Social environment affects juvenile dispersal in great tits (*Parus major*)

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Summary

1. Habitat selection can affect individual fitness, and therefore, individuals are expected to assess habitat quality of potential breeding sites before settlement.

2. We investigated the role of social environment on juvenile dispersal behaviour in the great tit (*Parus major*). Two main contradictory hypotheses can be formulated regarding social effects on juvenile dispersal as follows: (i) High fledgling density and sex ratio may enhance the intensity of local (kin) competition and, therefore, reduce individual survival chance, enhance emigration and reduce settlement ('repulsion' hypothesis) (ii) Alternatively, high fledgling density and sex ratio may signal high-quality habitat or lead to aggregation and thus increase individual survival chance, reduce emigration and enhance settlement ('attraction' hypothesis).

3. To disentangle positive from negative effects of high density and male-biased sex ratio on dispersal, we manipulated the social composition of the fledgling population in 12 semi-isolated nest-box areas (plots) via a change of fledgling density (low/high) as well as fledgling sex ratio (female-biased/balanced/male-biased) across 3 years. We then tested whether experimental variation in male and female fledgling densities affected variation in local survival, emigration and settlement of juveniles, and whether social effects on survival and dispersal support the 'repulsion' or 'attraction' hypothesis.

4. We found no experimental effects on local survival and emigration probabilities. However, consistent with the 'attraction' hypothesis, settlement was significantly and positively affected by local experimental sex ratio in each of the study years: both male and female juveniles avoided female-biased plots and settled more in plots that were balanced and male-biased the previous year.

5. Our study provides unprecedented experimental evidence that local sex ratio plays a causal role in habitat selection. We suggest that settlers avoid female-biased plots because a high proportion of females may reflect the absence or the low quality of local resources in the habitat. Alternatively, male territory acquisition may be facilitated by a high local density of 'candidate' males, and therefore, juveniles were less successful in settling in female-biased plots.

Key-words: Habitat selection, informed dispersal, intraspecific competition, natal dispersal, *Parus major*, prospecting, public information, social information

Introduction

The decision to leave the patch of birth and to settle in another patch (natal dispersal) can have large fitness consequences, and therefore, individuals are expected to be under strong selective pressure to make habitat choices that maximize their fitness (Clobert *et al.* 2001). Multiple factors can affect the costs and benefits of dispersal, thereby affecting individual optimal decisions at the distinct stages of departure, transience and settlement (Clobert *et al.* 2001). Classically, inbreeding, (kin) competition and local resource quality are considered to be important selective factors influencing an individual's fitness and driving the evolution of dispersal (Bowler & Benton 2005). Hence, to adopt optimal dispersal strategies, individuals often rely on external cues that predict future habitat suitability, that is, their fitness prospects if they settle in a certain location (Valone & Templeton 2002; Clobert *et al.* 2009). These cues may be derived from personal sampling of the resources (personal

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information) or by observing the behaviours or performance (e.g. reproductive success) of other individuals in the environment (social information) (Danchin *et al.* 2004; Dall *et al.* 2005). The use of social information should be a profitable habitat selection strategy because it can be gathered at low costs and it integrates habitat quality over a long period of time, potentially allowing individuals to produce a more adaptive response (Danchin *et al.* 2004).

Classically, dispersal studies corroborate the hypothesis that high conspecifics density generates high levels of intraspecific/kin competition for local resources and that dispersal is an adaptive response to avoid the negative fitness consequences of competition (Greenwood & Harvey 1982; Lambin, Aars & Piertney 2001). This explains why empirical studies have frequently found patterns of positive density-dependent emigration and negative density-dependent immigration (see review in Bowler & Benton 2005). Local sex ratio has also been suggested to play a role in dispersal decisions by promoting sex-specific emigration. For example, competitive asymmetries between the sexes, inbreeding or spatial variation in mating success may create sex-specific differences in the costs and benefits of dispersal (Greenwood 1980; Bowler & Benton 2005; Gros, Hovestadt & Poethke 2008). However, the net direction of social effects on dispersal is not easy to predict because multiple mechanisms with opposite effects may act simultaneously (Matthysen 2005).

In contrast to the classical perspective, there is growing evidence that high local densities can retain and attract individuals. This occurs when high local density impedes dispersal (Hestbeck 1982; Lambin, Aars & Piertney 2001), facilitates settlement (Drent 1983; Tinbergen *et al.* 1987), increases fitness through some Allee effects (Stamps 1988) or conveys inadvertent social information about habitat quality (Danchin *et al.* 2004). Inadvertent social information (i.e. produced unintentionally by others) may involve the presence of conspecifics, which could indicate the location of available resources (social attraction) or the performance of conspecifics, which reflects the quality of local resources (public information) (Danchin *et al.* 2004). To understand the role of social effects in the process of natal dispersal and to disentangle positive from negative effects of local (sex-specific) density of conspecifics, experimental manipulations of the social composition of the possible breeding habitats (both of departure and settlement) are needed.

In this study, we experimentally investigate how local social environment affects the natal dispersal pattern of juvenile male and female great tits (*Parus major*). Juvenile great tits typically roam around with their family for several weeks after fledging, before forming large mixed flocks in late summer (Drent 1983, 1984). Dispersal primarily occurs within the first 3 months of independence (Dingemanse *et al.* 2003; Michler *et al.* 2011b) and is biased towards the female sex (Greenwood, Harvey & Perrins 1979). Great tits are a resident species, and male territorial behaviour and pair formation start in autumn (Kluijver 1951). Previous studies have shown that passerine dispersal decisions might integrate complex social information about the local environment at each stage of the dispersal process (Doligez, Pärt & Danchin 2004; Parejo *et al.* 2007; Forsman & Thomson 2008). Social factors may include the density of local breeders (e.g. heterospecific density: Fletcher 2007; Forsman *et al.* 2008; conspecific density: Nilsson 1989), their breeding output (e.g. Ward 2005; Parejo *et al.* 2007) or both (e.g. Doligez *et al.* 2004; Parejo *et al.* 2008). In this study, we focused on the effects of local density and local sex ratio of conspecific juveniles on juvenile dispersal decisions in the great tit. We chose great tits for this study because (i) density-dependent dispersal patterns have been reported in this species (Greenwood, Harvey & Perrins 1979; Delestrade, McCleery & Perrins 1996), and (ii) producing more fledglings and/or more of the less-dispersive sex (males) in high-quality habitats is expected to provide higher fitness (Both, Tinbergen & Visser 2000; Doligez *et al.* 2008). Fledgling density and sex ratio could thus be used as public information for dispersal decisions.

