

# Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher

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## Summary

1. Public information, i.e. local reproductive performance of conspecifics, is expected to be a highly valuable cue for breeding habitat selection. However, the access to this cue may be spatially and temporally constrained. When public information is unavailable, individuals may use other integrative cues, such as the local density of breeders.

2. Departure decisions of collared flycatchers (*Ficedula albicollis*) were shown previously to be related to both public information and breeding density, in a long-term correlative study of a fragmented population. Here, we tested whether flycatchers also use public information (number and condition of fledglings produced locally) and breeding density to make individual settlement decisions in the following year.

3. Immigration rates were computed to measure the degree of attractiveness of patches to new breeders. We investigated the relative influence of public information and breeding density on immigration rates of yearlings and older adults separately. The access to public information for settlement decisions may indeed be more limited for yearlings.

4. Immigration rate in a patch increased with mean fledgling number in the previous year for older adults but not for yearlings. Yearling immigration rate was correlated positively to mean fledgling condition when patch breeding density in the previous year was low, but negatively when density was high.

5. Immigration rates of both yearlings and older adults increased with breeding density in the previous year. Breeding density explained a larger part of the variance in immigration rate than patch reproductive success.

6. The proportion of yearlings among breeders decreased with increasing patch reproductive success and breeding density in the previous year, suggesting that local competition was high in attractive patches.

7. Our results thus suggest that public information is also used for immigration decisions. However, decisions of yearlings are more complex than those of older adults, due to their more limited access to public information and the higher impact of intraspecific competition. Conversely, all individuals seemed to cue on breeding density in a similar way. Density is correlated to patch reproductive success, and may be a more easily accessible cue. We discuss the potential advantages of using conspecific density over conspecific reproductive performance for future immigration decisions.

*Key-words:* breeding habitat selection, dispersal, patch reproductive success, social attraction, spatial and temporal constraints in information gathering.

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## Introduction

For many species, factors affecting breeding habitat quality vary in time and space (Stephens 1989; Orians & Wittenberger 1991). Therefore, individuals have to rely on cues predicting local quality to make optimal breeding habitat selection decisions (Wiens 1976; Cody 1985). There is growing evidence that individuals are able to track local breeding patch quality (Cody 1985; Petit & Petit 1996), through the use of various cues (e.g. presence of parasites or predators: Marzluff 1988; Clobert *et al.* 2001; food availability: Brown & Brown 1996; or vegetation type: Clark & Shutler 1999).

The value of the information provided by different cues may, however, differ greatly (Giraldeau 1997; Clobert *et al.* 2001). In particular, using cues integrating the effects of many environmental factors on breeding success to select a breeding habitat should be a more parsimonious and powerful strategy than assessing every factor independently (Boulinier & Danchin 1997; Danchin & Wagner 1997). Among such integrative cues, individual reproductive success (Switzer 1997; Serrano, Tella & Forero 2001) and presence of conspecifics (i.e. social attraction: Kiester 1979; Stamps 1988; Reed & Dobson 1993; Muller 1998) have been shown to be used by individuals. Recent theoretical (Boulinier & Danchin 1997; Clobert *et al.* 2001; Doligez *et al.* 2003a) and empirical studies (Serrano *et al.* 2001; Blums *et al.* 2002; Doligez, Danchin & Clobert 2002 and references therein) also showed that 'public' information, i.e. information derived from the local reproductive performance of conspecifics (Valone & Giraldeau 1993; Clobert *et al.* 2001; Valone & Templeton 2002), is a highly valuable cue of local patch quality for breeding habitat choice in the following year(s), provided that the environment is sufficiently predictable. Public information may in particular be useful to individuals that cannot rely on their own reproductive success as an indicator of habitat quality (e.g. juveniles, non-breeders: Boulinier & Danchin 1997; Serrano *et al.* 2001).

Beyond the theoretical value of information, the use of information may, however, be constrained by spatial and temporal limitations in information gathering, i.e. prospecting behaviour (Orians & Wittenberger 1991; Reed *et al.* 1999; Matthysen, Adriaensen & Dhondt 2001; Giraldeau, Valone & Templeton 2002). Cues may be 'spatially unavailable' because of high costs of acquiring information on breeding habitat patches located far apart. In particular, individuals of species that do not usually prospect while breeding may gather public information only at the expense of their own breeding activities (Clobert *et al.* 2001). Only non-breeders may then afford to engage in intense prospecting (Cadiou, Monnat & Danchin 1994; Reed *et al.* 1999; Cam *et al.* 2002). Cues may also be 'temporally unavailable' because of limited time-windows during which they are reliably measurable (Boulinier *et al.* 1996; Reed *et al.* 1999). In particular, juveniles may not

be able to gather public information when it is available before the time of independence or departure from the natal site. The use of public information for breeding habitat selection might thus be restricted to categories of individuals such as non-breeders or early failed breeders, or to categories of species such as colonial species (Cadiou *et al.* 1994; Boulinier & Danchin 1997; Clobert *et al.* 2001).

Similarly, the use of public information might be restricted to one of the two dispersal decisions only, i.e. departure (emigration) or settlement (immigration). Different cues gathered at different spatial scales can be used for these two decisions (Clobert *et al.* 2001). Public information might be assessed more easily by individuals in their natal or current breeding patch than in other patches, and might thus be used especially for departure decisions (see Doligez *et al.* 2002). Conversely, breeders may rely on their own reproductive success to decide whether to depart from their current breeding patch (Switzer 1997); but they cannot have such personal information on the quality of other potential patches, hence they could use public information especially for settlement decisions (Danchin, Boulinier & Massot 1998). When public information is unavailable or costly to gather, individuals may use other integrative cues (see Templeton & Giraldeau 1995). However, when multiple information can be used, little is known about the relative influence of various cues on breeding habitat selection decisions in nature (but see Gundersen, Andreassen & Ims 2002; Massot *et al.* 2002), let alone the relative selective advantage of using a given type of information for breeding habitat selection in given conditions.

An experimental manipulation of patch reproductive success showed that juvenile and adult collared flycatchers (*Ficedula albicollis* Temm.) can use public information for both departure and settlement decisions (Doligez *et al.* 2002). However, such an experiment does not reveal to what extent individuals use public information cues for breeding habitat choice in non-manipulated situations, i.e. the relative influence of public information compared to other cues. Departure decisions were previously shown to be correlated to both public information and conspecific density in this population of flycatchers (Doligez *et al.* 1999). Here, using the same data set, we investigated whether individual settlement decisions in this population were also correlated to both public information and conspecific density, and the relative influence of these two pieces of information on settlement decisions. If flycatchers rely on public information and/or conspecific density to assess patch quality and choose where to settle in the following year, (i) recruitment of new breeders in a patch, i.e. immigration rate, should be positively related to patch reproductive success and/or patch breeding density in the previous year (Danchin *et al.* 1998), and (ii) patches where local success and/or density was high in the previous year should be very attractive, thus local competition for the access to nest

sites should be high (Doligez *et al.* 1999). We tested these predictions, and compared settlement decisions of yearlings and older adults. Yearlings may indeed not be able to use public information for settlement decisions, as this information should have been available mainly at a time when they could not gather it in the previous year, as juveniles, i.e. before or at fledgling (Boulinier *et al.* 1996).

