that it was more probably between 2 and 5 years (Clobert et al. 1994). The studied population is composed of one large colony and several small colonies. Small colonies are supposed to be of lower quality and with less competition than in the large colony. We first studied the influence of hatching date on age distribution of first-time breeders on the large colony. We predicted that individuals hatched late during the breeding season would start reproducing at an older age than individuals hatched earlier in the season. We then compared age distributions of breeders in the large colony and in the small ones. We predicted that relatively more young individuals would be observed in small colonies than in the main one. Therefore, small colonies may potentially offer opportunities for birds to breed at younger ages. Our study is one of the first to study the influence of the hatching date on age distribution of first-time breeders in a long-lived bird species with modern capture-mark-recapture methodology.

Materials and methods

Study area and data collection

The study site is located in the Forez basin, central France. Each year, approximately 20 colonies of black-headed gull occupy man-made ponds in a farmland mosaic (Lebreton 1987). The large colony, located at Crantilleux (45°35'N 4°14'E), attracts many more

breeding adults each year than other colonies (more than 4,000 breeding pairs, compared to an average of 250 breeding pairs in other colonies). The quality of this main colony seems higher than that of the small colonies, based on the large numbers of breeding pairs, the high breeding success (more than 1 young fledged per pair each year, compared to less than 1 in the other colonies, Prévot-Julliard 1996), and its stability: it is one of the two colonies that have persisted at least over the past 20 years. Most of the trapping and resighting effort was carried out at the main colony from 1977 to 1998 (we include in this paper data from 1977 to 1993). In addition, from 1994 to 1997, adults were resighted in three small colonies located 7–30 km from the main colony. At the main colony, gulls breed on vegetation growing on the border and on a large central islet of the pond. Nests are built in the centre or at the edge of vegetation. Eggs are laid from mid-April to the beginning of June (Lebreton and Landry 1979). Most of the individual variation in laying dates probably results from successive re-nesting after breeding failure, which occurs regularly in this colony (Prévot-Julliard 1996). Altogether, the annual mean laying date on this colony varied by less than 1 week from one year to another during the time of the study (V. Grosbois, unpublished work).

Pre-fledging young have been ringed during the first week of June in different colonies each year since 1976. Using plumage criteria, young were assigned to four stages corresponding to their approximate age in weeks (category 1–4 from the earliest to the latest hatched birds, Lebreton and Isenmann 1976). From 1977 to 1993, 20,364 young were ringed at the main colony.

Each year, observations of ringed adults were made at the main colony from a floating hide (Lebreton 1987). The breeding status of resighted adults was difficult to assess with certainty. While most gulls present in the colony are likely to be breeders, some individuals (notably at young ages) could be prospectors, as prospecting has been shown to occur in other colonial seabird species (e.g. Halley and Harris 1993; Boulinier and Danchin 1997). However, this problem was partly solved by the method of modelling recruitment. We analysed the recruitment pattern of cohorts born from 1977 to 1988 and resighted as adults from 1979 to 1993. In this period, 550 individuals (140, 245, 138 and 29 individuals from each category, respectively) were resighted at least once as adults at the colony. The sex of young gulls could not be determined at the time of ringing, and only a few breeding adults were sexed with confidence from behaviour. Thus, we could not separate the two sexes in the analysis. Breeding adults were resighted in the small colonies in the same way as at the main colony. However, we did not study age at first reproduction in small colonies with the same statistical procedure as at the main one.

Analysis of recruitment at the main colony

Recruitment was examined by capture-recapture analysis. Standard capture-recapture models use encounter histories (i.e. the sequence of capture and non-capture events) to estimate the probability of disappearance from a population (for a review see Lebreton et al. 1992). By analysing the encounter histories written in the reverse time sequence (such that the last encounter event becomes the first record in the reversed encounter history), and by removing the ringing occasion, it is possible to estimate the probability of entry into the population (Pradel 1996). Using age-specific modelling, these probabilities can be interpreted as the proportion of individuals of a given age present in a population for the first time (this methodology is explained in more detail in Pradel et al. 1997). As in classical capture-recapture modelling, resighting probabilities (p) are estimated.