To unravel the underlying mechanisms of juvenile dispersal decisions, we set-up an unprecedented experiment where the fledgling density (low/high) and fledgling sex ratio (female-biased/balanced/male-biased) of 12 semi-isolated nest-box areas (plots) were manipulated simultaneously for three consecutive years (2005–2007). Breeding densities were left unmanipulated. This experiment presumably altered the perceived quality of all the suitable settlement plots introducing a clear frequency-dependent framework to dispersal decisions because the fitness pay-off of individual dispersal decisions will also depend on the decision of other local juveniles. We predicted that (i) juveniles will use social information available during the post-fledging phase, to make dispersal decisions (departure/settlement) just after independence. During this period, juvenile birds are known to travel the largest distances, have no prior breeding experience and are still quite unfamiliar with the habitat (Greenwood & Harvey 1982) – conditions that render the use of socially acquired information particularly valuable (Muller *et al.* 1997). Information gathered just after fledging may also be used later to choose the best place of settlement, in spring for instance, when information on breeding success becomes relevant again. (ii) If high local density of young males conveys information about the expected local competition intensity, it should reduce local survival, promote emigration and reduce settlement (the 'repulsion' hypothesis). (iii) In contrast, if high local density of young males conveys information about the presence or quality of local resources, it should reduce emigration, be attractive for settlement and perhaps increase local survival (the 'attraction' hypothesis). (iv) Competitive asymmetries between the sexes and sex-specific requirements (Kluijver 1957; Hogstad 1989; Gosler & Carruthers 1999) may lead to sex-specific use of local social information (Michler *et al.* 2011a,b). If that is the case, sex-specific effects of the social environment on juvenile dispersal should be detected. For example, if competition occurs mainly between sexes, we expect juvenile females, the subordinate sex, to avoid high-density male-biased plots. If competition within sexes is more important, we expect the majority sex to avoid plots biased towards same-sex congeners. Alternatively, if the choice is

postponed to the spring, juvenile females may settle preferentially in male-biased plots to find a suitable partner.

Materials and methods

STUDY AREA

The study was carried out in a great tit population in the Lauwersmeer area located in the north-east of the Netherlands (53°23′N, 6°14′E). In March 2005, we created 12 new nest-box areas (plots) in a fragmented forest where woodlots are separated by open grasslands or sand paths (Fig. 1). Each plot consisted of 50 nest-boxes that were placed in a regular grid with inter-box distances of *c*. 50 m (mean plot surface ± SD = 10·39 ± 1·39 ha). The plots consisted primarily of 30-year-old deciduous forest and minimal distance between the plot edges ranged from 0·3 to 6 km (Fig. 1). Territory sizes of great tits range from *c*. 0·4 to 3 ha (Both & Visser 2000). The mean breeding density over the 3 years of this study was $1·84 ± 0·8$ pairs ha^{-1}. Few natural cavities were available in the study area so that the vast majority of the breeding attempts occurred in the nest-boxes. High temporal predictability of patch breeding output increases the value of social information use for habitat choice (Doligez *et al.* 2003). Overall, natural plot breeding densities but not nestling plot density or sex ratio were significantly correlated between years, implying that local breeding densities were temporally predictable (Data S1, Supporting information). Within years, the plot nestling densities were significantly and positively correlated to the plot breeding densities (2005: $r = 0·81$, $n = 12$, $P = 0·027$; 2006: $r = 0·97$, $n = 12$, $P < 0·001$; 2007: $r = 0·91$, $n = 12$, $P < 0·001$).

DATA COLLECTION

Each year, from the beginning of April, nest-boxes were checked weekly and parameters such as lay date (back-calculated assuming
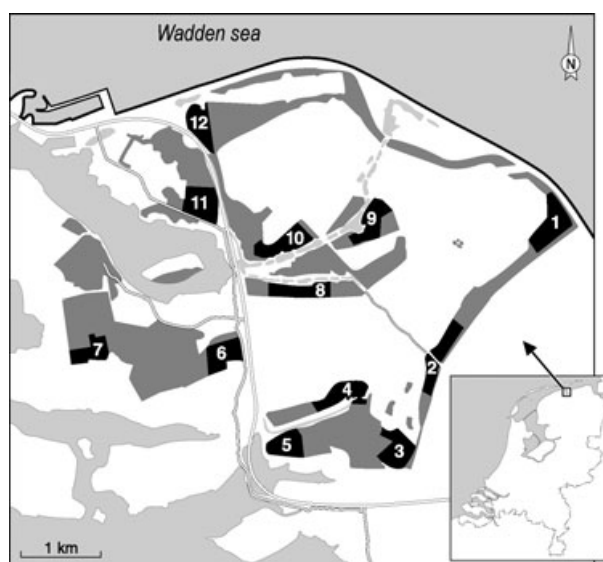
Fig. 1. Map of the study area in the Lauwersmeer (53°20′N, 06°12′E), NL. Each black area (1–12) represents a plot carrying 50 nest-boxes within a woodlot. Water is indicated in light grey, woodlots in dark grey, and open grass or agricultural areas in white. Six plot treatments (with two replicates) combining nestling density and nestling sex ratio were randomly assigned to a plot and changed every year.