## Materials and methods

### STUDY SITE AND SPECIES: FACTORS AFFECTING THE CAPTURE OF BREEDERS

The collared flycatcher is a short-lived, territorial and hole-nesting migratory passerine bird. The data were collected in a fragmented population breeding on the island of Gotland, Southern Baltic (57°10' N, 18°20' E), 1980–99. Nestboxes were distributed regularly and with a similar density in 20 discrete woodland patches. Each year, adult flycatchers breeding in nestboxes were trapped, identified (with individually numbered aluminium rings) and aged based on morphological characteristics (yearlings vs. older individuals). Laying date, clutch size and fledgling success were monitored throughout the season. All nestlings were ringed. For details on the breeding ecology of the collared flycatcher and the study area, see Gustafsson (1987), Gustafsson (1989), Pärt & Gustafsson (1989) and Pärt (1994).

Adult capture probability was linked to reproductive status and success. Breeding females were trapped during incubation, and most males when feeding nestlings. Thus, males were more likely to be missed than females due to early breeding failures. Breeding females were caught on average at 92.9% of nests with eggs (ranging from 85.0% to 99.7% between years), whereas breeding males were caught on average at 72.6% of nests (56.8% to 84.3%). When considering only successful nests (i.e. where at least one chick fledged), mean capture probability raised up to 98.0% for females and 89.1% for males, indicating that early breeding failure is a major reason for missing breeding adults. The collared flycatcher is a facultatively polygynous species (approximately 10–15% of males are polygynous). Males provide parental care mainly to the young of their primary female (Gustafsson 1989). As a consequence, they are sometimes very difficult to trap at their secondary nests (approximately 50% caught only). Polygyny is thus the second major reason for missing breeding males.

### IMMIGRATION STATUS OF BREEDERS AND DEFINITION OF IMMIGRATION RATE

A breeding adult was considered as immigrant in a patch when (i) it was unringed or, if ringed, (ii) it had been caught breeding in another patch on its last capture as a breeder (for individuals aged 2 years or more) or was ringed as a chick in another patch (for yearlings and older individuals that had not been caught as

breeders previously). Any other adult was considered as resident. Among caught immigrants, 68.2% of males (2046 of 2998) and 62.7% of females (2922 of 4663) were unringed (case i), i.e. their origin was unknown, reflecting frequent movements beyond the limits of the study area.

Because the total number of breeding sites (nestboxes) was known, immigration rate was computed as the proportion of nestboxes available to immigrants that were actually occupied by immigrants (the number of natural holes was low and was not expected to differ according to other patch characteristics). This estimate of immigration rate quantifies the relative attractiveness of different breeding patches to new breeders, by accounting for breeding patch occupancy. Indeed, the mere proportion of immigrants among caught breeders in a patch in a given year may not reflect their willingness to settle in this patch. Consider a population of 50 breeding males, 25 of which are immigrants. If the patch contains 50 breeding sites, i.e. the patch is saturated, our immigration rate is 100% because immigrants occupy all nestboxes available to them. If the patch contains 100 breeding sites, 75 immigrants could have settled, but only 25 did so, i.e. our immigration rate is 33%. In both cases, the proportion of immigrants is 50%, but the two patches did not have the same attractiveness to immigrants.

### NUMBER OF IMMIGRANTS AND NUMBER OF NESTBOXES AVAILABLE

The number of immigrants in each age and sex class was estimated among uncaught individuals by assuming that the proportions of both immigrants and yearlings are the same among caught and uncaught individuals. This in turn implies that capture probabilities do not differ between resident and immigrant breeding adults, nor between yearlings and older adults (see Appendix I for the test of this hypothesis and its implications).

The number of nestboxes available to immigrants was computed as the total number of boxes in the patch minus the number of boxes occupied by already settled breeders. Because birds arriving first at a nestbox have an advantage in a contest for that box, less boxes are available for late than early arriving birds (Pärt 1994). Yearlings come back from migration on average 1 week later than older adults (Gustafsson 1989; Pärt 1994). Thus, boxes occupied by older adults were considered unavailable to yearling immigrants. Conversely, there is no evidence that immigrant birds arrive later than resident birds, either in males or in females (Pärt & Gustafsson 1989; Pärt 1991, 1994). However, resident individuals have been shown to be competitively dominant over immigrants in different species (Eden 1987; Sandell & Smith 1991; Tobias 1997), and this was also suggested in the collared flycatcher (Pärt 1994). Thus, boxes occupied by residents were also considered unavailable to immigrants of the same age class (see Appendix I).

## EXPLANATORY VARIABLES

Both fledgling number and condition have been shown to covary with juvenile survival and local recruitment in the following year(s) (Gustafsson 1989; Lindén, Gustafsson & Pärt 1992), and may thus be used by individuals for breeding habitat selection. Therefore, two components of patch reproductive success in the previous year were tested in separate analyses: (i) mean number of fledglings per breeding pair, and (ii) mean body condition of fledglings, in the patch. Body condition was computed as the ratio of weight on tarsus length, both measured on day 13 (using the residuals of the linear regression of weight on tarsus length gave the same qualitative results). Nests in which clutch or brood size manipulations had been performed were included in the computation of components of patch reproductive success (Doligez *et al.* 1999). However, patches where reproductive success had been manipulated at the scale of the entire patch (Doligez *et al.* 2002) were excluded from the analyses. Patch reproductive success can be used for breeding patch selection in the following year only if it is temporally predictable (Danchin *et al.* 1998; Clobert *et al.* 2001; Doligez *et al.* 2003a). We tested this assumption by investigating the temporal autocorrelation of the two components of patch reproductive success between successive years.

The density of breeding pairs in the patch was computed as the proportion of nestboxes occupied by breeding flycatchers. Flycatchers lay only one clutch per year, thus the number of breeding pairs was estimated as the number of nests with eggs, i.e. active nests. The correlations between breeding density and components of patch reproductive success were investigated. Year (considered as a fixed factor – Doligez *et al.* 1999) and patch size, measured by the total number of nestboxes in the patch, are also likely to affect immigration rate, and were thus included as explanatory variables in the analyses of immigration rates.