We modelled the age-specific proportion of individuals present for the first time at the main colony (denoted β hereafter) as a function of time (year of breeding), cohort (year of birth), and birth date in the season (four categories). Starting from a general model which fits the data, we used the Akaike information criterion (AIC, Akaike 1981) to select the best model and likelihood-ratio tests (LRT) to test specific hypotheses (Lebreton et al. 1992). Confidence intervals of resighting probabilities were estimated by profile likelihood (Lebreton et al. 1992).

Table 1 Notations used in the model presentation

Notations	Meaning
t	Time (in years)
age	Age of individuals
cat	Categories of individuals (from 1 to 4)
age lin	Linear function of age (treated quantitatively)
cat lin	Linear function of categories (treated quantitatively)

In a previous analysis of survival rates using the same data, an important resighting heterogeneity (some individuals are more difficult to resight than others) was detected (Prévoit-Julliard et al. 1998a). This heterogeneity was probably due to varying accessibility of the breeding sites to the observer (it is easier to resight ringed individuals breeding on the edge of vegetation than in the centre), coupled with individual site-fidelity between years (Prévoit-Julliard et al. 1998b). Heterogeneity in resighting probability typically produces an excess of individuals seen only once. This results in negatively biased survival estimates (Francis and Cooke 1993). This bias is greatly reduced by estimating separately survival during the time step following first resighting and survival over later time steps (Francis and Cooke 1993). This was indeed done in a previous analysis on survival of adult black-headed gulls in the study population (Prévoit-Julliard et al. 1998a): when a survival probability following first resighting was added and estimated to be equal to 0.59, the adult survival estimate reached 0.90. The influence of resighting heterogeneity in obtaining this survival pattern was demonstrated by simulations: the same survival estimations were obtained with a simulated data set that had 10% and 90% of individuals with resighting probabilities of 0.30 and 0.07 respectively (Prévoit-Julliard et al. 1998a).

Resighting heterogeneity is likely to affect similarly the estimated proportion of individuals breeding for the first time. Individuals with resighting probability lower than average are typically resighted for the first time later than expected. Since these individuals are also more likely than expected to be resighted only once, resighting heterogeneity will typically result in many encounter histories consisting of a single resighting event at a relatively old age. This may bias the proportion of new individuals at a given age (i.e. first-time breeders, denoted β). Preliminary analyses using simulated data sets with the same amount of resighting heterogeneity as in Prévoit-Julliard et al. (1998a) showed that this may indeed be the case. Fortunately, biases are almost cancelled by using a model similar to the one used for survival analysis (simulation analysis not reported in the paper). Therefore, we used this kind of modelling for the analysis of the real data set. We analysed the capture-recapture data using SURGE5.1 software (Reboulet et al. 1999). Model notation is summarised in Table 1.

Modelling design of analysis of recruitment in the main colony

As in all capture-recapture analyses, we had to model and to estimate two sets of parameters, the proportion of first-time breeders (β) and the resighting probabilities (p). Our aim was to compare the age-specific proportion of first-time breeders in the main colony of four categories of individuals, depending of their hatching date in the season.

First, we modelled resighting probabilities for each category by testing their time-dependence (denoted t), before comparing them between categories (denoted cat). We then started the analysis of the proportion of first-time breeders by testing a potential time-dependence for each category. Then, we modelled age-dependence (denoted age) of the proportion of first-time breeders for each category separately. We particularly tested whether, after a given age, all individuals have started to breed (i.e. there are no more new breeders after the age at full breeding, and $\beta=0$). After having determined this age at full breeding, we tried to model the progressive accession to reproduction before this age by a linear

decrease of the proportion of first-time breeders with age (denoted $age\ lin$).