that one egg was laid per day), clutch size and onset of incubation were monitored. Around the expected hatching date (12 days of incubation), nest-boxes were checked daily to determine hatching date (day 0). All great tit nestlings were bled at day 2 (5–10 μL of blood collected) and their toenails were clipped for individual identification. The nestling sex was then determined using molecular markers (Griffiths *et al.* 1998). At day 6, nestlings were weighed, ringed with an aluminium ring and swapped between nests of the same age within or between plots according to the manipulation (see below and Table 1). We always moved or exchanged at least one nestling per nest to control for any effect of swapping. Swapped nestlings were chosen according to their sex but independently from their body size. At day 7, both parents were caught with a spring trap in the nest-box, measured, weighed and ringed if they were unringed. At day 14, juveniles were weighed and measured. Only first broods were manipulated (defined as clutches started within 30 days of the earliest clutch in that year), but standard measurements of adults and nestlings of the second broods (defined as broods laid by females that were known to have successfully fledged a first brood) and of replacement broods of known females after failure were also taken. The mean values of the breeding parameters of the first broods and the mean number of second broods are presented per year in the Data S2 (Supporting information).

Recruitment probability and settlement decisions of juveniles were estimated on the basis of recaptures of breeding birds in the whole study area the next year. Spring data of 2005, 2006, 2007 and 2008 were used in these analyses. Locally born juveniles that did not enter the breeding population in their second year but later in life (30 individuals of 759 recruited juveniles since 2005) were not included in the analyses because their natal dispersal decisions were unknown (they may have first bred in a natural cavity or outside the study area).

Table 1. Details about the experimental design applied in the Lauwersmeer great tit population across three consecutive years (2005–2007) in the Netherlands. The social composition of 12 plots (i.e. woodlots carrying 50 nest-boxes) was changed via a manipulation of plot nestling sex ratio (female, balanced or male-biased plots) and plot nestling density (low- or high-density plot) at day 6. To achieve the plot treatments, the frequencies (in %) of the different brood treatments that combined both a brood sex ratio (female, control or male-biased broods) and a brood size (small, intermediate or large broods) treatment were altered in a specific direction within each plots

| | Plot treatments | | | | | |
| | Female | | Balanced | | Male | |
Brood treatments (%)	Low	High	Low	High	Low	High
Female						
Small	60	20	–	–	–	–
Intermediate	20	20	–	–	–	–
Large	20	60	–	–	–	–
Control						
Small	–	–	60	20	–	–
Intermediate	–	–	20	20	–	–
Large	–	–	20	60	–	–
Male						
Small	–	–	–	–	60	20
Intermediate	–	–	–	–	20	20
Large	–	–	–	–	20	60

Breeding dispersal was very limited in our population (2005–2007: mean breeding dispersal distance (±SD): females: 150 ± 322 m, $n = 177$ and males: 113 ± 195 m, $n = 157$), and in our population, adult recapture probability in the whole study area from 1995 onwards is very high (0·90 see Tinbergen & Sanz 2004). This shows that once a juvenile bird selects a breeding habitat it remains in this place the rest of its life and indicates that habitat selection is mostly important the first year. Therefore, we did not investigate dispersal patterns in adults.

MANIPULATIONS

Plot level manipulation

To study the effect of local social environments on natal dispersal, we altered simultaneously the nestling density and the nestling sex ratio of the 12 study plots for three consecutive years (2005, 2006 and 2007). These manipulations were achieved by altering the frequencies of the brood size (number of nestlings in a nest at day 6) and brood sex ratio (proportion of nestling males in a nest at day 6) treatments differentially among the 12 study plots (Table 1 and see below). In that way, we created six different experimental treatments combinations of manipulated nestling density (low/high) and sex ratio (female/balanced/male). Low- and high-density plots were manipulated to $c. \pm 13\%$ of the natural number of nestlings in a plot (Fig. 2a; Data S2, Supporting information). Female- and male-biased plots were manipulated to $c.$ 25% or 75% nestling males, respectively, while balanced plots were manipulated to $c.$ 50% that reflects a natural situation (Fig. 2c; Data S2, Supporting information). Each treatment was randomly assigned to a plot, semi-randomized between years (i.e. each plot received a different treatment in every study year) and occurred in two replicates per year. Nestlings from first broods only were

included in the calculations of plot density and plot sex ratio. We left the natural breeding densities (number of breeding pairs per plot) unchanged.

Brood level manipulation

Brood manipulations were carried out such that broods were categorized as 'female', 'control' or 'male' biased broods and as 'small', 'intermediate' or 'large' broods (Table 1). We assigned all nests a brood size and a brood sex ratio treatment before the completion of the clutch. We defined 'female', 'control' and 'male' biased broods as broods with $c.$ 25%, 50% and 75% male nestlings, respectively. We defined 'intermediate' broods as being equal to the average population brood size of a given year (e.g. 8) and 'small' and 'large' broods as broods that differed, respectively, by −3 or + 3 nestlings from the average brood size (e.g. 5 or 11). To achieve the plot sex ratio treatments, all broods within a plot were manipulated in the direction of the plot treatments (Table 1). To achieve the plot density treatments, 60% of the brood size were manipulated in the direction of the plot treatment while keeping 40% as control broods (20% manipulated towards the opposite brood size treatment and 20% manipulated towards the annual mean brood size) (Table 1).