## IMMIGRATION RATE DATA AND STATISTICAL ANALYSES

One immigration rate was computed for each age and sex class per patch and year, because (i) the use of patch reproductive success for settlement decisions is expected to depend on age in this species and (ii) males and females have already been suggested to use patch reproductive success differently in departure decisions (Doligez *et al.* 1999). Age and sex differences in dispersal are widespread in birds (Greenwood & Harvey 1982; Johnson & Gaines 1990), including the collared flycatcher (Pärt & Gustafsson 1989; Doligez *et al.* 1999). Immigration rates in the first year of monitoring of each patch were excluded, because in that case all breeders were by definition immigrants.

Autocorrelation coefficients (Moran's  $I$ ) and significance were obtained using the R software (Legendre & Vaudor 1991). Patches/years with less than 10 breeding

pairs were excluded from correlation and autocorrelation analyses to ensure sufficient precision. Immigration rates and proportions were analysed with multiple logistic regressions (SAS Institute 1990). Immigration rates in a given patch in different years were not independent. This generated limited overdispersion (dispersion parameter usually between 1.5 and 2.5);  $\chi^2$  tests were therefore adjusted for this parameter to  $F$ -tests (SAS Institute 1990). Logistic regression models were compared using their Akaike Information Criteria (AIC) values: the model with the lowest AIC best fitted the data when AIC values differed by more than two (Burnham, White & Anderson 1995). Starting models contained the main effects plus all possible pairwise interactions; the significance of differences between yearlings and older adults was also tested using three-way interactions including age as a factor. Sample sizes vary between analyses because data on mean fledgling body condition was missing for some patches in some years.

## Results

## PREDICTABILITY OF PATCH REPRODUCTIVE SUCCESS AND RELATION WITH BREEDING DENSITY

Mean number of fledglings per breeding attempt ( $N = 151$ , Moran's  $I = 0.281$ ,  $P < 0.001$ ) and mean fledgling body condition ( $N = 143$ , Moran's  $I = 0.337$ ,  $P < 0.001$ ) in a patch were both autocorrelated positively between successive years. The autocorrelation was significant for time lags of 1 year only (for time lags of 2 years: mean fledgling number:  $N = 124$ , Moran's  $I = 0.030$ ,  $P = 0.287$ ; mean fledgling body condition:  $N = 114$ , Moran's  $I = 0.086$ ,  $P = 0.083$ ). The two components of reproductive success were weakly but significantly correlated positively both at the patch scale ( $N = 175$ , Pearson's correlation coefficient  $r = 0.264$ ,  $P < 0.001$ ) and at the nest scale ( $N = 2067$ ,  $r = 0.205$ ,  $P < 0.001$  – excluding all nests where the number of young had been manipulated).

Breeding density in a patch in year  $t$  was related weakly but positively to mean fledgling number in the same year ( $N = 215$ ,  $F_{1,213} = 4.52$ ,  $P = 0.035$  –  $R^2 = 2.1\%$ ), but also in the following year  $t + 1$  ( $N = 196$ ,  $F_{1,193} = 8.03$ ,  $P = 0.005$ , accounting for mean fledgling number in year  $t$  – model  $R^2 = 13.9\%$ ). Breeding density was also related positively to mean fledgling condition in the same year ( $N = 174$ ,  $F_{1,172} = 4.50$ ,  $P = 0.035$  –  $R^2 = 2.5\%$ ), but not in the following year  $t + 1$  ( $N = 143$ ,  $F_{1,140} = 0.44$ ,  $P = 0.506$ , accounting for mean fledgling condition in year  $t$ ). The two components of patch reproductive success in year  $t$  were also related positively to breeding density in the following year  $t + 1$ , even when accounting for breeding density in year  $t$  (mean fledgling number:  $N = 197$ ,  $F_{1,194} = 14.11$ ,  $P < 0.001$  – model  $R^2 = 0.391$ ; mean fledgling condition:  $N = 164$ ,  $F_{1,161} = 10.61$ ,  $P = 0.001$  – model  $R^2 = 0.308$ ).

**Table 1.** Effects of year, local density of breeding pairs in year  $t$ , number of nestboxes in year  $t + 1$ , sex, and patch reproductive success in year  $t$ , on immigration rates in year  $t + 1$ . Patch success was measured by (a) the mean number of fledglings per breeding attempt, or (b) the mean body condition of fledglings, in the patch. Non-significant main effects are shown in italics; they were excluded in the final model. Immigration rate decreased with increasing number of nestboxes for both sex and age classes: partial regression coefficient  $\pm 1$  SE: yearlings:  $(-1.5 \pm 0.6) 10^{-3}$ ; older adults:  $(-1.7 \pm 0.6) 10^{-3}$  (model with mean fledgling number – interaction number of nestboxes  $\times$  age non significant:  $F_{2,841} = 1.17$ ,  $P = 0.310$ ). Immigration rate of older females was higher than that of older males: relative coefficient for females compared to males:  $0.115 \pm 0.055$  (model with mean fledgling number)

| Age class    | Source   | (a) Mean number of fledglings     |          | (b) Mean fledgling body condition |          |
|--------------|--|-----------------------------------|----------|-----------------------------------|----------|
|              |  | <i>F</i> -value                   | <i>P</i> | <i>F</i> -value                   | <i>P</i> |
| Yearlings    | Year   | <i>F</i> <sub>17,409</sub> = 4.80 | < 0.001  | <i>F</i> <sub>16,325</sub> = 3.03 | < 0.001  |
|              | Density ( $t$ )                                | <i>F</i> <sub>1,409</sub> = 55.51 | < 0.001  | <i>F</i> <sub>1,325</sub> = 9.66  | 0.002    |
|              | Year $\times$ density ( $t$ )                  | <i>F</i> <sub>17,409</sub> = 4.21 | < 0.001  | <i>F</i> <sub>16,325</sub> = 3.19 | < 0.001  |
|              | No. boxes ( $t + 1$ )                          | <i>F</i> <sub>1,409</sub> = 6.46  | 0.011    | <i>F</i> <sub>1,325</sub> = 10.18 | 0.002    |
|              | Sex  | <i>F</i> <sub>1,408</sub> = 2.60  | 0.108    | <i>F</i> <sub>1,324</sub> = 2.48  | 0.117    |
|              | Patch success ( $t$ )                          | <i>F</i> <sub>1,404</sub> = 0.01  | 0.931    | <i>F</i> <sub>1,325</sub> = 9.69  | 0.002    |
|              | Patch success ( $t$ ) $\times$ density ( $t$ ) | <i>F</i> <sub>1,403</sub> = 2.03  | 0.156    | <i>F</i> <sub>1,325</sub> = 9.16  | 0.003    |
| Older adults | Year   | <i>F</i> <sub>17,403</sub> = 3.53 | < 0.001  | <i>F</i> <sub>17,408</sub> = 3.63 | < 0.001  |
|              | Density ( $t$ )                                | <i>F</i> <sub>1,403</sub> = 55.83 | < 0.001  | <i>F</i> <sub>1,408</sub> = 59.55 | < 0.001  |
|              | Year $\times$ density( $t$ )                   | <i>F</i> <sub>17,403</sub> = 2.85 | < 0.001  | <i>F</i> <sub>17,408</sub> = 2.91 | < 0.001  |
|              | No. boxes ( $t + 1$ )                          | <i>F</i> <sub>1,403</sub> = 8.26  | 0.004    | <i>F</i> <sub>1,408</sub> = 10.28 | 0.002    |
|              | Sex  | <i>F</i> <sub>1,403</sub> = 4.31  | 0.039    | <i>F</i> <sub>1,408</sub> = 4.49  | 0.035    |
|              | Patch success ( $t$ )                          | <i>F</i> <sub>1,403</sub> = 5.16  | 0.024    | <i>F</i> <sub>1,325</sub> = 2.84  | 0.093    |
|              | Patch success ( $t$ ) $\times$ density ( $t$ ) | <i>F</i> <sub>1,402</sub> = 0.07  | 0.794    | <i>F</i> <sub>1,324</sub> = 0.71  | 0.400    |