The final step of the analysis was to compare the pattern of accession to reproduction of the four categories. We tested whether these patterns were the same (i.e. no group effect), similar but shifted with age for different categories (i.e. additive effect, symbolised by +), or different (i.e. interaction between age and categories, symbolised by *).

Analysis of recruitment in the small colonies

We investigated the effects of year, age and hatching date of individuals born at the main colony on the proportion, among adults resighted at the main or small colonies, of individuals resighted at the main colony. In this analysis, we pooled individuals in two groups: individuals born early in the season (i.e. categories 1 and 2; 290 individuals) and individuals born late in the season (categories 3 and 4; 65 individuals). We were not able to use capture-recapture methodology because of the small amount of data from the small colonies. However, we used general linear modelling with a binomial error and logit link function, using GLIM software (Crawley 1993). We used AIC to select the best model, and LRT to test hypotheses.

Results

Analysis of recruitment at the main colony using capture-recapture modelling

Modelling resighting probabilities

For each category separately, temporal variation of resighting probabilities was not significant [model (p_{t*cat}) vs. model (p_{cat}), $\chi^2_{60}=50.48$, $P=0.80$]. However, resighting probabilities of the four categories of individuals differed significantly [model (p_{cat}) vs. model (p), $\chi^2_3=11.78$, $P=0.008$; $\hat{p}_{cat1}=0.17$, 95% confidence interval (C.I.) 0.12–0.27; $\hat{p}_{cat2}=0.12$, 95% C.I. 0.09–0.17; $\hat{p}_{cat3}=0.22$, 95% C.I. 0.17–0.29; $\hat{p}_{cat4}=0.39$, 95% C.I. 0.29–0.50].

Modelling age-dependent proportion of first-time breeders

For each category separately, no significant temporal variation of the age-specific proportion of first-time breeders was detected [model ($\beta_{age*t*cat}$) vs. model ($\beta_{age*cat}$), $\chi^2_{618}=232.76$, $P=0.99$]; this lack of detectable temporal variation is likely to be due to the low sample sizes.

The results of the model selection process are shown in Table 2. According to the best model, individuals born early in the season (i.e. categories 1 and 2) were present for the first time at the main colony at ages 2 or 3 years ($\beta=0$ for age ≥ 4). Individuals from category 3 arrived more gradually, from age 2 to age 4 years ($\beta=0$ for age ≥ 5). Individuals from category 4 arrived the latest: none of them were resighted at the main colony before age 5 years ($\beta=1$ at ages 2, 3 and 4, $\beta=0$ for age ≥ 5). Recruitment patterns of the four categories are shown in Fig. 1.

Table 2 Model selection to estimate the minimum age at stabilisation of the proportion of first-time breeders at 0 for each group separately. The modelling started with the analysis of category 4, followed by categories 3, 2 and 1. Each model included a category-dependent value of p [i.e. models (β^{**}, p_{cat})]. Akaike information criterion (AIC) of the best models indicated in *bold*

Modelling β	Deviance	df	AIC
1. β age*cat	1305.36	129	1563.36
2. cat. 4 β from age 8=0	1305.36	121	1547.36
3. cat.4 β from age 6=0	1308.71	119	1546.71
4. cat. 4 β from age 5=0	1308.97	118	1544.97
5. cat. 4 β from age 4=0	1317.99	117	1551.99
Model selected for category 4: β from age 5=0			
6. cat. 3 β from age 7=0	1311.20	109	1529.20
7. cat. 3 β from age 6=0	1312.21	108	1528.21
8. cat. 3 β from age 5=0	1313.92	107	1527.92
9. cat. 3 β from age 4=0	1318.79	106	1530.79
Model selected for category 3: β from age 5=0			
10. cat 2 β from age 8=0	1316.45	99	1514.45
11. cat. 2 β from age 6=0	1318.86	97	1512.86
12. cat. 2 β from age 5=0	1318.86	96	1510.86
13. cat. 2 β from age 4=0	1318.86	95	1508.86
14. cat. 2 β from age 3=0	1322.03	94	1510.03
Model selected for category 2: β from age 4=0			
15. cat. 1 β from age 6=0	1321.11	85	1491.11
16. cat. 1 β from age 5=0	1321.85	84	1489.85
17. cat. 1 β from age 4=0	1324.27	83	1490.27
18. cat. 1 β from age 3=0	1330.96	82	1494.96
Model selected for category 1: β_2 from age 4=0 ^a			