LOCAL RECRUITMENT AND EMIGRATION ANALYSES

To account for sources of inter-dependency between measurements at various levels, we used generalized hierarchical linear mixed models (MLwiN versions 2.02; Rasbash *et al.* 2004) distinguishing between variance at four levels: plot, plot-year, nest and individual. We analysed the *local recruitment probability* (probability of a known fledgling to be recaptured as a breeder in the whole study area the subsequent breeding season) and the *emigration probability* (probability of a fledgling surviving until the next year to leave the plot of
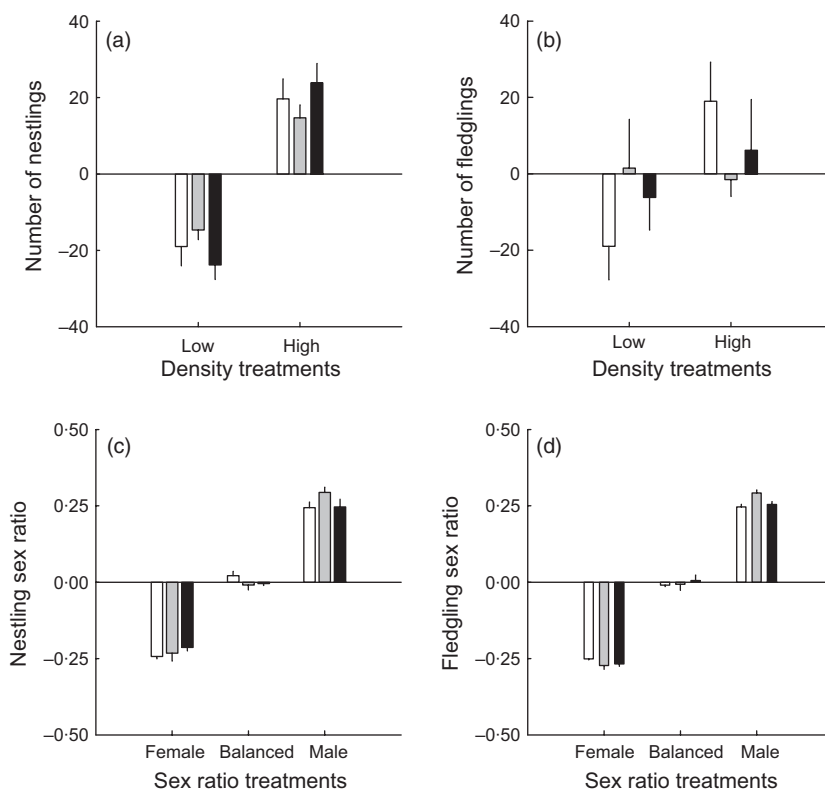
Fig. 2. Overview of the experimental changes in mean plot offspring density (low- and high-density treatments) and in mean plot offspring sex ratio (female-biased, balanced sex ratio or male-biased treatments) at day 6 and at fledging for 3 years in the Lauwersmeer great tit population in the Netherlands (white: 2005, grey: 2006 and black: 2007). Figures represent (a) the mean change in the number of nestlings per plot at the day of manipulation (day 6), (b) the difference between the mean number of fledglings per density treatment and the population mean number of fledglings, (c) the mean change in nestling sex ratio per plot at the day of manipulation (day 6) and (d) the difference between the mean fledgling sex ratio per sex ratio treatment and the population mean fledgling sex ratio. Means are presented with their standard error ($n = 6$ plots per density treatment per year; $n = 4$ plots per sex ratio treatment per year).

birth in year n and breed in another plot in year $n + 1$) for juveniles of the first broods. The variation in local recruitment ($n = 4073$ fledglings) and emigration probability ($n = 447$ recruited individuals, ranging from 4 to 28 recruits per plot per year) was studied using a binomial response model with a logit link function.

We analysed these parameters in relation to the sex ratio treatment (female/balanced/male) and the density treatment (low/high) of the plot of origin. We controlled for the natural plot sex ratio and plot density (nestling sex ratio and nestling density before manipulation at day 6) and individual sex (female/male). To disentangle social effects because of sibling interactions from conspecific interactions at the plot scale, we included the natural brood size (number of nestling per brood before manipulation at day 6) and the brood size manipulation as a factor (small/intermediate/large). We further included date, year (2005/2006/2007) and the two- and three-way interactions between treatment, sex and years. Apart from the factors such as sex ratio, sex, brood size and year, all the other explanatory variables were continuous and centred on the population mean.

Local recruitment estimates may be biased by the occurrence of permanent emigration outside the study area (Tinbergen 2005; Doligez, Gustafsson & Pärt 2009). The probability of such permanent emigration may depend on the plot position in the study area (edge vs. centre). However, the randomization of the plot treatments over the plots between years and the two replicates within years should have minimized this potential bias. Recruitment estimates represent thus local estimates for the study area.

SETTLEMENT ANALYSIS

For each combination of plots, we calculated the *number of juvenile males and females originating from one plot and settling in the other plot* (e.g. for a plot combination $i - j$, we obtained a count of females born in i and breeding in j and a count of males born in i and breeding in j) for each of the three study years. We thus obtained counts for 864 groups [12 (plots) × 12 (plots) × 2 (sexes) × 3 (years)]. These counts, ranging from 0 to 9 individuals per group, were analysed using a Poisson response model with a log link function with the log of the number of fledgling males or females of the plot of origin used as an offset. We used generalized linear mixed models (MLwiN versions 2.02; Rasbash *et al.* 2004) distinguishing between variance on two levels: plot combination and plot combination-year.

In this analysis, we considered all plots as settlement options for the fledglings, including their plot of origin. Variation in the count of male and female settlers relative to the number of fledglings was thus analysed in relation to the sex ratio and the density treatment of the plot of settlement. We also fitted in the analyses the natural plot sex ratio and plot density of the plot of settlement. To control for the fragmented structure of the population that could affect the distribution of the birds (i.e. decrease the number of exchanged birds with increased inter-plot distance; Matthysen, Adriaensen & Dhondt 2001), the distance between the centre of the focal plot and the centre of each other plot (m) was included in the model. We also fitted great tit sex (female/male), year (2005/2006/2007) and all the two-way interactions between sex, distance, year and the plot treatments. As with the previous analyses, plot sex ratio, sex and year (2005/2006/2007) were fitted as factors, whereas the other explanatory variables were fitted as continuous variables centred on the population mean.