#### PATCH REPRODUCTIVE SUCCESS AND IMMIGRATION RATE

Immigration rate of older males and females in a patch in year  $t + 1$  increased with patch reproductive success in the previous year  $t$ , measured by the mean number of fledglings per breeding pair (Table 1, Fig. 1a). It also increased with increasing mean body condition of fledglings, but the relationship was only marginally significant (Table 1; partial regression coefficient  $\pm 1$  SE:  $2.38 \pm 1.42$ ). The interactions between components of patch reproductive success and breeding density in year  $t$  were not significant for older adults (Table 1).

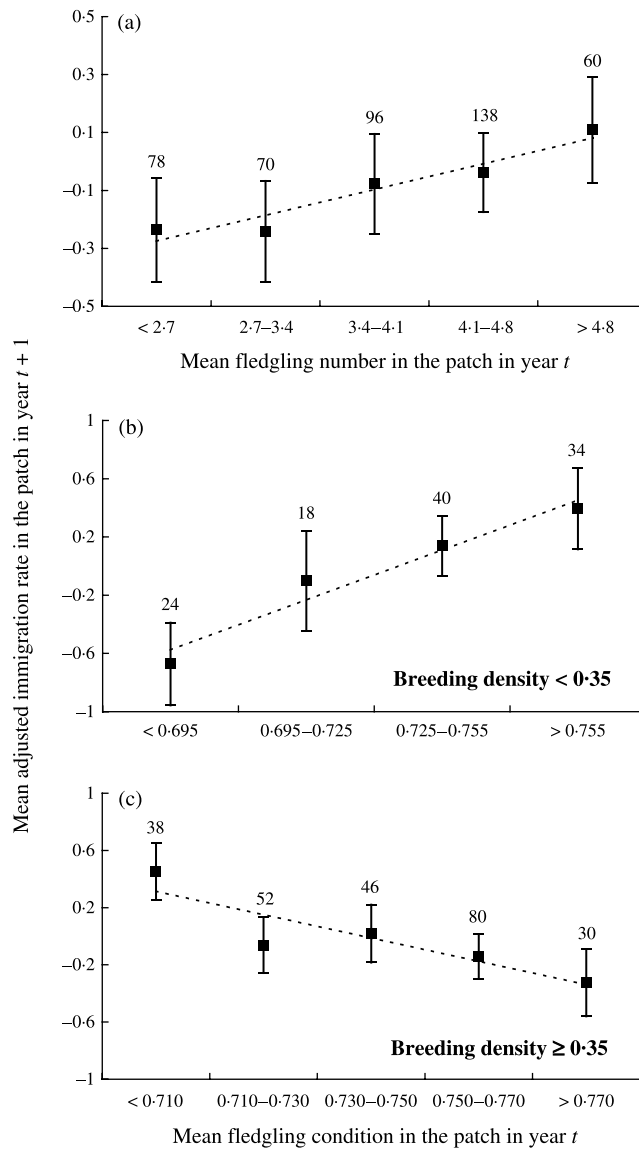
Conversely, the relation between immigration rate of male and female yearlings in year  $t + 1$  and mean fledgling condition in the patch in year  $t$  depended on patch breeding density in year  $t$  (significant interaction between mean fledgling condition and breeding density: Table 1; the three-way interaction mean condition  $\times$  breeding density  $\times$  age was significant when considering all individuals together:  $N = 724$ ,  $F_{1,666} = 4.71$ ,  $P = 0.030$ ). Yearling immigration rate increased with increasing mean fledgling condition when breeding density was low in the previous year (density  $< 0.35$ :  $N = 116$ ,  $F_{1,99} = 9.52$ ,  $P = 0.003$ ; Fig. 1b), while the relationship was reversed when breeding density was high (density  $\geq 0.35$ :  $N = 246$ ,  $F_{1,226} = 11.33$ ,  $P < 0.001$ ; Fig. 1c). However, yearling immigration rate was not related to mean fledgling number in the previous year (Table 1); the relationship between immigration rate and mean fledgling number differed significantly between age classes (interaction mean fledgling number  $\times$  age when considering yearlings and older adults together:  $N = 884$ ,  $F_{1,843} = 6.12$ ,  $P = 0.014$ ). The interaction between mean

fledgling number and breeding density was not significant for yearlings (Table 1).

#### BREEDING DENSITY AND IMMIGRATION RATE

Immigration rate in a patch was also related to the density of breeding pairs in the patch in the previous year (Table 1): for both sexes and both age classes, immigration rate increased with increasing breeding density in the previous year (Fig. 2). The relationship between immigration rate and breeding density varied between years (Table 1), but was overall positive and significant when removing the interaction with year ( $N = 884$ ,  $F_{1,860} = 119.88$ ,  $P < 0.001$ ), and did not depend on age (interaction breeding density  $\times$  age:  $F_{1,859} = 0.15$ ,  $P = 0.696$ ) or sex (interaction breeding density  $\times$  sex:  $F_{1,859} = 0.66$ ,  $P = 0.418$ ).