^a In general, models with only a small difference in AIC are not significantly different. In this case, we selected the most parsimonious model (with the least number of parameters)

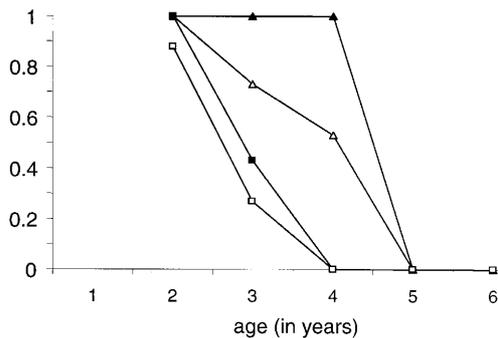


Fig. 1 Variation in the estimates of proportion of first-time breeders according to age in years: individuals of categories 1 (*open squares*), 2 (*filled squares*), 3 (*open triangles*) and 4 (*filled triangles*). The proportions of first-time breeders were estimated separately for each category

A linear effect of age was accepted for each category separately ($\beta_{age \cdot cat}$ vs. $\beta_{age \cdot cat}$, $\chi^2_4=2.65$, $P=0.62$).

An additive linear effect of age and category was then accepted ($\beta_{age \cdot cat}$ vs. $\beta_{age \cdot cat}$, $\chi^2_5=3.76$, $P=0.58$). However, age-specific proportions of first-time breeders were different for each category (β_{age} vs. $\beta_{age \cdot cat}$, $\chi^2_1=10.71$, $P=0.001$).

Table 3 Model selection for studying the difference in age-specific proportion of philopatric individuals between early-hatched and late-hatched individuals. Tested effects included age (2 years old, 3 years old, more than 4 years old), resighting year (1994, 1995, 1996, 1997), status (early- or late-hatched), and all possible interactions. The two best models are indicated in *bold*. Since the AIC did not differ much, we preferred the model with the lowest number of parameters and with more biological meaning

	Deviance	df	AIC
Full model	42.93	24	90.23
Year+age+status+age.status+age.year	44.54	18	80.54
+year.status			
Year+age+status+age.status+age.year	55.69	15	85.69
Year+age+status+age.status+status.year	61.03	12	85.03
Year+age+status+age.status	64.03	9	82.03
Year+age+status	74.05	7	88.05

Breeders on small colonies

Birds born at the main colony may have been resighted as adults either at the main colony (i.e. philopatric individuals) or at small colonies (i.e. dispersers). We modelled the proportion of philopatric birds with age. No age-dependence was found from age 4 onwards [(no age-dependence after age 4) vs. (no age-dependence after age 5), $\chi^2_1=0.74$, $P=0.39$], indicating that the age-specific relative importance of philopatric birds and dispersers was similar after age 4. However, the distribution of gulls resighted at the main versus small colonies differed for ages 2, 3 and ≥ 4 [(no age-dependence after age 3) vs. (no age-dependence after age 4), $\chi^2_1=9.48$, $P=0.002$].

We tested for the effects of resighting year (4 years from 1994 to 1997), age (3 classes), status (early-hatched vs. late-hatched, see Materials and methods) and all possible interactions between effects. The most parsimonious model based on comparisons of the AIC included additive effects of resighting year, status, and age, together with an interaction between status and age (Table 3). This means that, in a given year, the age dependence of the proportion of philopatric birds was different between early- and late-hatched individuals. In particular, at age 2 years, late-hatched individuals were present in higher proportions than early-hatched individuals in small colonies (Fig. 2).