We did not perform any of the analyses using mark-recapture method that controls for heterogeneity in detection probability because during the 3 years of manipulation, the capture probability of birds breeding in our boxes was high, that is, 0·95 (49 breeding birds missed vs. 959 captured between 2005 and 2007). Also virtually all local breeding attempts occur in our boxes (there are few natural cavities).

We used a hypothesis testing approach to accommodate tests of the experimental effects. In all the analyses, model selection was based on backwards elimination of the non-significant terms in the order of their significance assessed by their Wald statistic. Because the final models may be sensitive to the order of exclusion of independent variables, model selections were also performed using information theoretic approach that takes into account model uncertainty (e.g. Grueber *et al.* 2011). Model selection based on Akaike's information criteria and model averaging revealed qualitatively similar results as the stepwise method, indicating that there was no effect of the order of exclusion of the independent variables. Therefore, we will present results based on the stepwise approach because it allows reporting the non-significance of parameters that are important for validating our hypotheses. These non-significant parameters were retested after elimination in the final model. Other non-significant effects are not mentioned. Means are expressed with standard error.

Results

SUCCESS OF THE PLOT MANIPULATIONS AND LONG-LASTING EFFECTS

Our manipulation successfully affected the frequencies of brood sizes and brood sex ratios within plots resulting in significant changes in plot densities and plot sex ratios after manipulation at day 6 (Data S2 and S3, Supporting information; Fig. 2a,c).

Experimental changes in plot density and sex ratio were still significant at fledging (Data S2 and S3, Supporting information; Fig. 2b, d). However, the significant correlation between final fledgling densities and natural nestling densities before manipulation ($r = 0·47$, $P = 0·004$, $n = 36$) indicates that the magnitude of the density manipulation was small. Differential mortality among the brood size treatments may have contributed to reduce the strength of the density manipulation at fledging: nestling mortality significantly increased with brood enlargement but was not affected by the brood sex ratio manipulation (Nicolaus *et al.* 2009). Because experimentally enlarged broods were more frequent in high-density than in low-density plots, nestling mortality was higher in high-density plots (Fig. 2b; Data S3, Supporting information).

From bi-weekly direct observations of ringed birds during the post-fledging phase in 2005 and 2006, we know that the experimental changes of plot sex ratio were detectable at least until September (Michler *et al.* 2011a,b), unlike the density manipulation that disappeared quickly after fledging (Michler 2010). Additionally, further analyses based on roosting checks performed each year in December revealed that variation in the number of locally born juveniles roosting in the nest-boxes was affected by the previous experimental change in the plot sex ratio (Table 2) but did not relate to the experimental change in density ($\chi^2_{d.f. = 1} = 0·001$, $P = 0·975$) nor to the natural variation in plot nestling sex ratio ($\chi^2_{d.f. = 1} = 0·306$, $P = 0·580$) or density ($\chi^2_{d.f. = 1} = 0·087$,

$P = 0.768$). Consequently, the sex ratio but not the density treatment was still reflected in the social composition of locally fledged juveniles in winter.

LOCAL RECRUITMENT PROBABILITY

Juvenile local recruitment probability was not affected by the plot manipulations (density: $\chi^2_{d.f. = 1} = 1 \cdot 59$, $P = 0.207$; sex ratio: $\chi^2_{d.f. = 2} = 1 \cdot 15$, $P = 0.563$) and it did not differ between the sexes ($\chi^2_{d.f. = 1} = 0 \cdot 046$, $P = 0.496$; average recruitment probability over all the years for females: $11 \cdot 21 \pm 31 \cdot 56\%$, $n = 2087$; for males: $11 \cdot 38 \pm 31 \cdot 76\%$, $n = 1986$). However, juveniles that fledged in plots with a naturally high density had a lower probability of recruiting (Table 3).

In this analysis, we statistically controlled for brood traits that may also influence the local survival of the juveniles (natural brood size, brood size treatment and date). Brood size enlargement reduced the recruitment probability of juveniles (Table 3; *post hoc* tests: small vs. intermediate: $\chi^2_{d.f. = 1} = 1 \cdot 07$, $P = 0.301$; small vs. large: $\chi^2_{d.f. = 1} = 10 \cdot 74$, $P = 0.001$ and large vs. intermediate: $\chi^2_{d.f. = 1} = 4 \cdot 16$, $P = 0.041$). The effect of the brood size manipulation did not interact with the plot sex ratio manipulation ($\chi^2_{d.f. = 4} = 3 \cdot 24$, $P = 0.518$) and did not differ between the sexes ($\chi^2_{d.f. = 2} = 1 \cdot 94$, $P = 0.378$). Juvenile recruitment probability changed with season (date), but the slope of this effect differed among years (year × date interaction, Table 3).