Breeding density explained a larger part of the variance in immigration rate than patch reproductive success. For older adults, the AIC value of the model increased by 11.7 when excluding mean fledgling number, while it increased by 95.0 when excluding the interaction density  $\times$  year, and by a further 209.0 when excluding breeding density. Similarly, the AIC value increased by 7.1 when excluding mean fledgling condition, while it increased by 69.1 when excluding the interaction density  $\times$  year, and by a further 97.3 when excluding breeding density. The same qualitative differences in the increase of AIC values were observed for yearlings (smaller increase when excluding mean fledgling condition from the model than when excluding density). Thus, in all cases, excluding density from the model resulted in a much lower fit to the data than excluding the components of patch reproductive success.



**Fig. 1.** Relationship between immigration rate in a patch and patch reproductive success in the previous year, measured by (a) mean fledgling number for older adults, and (b, c) mean fledgling body condition for yearlings. (a) Partial regression coefficient (PRC)  $\pm$  1 SE:  $0.088 \pm 0.039$  (the relationship was similar, but only marginally significant, with mean body condition of fledglings: PRC  $\pm$  1 SE:  $2.38 \pm 1.42$ ). (b, c) The relationship between yearling immigration rate and mean fledgling condition depended on breeding density: (b) breeding density  $< 0.35$ : PRC  $\pm$  1 SE:  $7.03 \pm 2.31$ ; (c) breeding density  $\geq 0.35$ : PRC  $\pm$  1 SE:  $-6.85 \pm 2.05$ . The y-axis represents the mean residuals ( $\pm$  1 SE) of the logistic regression model with all the significant effects except patch reproductive success (see Table 1). These relationships did not differ between sexes (interactions with sex not significant).

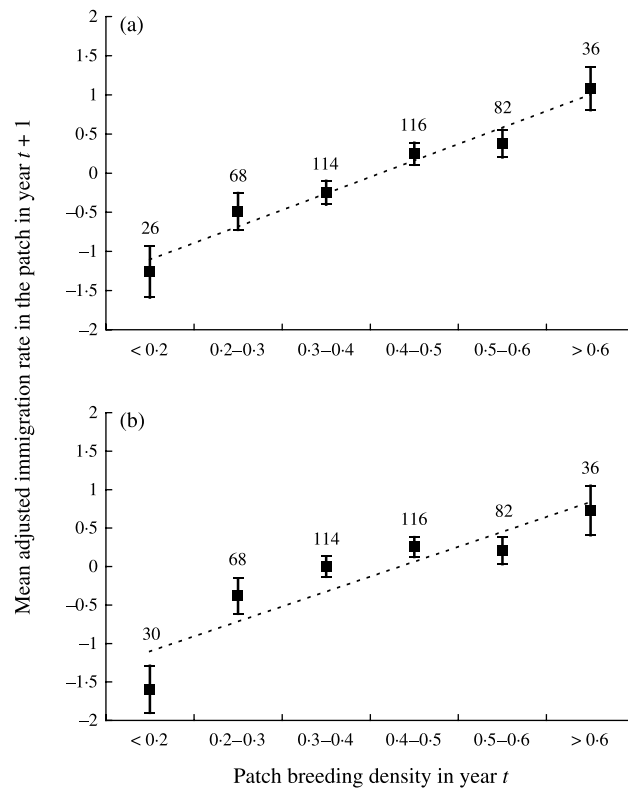
**PATCH REPRODUCTIVE SUCCESS, BREEDING DENSITY AND LOCAL COMPETITION**

The proportion of yearlings among caught breeders of both sexes decreased with increasing patch reproductive success in the previous year, measured by mean fledgling number ( $N = 441$ ,  $F_{1,419} = 6.46$ ,  $P = 0.011$ ; Fig. 3a), and increasing density of breeding pairs in the previous year ( $F_{1,419} = 13.19$ ,  $P < 0.001$ ; Fig. 3b; no significant interaction with sex). These results suggest that local competition for breeding sites was high in the year following high patch reproductive success and breeding density, although the proportion of yearlings was not related to mean fledgling body condition ( $N = 361$ ,  $F_{1,340} = 0.16$ ,  $P = 0.687$ ). Such a high level of competi-

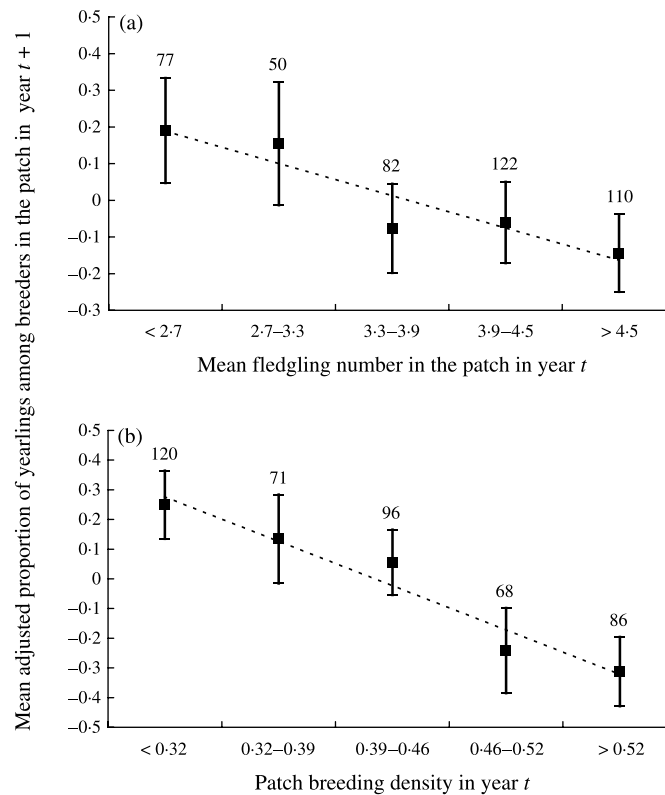
tion is also supported by (i) the high average nestbox occupation rate (65–70%; Fig. 4) and (ii) the increase in breeding density with increasing patch reproductive success and density in the previous year (see above).