Delayed reproduction as a strategy?

The recruitment pattern of philopatric individuals at the main colony differed according to the hatching date in the season. Individuals born earlier in the breeding season bred for the first time at a younger age than birds born later on in the same breeding season. This observed difference in age at first breeding could result from different breeding strategies, whereby later-hatched individuals would counterbalance delayed recruitment by increasing adult survival or reproductive success. We defined two breeding strategies: individuals using the first strategy were assumed to start to breed between ages 2

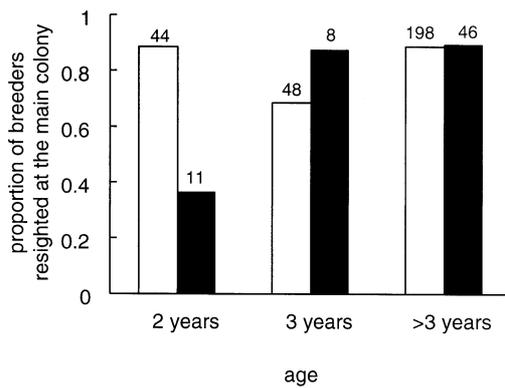


Fig. 2 Proportions of philopatric birds (i.e. breeding at the main colony) among all early-hatched (*open bars*) and late-hatched (*filled bars*) adults resighted in 1994–1997 at the main colony and at three small colonies (all years pooled). *Sample sizes* are indicated above the bars

and 3 years (65% at age 2 and 100% at age 3), and individuals using the second strategy were assumed to start to breed between ages 2 and 4 years (3% at age 2, 23% at age 3 and 100% at age 4). We compared the fitness of these two breeding strategies reflecting the recruitment patterns we found for the four categories of birds, using ULM software (Legendre and Clobert 1995). The proportions of breeders in each age class were computed from age-specific proportions of first-time breeders among individuals of categories 1 and 2 for the first strategy, and 3 and 4 for the second strategy. Assuming equal adult survival for the two strategies (i.e. 0.90, Prévot-Julliard et al. 1998a), a similar fitness would be obtained with delayed individuals producing 0.45 more young per breeding pair each year than individuals which have bred earlier. Assuming an equal breeding success for the two groups of birds (i.e. 1.2 young per breeding pair, Prévot-Julliard 1996), the survival of delayed individuals should be 95%, as compared to 90% for less delayed individuals.

Discussion

Among philopatric black-headed gulls which establish in the main colony of the Forez plain, age at recruitment was negatively correlated with hatching date: individuals hatched earlier in the season tended to recruit at a younger age than individuals born later on in the season. We found that the estimated age at first reproduction of the less abundant group (i.e. individuals from category 4) was older than that of the other ones. Because a large number of individuals is needed to estimate accurately the age at full breeding, small data sets should result in underestimation of the age at full breeding. This was not the case in our study, because we estimated that the least abundant group recruited the latest, which supports our result. Moreover, our method of modelling took into account the excess of encounter histories composed of a

single resighting event; we were thus able to eliminate potential prospectors or transients (i.e. individuals that remained only 1 year on the colony) from the analysis of age-specific proportion of first-time breeders. We thus studied the age of appearance in the colony of individuals that eventually established in the colony, and not of potential prospectors. Thus, we argue that there are differences in age at recruitment of individuals depending on their hatching date. This result is supported by the resightings of individuals aged 1 year at the colony: three individuals were resighted at this age. Two of them (categories 1 and 2 respectively) were never seen again. The last one, belonging to category 1, was re-observed two more times as a breeder (paired or nesting) within the same colony area each time. The only individual seen at 1 year old and subsequently breeding at the colony was therefore born early in the season.