EMIGRATION PROBABILITY

Females, the most dispersive sex in this species, were more likely to leave their natal plot than males (Table 4; percentage of juveniles that emigrated: females: $78 \cdot 70\%$, $n = 230$ vs. males: $60 \cdot 37\%$, $n = 217$). For those juveniles that recruited into the population, we found no effect of the plot manipulations on their emigration probability (density: $\chi^2_{d.f. = 1} =$

Table 3. Model summary examining the local recruitment probability for juvenile great tits in relation to the social environment of their plot and nest of origin in the Lauwersmeer population in the Netherlands (nat. density = natural plot nestling density; BS = brood size; date = hatching date). 'Intermediate' brood size and '2005' are chosen as reference categories (three study years; $n = 4073$ individuals)

Parameters	Level	β	SE (β)	χ^2	d.f.	P
Intercept		−2·450	0·160			
Nat. density	Year	−0·007	0·003	7·57	1	0·006
BS						
Small	Nest	0·158	0·153	11·09	2	0·004
Large		−0·310	0·152			
Date	Nest	−0·057	0·024	5·81	1	0·016
Year						
2006	Year	0·772	0·189	16·62	2	<0·001
2007		0·307	0·176			
Year × date						
2006 × date	Nest	0·038	0·041	10·02	2	0·007
2007 × date		0·111	0·035			
Random effects	σ^2_{plot}	0·056	0·044			
	σ^2_{year}	0·015	0·041			
	σ^2_{nest}	0·313	0·112			

$0 \cdot 01$, $P = 0.975$; sex ratio: $\chi^2_{d.f. = 2} = 1 \cdot 68$, $P = 0.430$). Yet, juveniles that fledged in naturally high-density plots were more likely to emigrate (Table 4), and this pattern tended to be stronger for males than for females ($\chi^2_{d.f. = 1} = 3 \cdot 27$, $P = 0.070$). The positive effect of natural density was only present in two of the 3 years with natural high breeding densities, that is, in the years 2005 and 2007 that had, respectively, $1 \cdot 5$ and $1 \cdot 6$ times higher breeding densities than in 2006 (year × nat. density interaction, Table 4 and Data S2, Supporting information).

We also controlled for brood traits that may influence the emigration probability of juveniles (natural brood size, brood size treatment and date). We found no effect of natural brood

Table 2. Model summary examining the effect of the manipulated plot sex ratio (SR) on the number of roosting male and female juveniles in the Lauwersmeer great tit population in the Netherlands ($n = 72$ counts). 'Balanced' plots, 'female' sex and '2005' are chosen as the reference categories

Parameters	Level	β	SE (β)	χ^2	d.f.	P
Intercept	Plot	1·092	0·201			
SR						
Female	Plot	0·834	0·203	48·21	2	<0·001
Male		−1·421	0·382			
Sex	Plot	0·863	0·200	18·56	1	<0·001
Sex × SR						
Sex × female	Plot	−1·328	0·268	73·66	2	<0·001
Sex × male		1·902	0·406			
Year						
2006	Plot	0·197	0·117	14·54	2	<0·001
2007		−0·288	0·132			
Random effects	σ^2_{plot}	0·083	0·046			

Table 4. Model summary examining the effect of the local social environment (plot of origin) on the probability of emigrating outside the fledging plot for juvenile great tits in the Lauwersmeer population in the Netherlands (nat. density = natural plot nestling density). 'Female' sex and 2005 were chosen as reference categories (three study years; $n = 447$ individuals)

Parameters	Level	B	SE (β)	χ^2	d.f.	P
Intercept		1·339	0·316			
Nat. density	Year	0·015	0·011	1·91	1	0·167
Sex	Indiv.	−0·926	0·220	17·7	1	<0·001
Year						
2006	Year	−0·156	0·337	0·91	2	0·634
2007		−0·321	0·346			
Year × nat. density						
2006 × nat. density	Year	−0·020	0·012	6·66	2	0·036
2007 × nat. density		0·000	0·013			
Random effects	σ^2_{plot}	0·059	0·080			
	σ^2_{year}	<0·001	<0·001			
	σ^2_{nest}	<0·001	<0·001			

size or the brood size manipulation (in contrast to earlier findings in this population, Tinbergen 2005) and no effect of date. Effects of brood size manipulation did not interact with the plot sex ratio manipulation and did not differ between the sexes.

SETTLEMENT PATTERNS

Juvenile females settled farther from their plot of origin than males (mean natal dispersal distance ± SD: females = 1·43 ± 1·01 km, n = 231; males = 1·09 ± 1·01 km, n = 216), but all juveniles preferentially settled in a plot close to their plot of origin (Table 5).

We found a significant positive effect of the plot sex ratio treatment on juvenile settlement: Juveniles settled less in female-biased plots than in balanced or male-biased plots (Table 5, Fig. 3, *post hoc* tests: female vs. balanced: $\chi^2_{d.f. = 1} = 5 \cdot 08$, $P = 0·024$; female vs. male: $\chi^2_{d.f. = 1} = 6 \cdot 07$, $P = 0·014$; male vs. balanced: $\chi^2_{d.f. = 1} = 0 \cdot 06$, $P = 0·806$). This effect was not sex-specific ($\chi^2_{d.f. = 2} = 1 \cdot 30$, $P = 0·521$). Juvenile settlement was not affected by the density manipulation ($\chi^2_{d.f. = 1} = 0 \cdot 32$, $P = 0·573$). Yet, juveniles settled significantly less in plots that had a high natural density the previous year, and this effect was stronger for juvenile males than females (sex × nat. density, Table 5). Density-dependent settlement was stronger in 2007 than in 2005 or 2006 (year × nat. density, Table 5).