**Discussion**

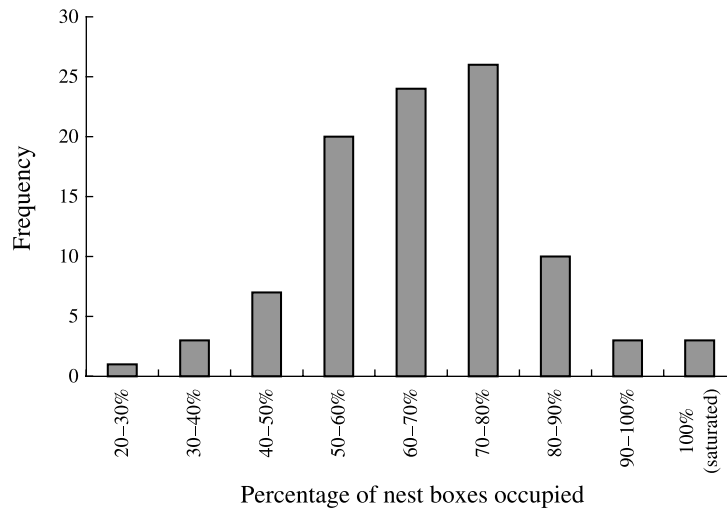
Understanding complex individual dispersal decisions has long been identified as a key issue for the study of many evolutionary processes, such as metapopulation dynamics and local adaptation (e.g. Lidicker 1975; Endler 1977) and, more recently, for the implementation of conservation and management strategies (e.g. Curio 1996; Sutherland 1998). In this perspective, information used for both departure (emigration)



**Fig. 2.** Relationship between immigration rate in a patch and patch density of breeding pairs in the previous year, for (a) older adults and (b) yearlings. The y-axis represents the mean residuals ( $\pm 1$  SE) of the logistic regression model with all the significant effects except breeding density (see Table 1). Partial regression coefficients  $\pm 1$  SE: (a)  $2.25 \pm 0.27$ ; (b)  $2.06 \pm 0.27$  (interactions sex  $\times$  breeding density not significant).



**Fig. 3.** Relationship between the proportion of yearlings among breeders in a patch and (a) mean fledgling number in the patch, and (b) patch breeding density, in the previous year. The y-axis represents the mean residuals ( $\pm 1$  SE) of the logistic regression model with year, number of nestboxes, sex, and (a) breeding density or (b) mean fledgling number. Partial regression coefficients  $\pm 1$  SE: (a)  $-0.088 \pm 0.035$ ; (b)  $-0.940 \pm 0.259$ .



**Fig. 4.** Frequency distribution of occupation rate of the breeding patches during the course of the study. Occupation rate of a patch in a given year was defined as the percentage of nestboxes in that patch occupied by either flycatchers or tits (great tits *Parus major* L. and blue tits *P. caeruleus* L.), with which flycatchers compete for the access to nestboxes (Gustafsson 1987).  $N = 97$  (data on tit presence was not recorded for all the 20 patches over all years).

and settlement (immigration) decisions have received considerably increased interest (e.g. Reed *et al.* 1999; Clobert *et al.* 2001). Departure and settlement decisions are nevertheless rarely considered as independent processes (Clobert *et al.* 2001), although individuals may base both decisions upon different cues because of spatial and temporal limitations in information availability. Conspecific cues (local reproductive success and breeding density) were shown previously to be related to departure decisions in the collared flycatcher (Doligez *et al.* 1999, 2002). Here, our results suggest that different conspecific cues may be used by different individuals for settlement decisions depending on competition pressure and information availability. Recruitment of older adults in a patch was linked positively to both patch conspecific reproductive success and breeding density in the previous year, suggesting that their settlement decisions are based partly on these two conspecific cues. Immigration decisions by yearlings are more complex, because some information may be unavailable to them and because more processes are involved in natal dispersal, in particular intraspecific competition (Clobert *et al.* 2001). Yearling immigration rate was related positively to local breeding density in the previous year; it was also related positively to mean fledgling condition when breeding density was low, but negatively when density was high. Yearlings thus responded differently to potential competition with older adults and other yearlings. In all cases, breeding density explained a larger part of the variation in settlement decisions than patch reproductive success.

success suggests that public information is also used by older adults for settlement decisions in the collared flycatcher. This relationship confirms the results of an experimental study (Doligez *et al.* 2002) in a non-manipulated situation. As for many migratory species, the strong time constraints on mating and breeding (Gustafsson 1989; Pärt 1994; Wiggins, Pärt & Gustafsson 1994; see Siikamäki 1998) are likely to favour the use of patch quality cues gathered before leaving to the wintering grounds for settlement decisions in the following year (see Lawn 1994), as soon as the environment is temporally predictable (Boulinier & Danchin 1997; Clobert *et al.* 2001; Doligez *et al.* 2003a). The use of public information for settlement decisions was described previously mainly in colonial bird species (Danchin *et al.* 1998; Brown, Brown & Danchin 2000; Frederiksen & Bregnballe 2001; but see Zicus & Hennes 1989). Our results suggest that the value of this information may also be high in a territorial species, where the low 'spatial availability' of public information is reflected by the high proportion of non-breeders among prospecting birds (Doligez, Pärt & Danchin 2003b), and the restricted prospecting activity of breeders (see Slagsvold & Lifjeld 1990; Ottosson, Backman & Smith 2001).

The positive relationship between immigration rate of older adults and breeding density of conspecifics in the previous year suggests that density is also used by older adults for settlement decisions. As a consequence, settlement of older adults, like departure (Doligez *et al.* 1999), appears to be multideterministic in this species (Clobert *et al.* 2001). Breeding density did not affect immigration rates following the experimental manipulation of public information (Doligez *et al.* 2002). However, the range of breeding density was much narrower during the few years of the experiment ( $N = 32$ , mean breeding density  $\pm 1$  SE:  $0.37 \pm 0.01$ , range:

#### MULTIDETERMINISM OF SETTLEMENT DECISIONS FOR OLDER ADULTS

The positive relationship between immigration rate of older adults and components of patch reproductive

0.220–0.545) than during the course of the long-term study ( $N = 258$ , mean breeding density  $\pm 1$  SE:  $0.39 \pm 0.01$ , range: 0.043–0.875).

Breeding density explained a larger part of the variation in immigration rate of older adults than public information. Traditionally, a preference for high density patches is viewed as support for social (or conspecific) attraction (Smith & Peacock 1990; Reed & Dobson 1993). However, a breeding habitat selection based on the mere presence of conspecifics is theoretically unlikely to be evolutionary stable (see Doligez *et al.* 2003a for a discussion). Because breeding density is related positively to patch reproductive success in the following year, breeding density could also be used to assess expected breeding success. Despite the low power of breeding density in predicting next year's patch reproductive success, density is likely to be easier and less costly to gather than public information (e.g. due to its wider temporal availability). This suggests that the trade-off between the predictive value of a cue and the costs of gathering this cue will determine whether it will be used for assessing habitat quality (Templeton & Giraldeau 1995; Giraldeau *et al.* 2002). Finally, breeding density may also reveal local quality in terms of potential mate availability. Patch breeding density is related strongly to its value in the following year, and may therefore predict expected mating success. Mating success may be a component of breeding success that is more important than number and condition of fledglings. This is supported by the high proportion of non-breeding individuals (Gustafsson 1989 and unpublished results), which may partly reflect high constraints on the access to mates, especially for males in this polygynous species (Gustafsson 1989; Pärt 1994). None of these explanations are mutually exclusive.