Previous studies on the effect of hatching date on the probability of recruitment, have found that the return rate of young to their birth place for breeding was lower for late-hatched individuals than for early-hatched ones (Nisbet and Drury 1972; Perrins and Moss 1975; Daan et al. 1990; Spear and Nur 1994; Thompson et al. 1994; Harris et al. 1996; Verboven and Visser 1998). This difference in return rate could result either from lower survival of late-hatched individuals after fledging (Newton 1986; Spear and Nur 1994; but see Korpimäki and Lageström 1988), or from a higher probability of dispersing for late-hatched individuals (Miller and Smallwood 1997; Spear et al. 1998; but see Verboven and Visser 1998). Our study examines a step further in the process, that is, the age at which individuals are recruited. The influence of body size on the age at recruitment has been recently studied in some arctic-nesting geese, where body size is directly related to hatching date (e.g. black brant *Branta bernicla*: Sedinger et al. 1995; snow geese *Anser caerulescens*, Cooch et al. 1999). To our knowledge, our study is one of the few that demonstrates an effect of hatching date on age at first reproduction in a long-lived bird species.

Late-hatched individuals could compensate for delayed reproduction without breeding elsewhere by increasing reproduction from 1.2 to 1.65 young each year, or by increasing their survival from 0.90 to 0.95 per year (i.e. by decreasing the probability of mortality from 10% to 5%, see Results). These increases in reproductive output and adult survival seemed to us rather unlikely.

In some species, early-hatched individuals have been found to be dominant over late-hatched young after fledging (e.g. magpie *Pica pica*: Eden 1987; marsh tit *Parus palustris*: Nilsson 1990), especially in access to food resources (herring gull *Larus argentatus*: Nisbet and Drury 1972; western gull *Larus occidentalis*: Spear and Nur 1994). In the magpie, this dominance has been shown to persist until recruitment (Eden 1987). In other species, persistence of the social dominance of early-hatched individuals was not demonstrated (marsh tit: Nilsson and Smith 1988; pied flycatchers *Ficedula hypoleuca*: Potti and Montalvo 1991; western gull: Spear and Nur 1994).

Late-hatched individuals delayed first reproduction on their birth colony. However they may have bred in other colonies, where competition was less intense. This hypothesis was strongly supported by the observation of breeding individuals on small peripheral colonies: significantly more late-hatched than early-hatched individuals were resighted as adults on small colonies at age 2 years (Fig. 2, Table 3). This difference disappeared at older ages. We suspect that a large proportion of the late-hatched individuals breeding at age 2 years on small colonies will eventually settle in their natal colony when older. This could represent a "best-of-a-bad-job" strategy: late-hatched individuals, being constrained to delay recruitment at their birth colony, settle for few years in colonies where competition is less intense. They can thus gain experience and increase their competitive ability.

There is only 1 week difference on average between individuals of each category. Laying dates of early-hatched (categories 1 and 2) and late-hatched philopatric (categories 3 and 4) breeders were not found to be significantly different at this colony (A. Besnard and J.D. Lebreton, unpublished work). However, breeding failures during incubation occur regularly at the main colony (Prévot-Julliard 1996). Thus, most late-hatched individuals could be the offspring of replacement clutches. Whether breeding failures are randomly distributed among individuals or are due to parents of lower quality breeding in lower quality nest locations remains unknown. However, recent unpublished studies on sex determination of young black-headed gulls born at the main colony have detected a biased secondary sex ratio in relation to hatching date: there were proportionally more males than females in early broods whereas the reverse is true in late broods (A. Besnard and V. Grosbois, unpublished work). This result is consistent with what has been found in other species (e.g. kestrel, Dijkstra et al. 1990). This biased sex ratio could be related to the differences we found in reproductive strategies. Nonetheless, a difference of 1 or 2 weeks in hatching date seems to have consequences for the individual for several years.

Age at first reproduction and dispersal are thus closely linked in this black-headed gull population. Early-hatched individuals seem to breed in their natal colony as early as 2 years old. However, some late-hatched philopatric individuals seem to start breeding in smaller colonies where competition is likely to be less intense, rather than delaying recruitment. Thus, small colonies seem to represent, for some birds, a queuing opportunity before breeding in a good colony.

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