Discussion

We tested the idea that juvenile great tit dispersal decisions are affected by aspects of their social environment, particularly sex-specific fledgling density. Our results demonstrate

Table 5. Model summary examining the settlement of juvenile great tits that recruited into the Lauwersmeer population in relation to the social environment of the plot of settlement in the Netherlands (nat. density = natural plot nestling density; SR = manipulated plot sex ratio). 'Balanced' plot sex ratio, '2005' and 'female' sex were chosen as reference categories (three study years; n = 864 groups)

Parameters	Level	β	SE (β)	χ^2	d.f.	P
Intercept		−5·608	0·155			
Distance	Plot-combi	−0·671	0·075	80·24	1	<0·001
SR						
Female	Plot-year	−0·302	0·137	6·75	2	0·034
Male		0·037	0·117			
Nat. density	Plot-year	−0·001	0·005	0·03	1	0·863
Year						
2006	Plot-year	0·772	0·147	26·34	2	<0·001
2007		0·216	0·141			
Nat. density × year						
Nat. density × 2006	Plot-year	0·002	0·005	9·05	2	0·011
Nat. density × 2007		−0·010	0·006			
Sex	Plot-year	−0·549	0·157	12·29	1	<0·001
Sex × distance		−0·332	0·096	12·02	1	<0·001
Sex × nat. density		−0·007	0·003	5·95	1	0·015
Random effects	$\sigma^2_{plot-combi}$	0·273	0·081			
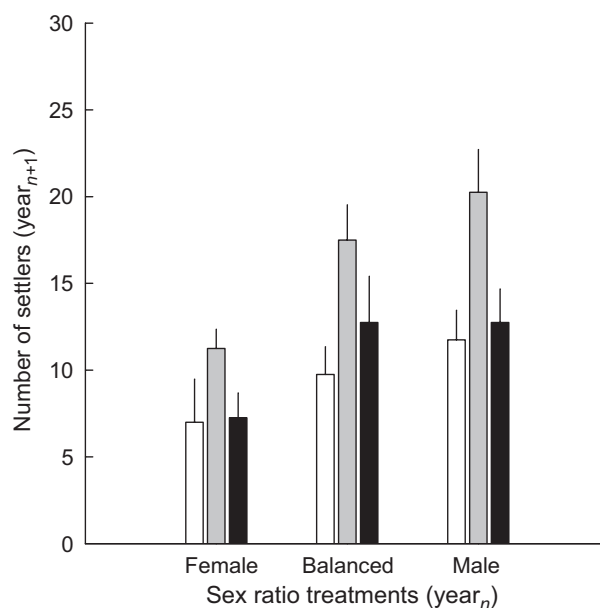
Fig. 3. Significant effect of the manipulated plot sex ratio on juvenile great tit settlement in the Lauwersmeer population in the Netherlands. For 3 years (white: 2005, grey: 2006 and black: 2007), juvenile great tits settled more in plots that had male-biased fledgling sex ratios the year before. Means are presented with their standard error (n = 441 individuals).

that the local fledgling sex ratio played a causal role in the redistribution of the juveniles over the habitat by affecting settlement. Experimental effects on juvenile emigration probability were not detected, maybe due to a lack of statistical power. Although non-experimental, we also found a pattern of positive density-dependent emigration and negative density-dependent survival and settlement. We discuss our results in the contexts of the 'attraction' or 'repulsion' hypotheses on the effects of the social environment, and we suggest potential mechanisms and associated functions that may explain the patterns found.

EXPERIMENTAL EFFECTS OF LOCAL SEX RATIO ON DISPERSAL

Consistent with the 'attraction' hypothesis, juveniles of both sexes consistently avoided plots that were female-biased the previous year and instead settled preferentially in plots that were previously balanced or male-biased. The experimental effect of the plot sex ratio on settlement was found in each of the three study years. Because each plot received all treatments, we can exclude the possibility that this pattern is driven by intrinsic plot differences. Nevertheless, conclusions should be formulated with caution because our experimental design did not allow teasing apart brood sex ratio effect from plot sex ratio effect. The fact that the brood sex ratio manipulation did not affect fledgling condition (Nicolaus *et al.* 2009) nor parental provisioning behaviour (Nicolaus *et al.* in press) suggests though that dispersal did not depend on the brood sex ratio experienced at an early stage. We propose several pathways by which fledgling sex ratio may influence settlement.

Our first interpretation is that fledgling sex ratio conveys public information about habitat quality. Sex allocation theory predicts that when the fitness of the offspring is affected differently by parental investment, parents should invest more in the sex that has the steepest fitness gain from the investment (Trivers & Willard 1973). In species with sex-biased dispersal and with spatial and temporal variation in habitat quality, pairs breeding in high-quality habitats should produce more of the less-dispersive sex (Julliard 2000). Avian and mammal studies have shown that parents may increase their fitness benefits in good habitats by biasing their offspring sex ratio towards the sex that benefits more from settling and reproducing locally (Johnson *et al.* 2001; Doligez *et al.* 2008; Hjernquist *et al.* 2009). In great tits, males disperse less and are the sex that acquire and defend territories (Greenwood, Harvey & Perrins 1979). Producing more males in high-quality plots may increase the chance for male offspring to settle and subsequently reproduce in good habitats (Doligez *et al.* 2008). By manipulating the local sex ratio to 25%, 50% or 75% males, we may have created variation in perceived plot quality and juveniles may have avoided settling in female-biased plots because they indicated low-quality areas that should be associated with low fitness prospects.

Alternatively, public information about habitat quality may have been conveyed by local variation in fledgling density induced by the sex ratio manipulations. Young females usually disperse more outside the breeding areas in winter than young males (Drent 1983, 1984). This may cause entire flocks to leave female-biased plots more. Consistent with this idea, in 1 year of our experiment, apparent post-fledging survival of juveniles was lower in female-biased plots than in control or male-biased plots (2006 mark-recapture analysis, apparent juvenile survival between June and September: female-biased plots: 0·14, balanced plots: 0·24 and male-biased plots: 0·35; Michler 2010). We assume this pattern was caused by local juvenile emigration from the study area rather than permanent juvenile emigration because juvenile recruitment probability was not affected by the plot sex ratio manipulation (this study). Female-biased plots may thus have appeared to be areas of poor quality at the end of the summer (as reflected by a low density of young conspecifics) and as less attractive to prospecting juveniles. Other studies are in line with this interpretation where adult dispersers used the nestling/fledgling density of conspecifics or heterospecifics with similar requirements as public information for habitat quality (direct cue: Doligez, Danchin & Clobert 2002; Serrano & Tella 2003; Parejo *et al.* 2007; Parejo, White & Danchin 2007; Parejo *et al.* 2008; via parental activity: Pärt & Doligez 2003). Other mechanisms not involving social information use may explain the avoidance of female-bias plots. For example, in low-density areas, juveniles may not benefit from other direct social effects such as decreased risk of predation, improved access to mate (Stamps 1988, 2001) or improved access to a territory for young males (Drent 1983; Tinbergen *et al.* 1987).