#### SETTLEMENT IN YEARLINGS: INFORMATION AVAILABILITY AND INTRASPECIFIC COMPETITION

Contrary to immigration rate of older adults, yearling immigration rate was not related to mean fledgling number in the patch in the previous year, suggesting that yearlings did not use this cue for settlement decisions. This information may actually be 'temporally unavailable' to yearlings due to the high breeding synchrony in this species. Juveniles should indeed gather information on mean fledgling number in patches other than their natal patch at the time of fledgling. Alternatively, yearlings may have access to this information, but may use it differently than older adults. The high attractiveness of patches following high reproductive success (reflected by low rates of emigration – Doligez *et al.* 1999 – and high rates of immigration of older adults) leads to high local intraspecific competition for mates and breeding sites. Such increased competition is revealed here by the low proportion of yearlings among immigrants and high occupation rates. Therefore, individuals of lower competitive ability

might avoid or be excluded from patches following high patch reproductive success (Doligez *et al.* 1999). For the subordinate yearling breeders, high patch reproductive success may reveal high local competition level, and thus reduced chances of breeding. Public information may be gathered by juveniles while prospecting patches during the post-breeding season and assessing local post-breeding densities, which integrate both breeding density of adults and fledgling success (i.e. juvenile density). In particular, juveniles in poor condition suffer from high mortality during the first weeks following fledgling (see Naef-Daenzer, Widmer & Nuber 2001).

This interpretation is supported by the complex relationship between yearling immigration rate and mean fledgling condition in the patch in the previous year. When breeding density was high in the previous year, yearlings might expect high levels of local competition with older adults. In that case, the higher the mean fledgling condition, the higher the post-breeding density and the higher the expected level of competition with philopatric yearlings. Because familiarity gives a mating advantage to yearlings (Pärt 1994), immigrant yearlings may avoid such patches or be unable to settle there due to the competition pressure. Conversely, when breeding density was low, low levels of competition with older adults are expected. In that case, high mean fledgling body condition will lead to intermediate levels of post-breeding density, thus less intensive expected intraspecific competition, i.e. higher patch quality. Finally, a low post-breeding density (i.e. low breeding density and low fledgling condition) reveals a low-quality patch that should be avoided by all individuals in the following year. The post-breeding density optimum to cue on for future immigration decisions should thus differ for yearlings and older adults, reflecting their different competitive ability, which is supported by our results. Older adults should choose patches with a high post-breeding density, which is likely to be a good integrative indicator of future success. Conversely, subordinate yearlings have to trade 'intrinsic' patch quality with the expected level of competition with both adults and other yearlings. Thus they should choose patches with lower levels of post-breeding densities, i.e. intraspecific competition.

Yearling immigration rate was found to increase following an experimental increase in the mean number of fledglings reared locally (Doligez *et al.* 2002). This difference with our present results is not explained by a different range of mean fledgling number or condition in the two data sets. This may suggest that some information not normally accessible may have been made available to juveniles by the experimental manipulation itself, for instance through the sharp and sudden local increase or decrease in number of fledglings. Alternatively, yearlings may not rely on the absolute value of patch reproductive success, but on its rank relative to the distribution of patch success in any given year, which was not accounted for here. In the experiment,

the main factor determining the level of competition, i.e. adult density, was not directly changed since only juvenile density was manipulated.

When determining which cues individuals are likely to use for breeding patch selection, (i) the theoretical value of the information conveyed by cues, (ii) their availability to prospecting individuals and (iii) the costs of gathering these cues have to be taken into account. Because the last two are likely to depend on information gathering processes, more work is required to characterize such behaviour in future studies, and include them into models of habitat selection. The selective pressures shaping the use of given cues will depend strongly on the species' breeding biology and life cycle. For example, (i) juveniles of less synchronous species, or immature individuals of long-lived species, may have higher access to public information; (ii) yearlings of non-territorial species or species using resources less defensible than nestboxes may experience lower levels of intraspecific competition; and (iii) colonial species may experience lower costs of gathering public information (Clobert *et al.* 2001). The issue of the constraints imposed by the breeding biology and life cycle on the type of information available and the costs of information gathering deserves more attention (Doligez *et al.* 2003a). The use of public information in breeding habitat selection has been shown experimentally (Doligez *et al.* 2002). Our results show that it is, however, not necessarily the main cue used, and that other cues, here breeding density, may integrate public information and level of competition for settlement, which are two crucial factors for future reproductive success. Such other cues may reveal local quality indirectly, and may be preferred because of their easier access and/or their higher ability to predict expected individual success.

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## Appendix I

### TESTS AND DISCUSSION OF THE HYPOTHESES UNDERLYING THE COMPUTATION OF IMMIGRATION RATES

#### *Differences in capture probability between individuals of different age and dispersal status*

The assumption of equal capture probability between breeding individuals of different age and dispersal status was tested by comparing (i) their probability of breeding failure (i.e. no chick fledged) and (ii) their probability of polygyny (for males).

*Probability of breeding failure.* The probability of breeding failure did not differ between immigrant and resident males ( $N = 5466$ ,  $\chi^2 = 0.75$ ,  $P = 0.388$ ), but yearling males were more likely to fail than older males ( $\chi^2 = 11.51$ ,  $P < 0.001$ ). Moreover, yearling and immigrant females were more likely to fail than older and resident females, respectively ( $N = 5939$ ; age:  $\chi^2 = 9.28$ ,  $P = 0.023$ ; dispersal status:  $\chi^2 = 11.92$ ,  $P < 0.001$ ).

Thus, our estimates of the number of immigrants among missed individuals in each age class are likely to be biased in both males and females. However, the number of uncaught breeding females was very low, so that a bias in the number of immigrants among uncaught females should not affect the results to a large extent. Conversely, the number of uncaught males was much higher. Older males were more likely to be caught than yearling males because of their higher breeding success. This leads to an overestimation of the proportion of older males, thus to (i) an overestimation of the number of both immigrant and resident older males, and (ii) an underestimation of the nestboxes considered available to older males. Therefore, the immigration rate of older males was overestimated. Such a bias was not random with respect to patch reproductive success: the higher the patch reproductive success, the lower the proportion of failed breeding attempts (Pearson correlation coefficient with (i) mean number of fledglings:  $-0.921$ ,  $N = 253$ ,  $P < 0.001$ , and (ii) mean fledgling body condition:  $-0.176$ ,  $N = 206$ ,  $P = 0.011$ ). Hence, immigration rate of older males was more likely to be overestimated when patch reproductive success was low in the same year, and thus when patch success was low in the previous year (as patch reproductive success is autocorrelated temporally). This bias is conservative with respect to the hypothesis of the use of public information for settlement decisions. Conversely, immigration rate of yearling males may either be underestimated or overestimated, depending on the proportion of immigrants among yearlings. The number of boxes available to immigrants was indeed both underestimated because of older males, and overestimated because of resident yearlings. In the worst case, immigration rate of yearling males could be overestimated when patch repro-

ductive success was high in the same year, thus when patch success was high in the previous year. In other words, in the worst case, the bias was non-conservative for yearling males.