NEGATIVE CORRELATIONS WITH NATURAL PLOT DENSITY

In all analyses, we found a significant but non-experimental pattern of density-dependent dispersal. Experimental effects of density could not be detected, perhaps because the magnitude of our density manipulation was rather small. Although we cannot infer causation, we speculate that density-dependent patterns are driven by the avoidance of negative fitness consequences stemming from intraspecific and/or intrasexual competition between juveniles and adults (Greenwood, Harvey & Perrins 1979; Drent 1984; Delestrade, McCleery & Perrins 1996).

In great tits, the outcome of competitive interactions is strongly affected by individual differences in state, such as age (Drent 1983), body condition (Gosler & Carruthers 1999) or prior residency (Krebs 1982; Sandell & Smith 1991). In our population, natural high-density plots were associated with reduced fledgling body mass (Nicolaus *et al.* 2009), reduced juvenile recruitment probability, increased juvenile emigration and reduced juvenile male settlement (this study). This pattern is consistent with the idea that in natural high-density areas, juveniles are out-competed by dominant adults. The fact that the negative density-dependence in settlement was stronger for juvenile males than for juvenile females indicates that high local densities increased male–male competition for territory (Drent 1983). Juveniles, and particularly males, may thus be constrained by intraspecific competition in their dispersal decisions.

Fledglings may also disperse more from natural-high-density plots to avoid inbreeding risk (e.g. Gundersen & Andreassen 1998; Szulkin & Sheldon 2008) or high competition level with kin (e.g. Lena *et al.* 1998; Cote, Clobert & Fitze 2007). If individuals disperse to avoid relatives and kin recognition is based on being together in the nest, manipulated brood size should have affected emigration probability because family size should directly affect the probability of mating with a relative and the level of kin competition. However, the absence of experimental brood size effects suggests that effects of high kin competition on the probability of emigration are negligible.

TIMING OF DISPERSAL

It has been shown that the success of an information-based habitat selection strategy depends on the availability of the social information, as well as on the costs and benefits associated with its use (Doligez *et al.* 2003). Using local reproductive success as a cue for habitat choice should be a powerful and parsimonious strategy because it integrates all of the environmental factors on breeding success; that is, it allows an individual to make more optimal decisions (Danchin *et al.* 2004). However, despite this apparent selective advantage, most avian studies have failed to find evidence that juvenile birds use public information to make dispersal decisions. The main reasons evoked are that time constraints and/or the subordinate status of juveniles limits their ability

to gather public information at fledging (Doligez, Danchin & Clobert 2002; Doligez *et al*. 2004; Parejo *et al*. 2007, 2008). Information on local breeding performance is usually available only for a short period of time after the breeding season (Danchin, Boulinier & Massot 1998), and competition with more dominant individuals for local resources in good quality patches may render public information use too costly (Doligez *et al*. 2004). Therefore, some authors have proposed that juveniles adaptively rely on long-lasting social cues such as local conspecific densities that are easier to obtain after fledging or early spring (Doligez *et al*. 2004; Nocera, Forbes & Giraldeau 2006; Parejo *et al*. 2008). In contrast, our results reveal that juvenile redistribution is affected by manipulated local breeding performance and is related to natural breeding densities. In our study, juveniles may have been able to use local public information at low costs because the experimental variation in sex ratio was long lasting (until winter) and the distribution of dominant adults and male fledglings was not correlated (the sex ratio treatments were assigned randomly among plots, which varied in their natural densities). The benefits of acquiring social information may thus have exceeded the costs of intraspecific competition with adult birds. Most likely, gathering social information happened before winter because the arrival and settlement of non-locally born individuals occurred later in the season (i.e. winter/early spring). Further, the arrival of these immigrants was not related to the plot manipulations the previous year but positively correlated with the natural plot density the next year ($r = 0.34$ for females, $r = 0.44$ for males, $n = 3 \times 12$ plots; Nicolaus 2009). These late arriving immigrants (32.7% and 28.9% of the yearling population in winter and spring, respectively) may not have had access to information regarding plot breeding output and may have used alternative cues for settlement decisions. This supports the idea that breeding site selection may be a two-step process with one selection made during the post-fledging period and another during territory establishment period in winter and early spring (Kluijver 1951; Nocera, Forbes & Giraldeau 2006; Arlt & Pärt 2008; Betts *et al*. 2008; Pärt *et al*. 2011). The timing of arrival in the future breeding area may thus determine which breeding habitat selection strategy individuals can adopt (public information use or conspecific attraction). Finally, the absence of a sex-specific effect of sex ratio on settlement suggests that the timing of informed dispersal decisions and the use of social information were similar for both sexes or that males settled first (e.g. using social information or benefiting directly from high male densities) and later attracted young females. Future studies should aim at differentiating between alternative mechanisms (e.g. direct/indirect social effects and sex-specific information use) that can yield similar dispersal outcomes.

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Supporting Information

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

Data S1. Correlations between the plot breeding traits of the Lauwersmeer great tit population in the Netherland between 2005, 2006 and 2007.

Data S2. Overview of the plot density and sex ratio manipulations and of the breeding parameters of the Lauwersmeer great tit population in the Netherlands.

Data S3. Success of the plot manipulations and long-lasting effects.

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