To summarize, immigration rates were biased with respect to patch reproductive success. No large bias is expected for females, a conservative bias is expected for old males and a non-conservative bias may be expected for yearling males.

*Probability of being polygynous (males).* Most secondary nests of polygynous males are in the same plot as their primary nests. Therefore, polygynous males are unlikely to be misclassified as immigrants or residents, even when missed at their secondary nests. However, the number of immigrants estimated among uncaught breeders may be affected by the lower capture rate of polygynous males at their secondary nests. The probability of being polygynous did not differ between immigrant and resident males ( $N = 5498$ ,  $\chi^2 = 2.58$ ,  $P = 0.108$ ), but yearling males were less likely to be polygynous than older males ( $\chi^2 = 72.57$ ,  $P < 0.001$ ). However, the number of males missed because of polygyny may be estimated to 5%, compared to the 25% missed because of breeding failure. Moreover, the probability of being polygynous did not differ among patches according to patch reproductive success ( $N = 278$ ,  $\chi^2 = 0.001$ ,  $P = 0.975$ ). Thus, differences in capture rate due to polygyny should not affect the results.

#### *Accounting for heterogeneities in individual capture rate*

The heterogeneities observed in capture rates of individuals of different age and dispersal status could be accounted for by using the recently developed time-reversed capture–recapture modelling (Lebreton *et al.* 1992; Clobert 1995; Pradel 1996). However, these models would give the individual probability of being an immigrant according to local characteristics (here, patch reproductive success and breeding density in the previous year). Such an individual probability would thus relate to the mere proportion of immigrants in the population, and would not be an estimate of patch attractiveness, as measured here by the rate of occupancy of nestboxes available to immigrants.

#### *Assignment of dispersal status*

Our calculation of immigration rates assumes that individual dispersal status was assigned correctly. However, older adults may be misclassified as immigrants or residents if they were breeding but not caught in the previous year (yearlings cannot be misclassified). Again, these misclassification problems should affect mainly males, because female capture probability was very high. Misclassification of residents as immigrants is more likely to occur following low patch reproductive success and is thus conservative. Misclassification of

immigrants as residents can occur only following two successive dispersal events, and should thus remain anecdotal, because breeding dispersal probability is low in males, even after a breeding failure (Pärt & Gustafsson 1989; Doligez *et al.* 1999).

#### *Estimation of the number of immigrants among uncaught individuals*

The influence of potential biases linked to the estimation of the number of immigrants among uncaught individuals was assessed by computing an immigration rate without accounting for uncaught individuals. The number of immigrants and residents in each age and sex class were assimilated to the number of caught individuals classified as immigrants and residents in this class, excluding uncaught individuals. The number of nestboxes where breeders of the sex class concerned had not been caught was subtracted from the number of nestboxes available to immigrants. The results obtained for this 'non-estimated' immigration rate were similar to those obtained previously. The 'non-estimated' immigration rate increased with increasing mean fledgling number for older adults ( $N = 441$ ,  $F_{1,402} = 6.77$ ,  $P = 0.010$ , partial regression coefficient:  $0.104 \pm 0.040$ ), but not for yearlings ( $N = 441$ ,  $F_{1,402} = 0.03$ ,  $P = 0.858$ : interaction mean fledgling number  $\times$  age:  $N = 882$ ,  $F_{1,841} = 3.73$ ,  $P = 0.054$ ). The effect of mean fledgling condition on yearling 'non-estimated' immigration rate still depended on breeding density in the previous year (interaction mean fledgling condition  $\times$  breeding density:  $F_{1,323} = 9.48$ ,  $P = 0.002$ ). 'Non-estimated' immigration rate also increased with increasing breeding density in the previous year, when the significant interaction density  $\times$  year was removed ( $F_{1,858} = 129.76$ ,  $P < 0.001$ ; partial regression coefficient:  $2.30 \pm 0.20$ ; no significant interaction with age:  $F_{1,840} = 0.86$ ,  $P = 0.353$ ).

#### *Advantage of residents over immigrants for the access to nestboxes*

The influence of the advantage of residents over immigrants for the access to nestboxes was assessed by computing an immigration rate without resident advantage. Half the nestboxes occupied by residents of the same age class were considered available to immigrants at the time of settlement. The results obtained for this immigration rate with no resident advantage were similar to those obtained previously. Immigration

rate with no resident advantage increased with increasing mean fledgling number in older adults ( $N = 442$ ,  $F_{1,403} = 3.73$ ,  $P = 0.054$ ; partial regression coefficient:  $0.074 \pm 0.038$ ), but not in yearlings ( $N = 442$ ,  $F_{1,404} = 0.04$ ,  $P = 0.840$ ; interaction mean fledgling number  $\times$  age:  $N = 884$ ,  $F_{1,843} = 6.17$ ,  $P = 0.013$ ). The effect of mean fledgling condition on yearling immigration rate still depended on breeding density in the previous year (interaction mean fledgling condition  $\times$  breeding density:  $F_{1,325} = 9.38$ ,  $P = 0.002$ ). Immigration rate also increased with increasing breeding density the previous year, when the significant interaction density  $\times$  year was removed ( $N = 884$ ,  $F_{1,860} = 107.14$ ,  $P < 0.001$ ; partial regression coefficient:  $2.00 \pm 0.20$ ; no significant interaction with age:  $F_{1,842} = 0.09$ ,  $P = 0.765$ ). The same results were still found when considering that all nestboxes occupied by residents of the same age class were available to immigrants at the time of settlement, i.e. an advantage of immigrants over residents for the access to nestboxes: immigration rate still increased with increasing mean fledgling number in older adults but not in yearlings (interaction mean fledgling number  $\times$  age:  $F_{1,843} = 6.19$ ,  $P = 0.013$ ); for yearlings, the interaction mean fledgling condition  $\times$  breeding density was still significant ( $F_{1,325} = 9.40$ ,  $P = 0.002$ ); immigration rate still increased with increasing breeding density in the previous year ( $F_{1,860} = 94.60$ ,  $P < 0.001$ ; partial regression coefficient:  $1.89 \pm 0.20$ ).

In conclusion, we were confident that our results were robust to the different hypotheses underlying the computation of immigration rates.

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