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ORIGINAL PAPER

Do great tits rely on inadvertent social information from blue tits? A habitat selection experiment

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Abstract Sympatric species sharing requirements are competitors, but recent evidence suggests that heterospecifics may also be used as a source of information. The heterospecific habitat copying hypothesis proposes that individuals of one species might use information inadvertently produced by the breeding performance of individuals of other species to assess habitat quality whenever the two species share needs. In this study, we provide the first experimental test of this hypothesis by examining whether the manipulated reproductive success of blue tits (*Cyanistes caeruleus*) is used as heterospecific inadvertent social information (ISI) in breeding-habitat selection by sympatric great tits (*Parus major*). The reproductive success of blue tits was manipulated 1year at the scale of patches by transferring nestlings from decreased to increased patches. No evidence was found of great tits using the reproductive success of blue tits as a source of heterospecific ISI. However, dispersal decisions by adult great tits correlated with information on con- and heterospecific densities, which constitute other sources of ISI. As density and breeding performance are tightly intertwined forms of information, the difficulty in distinguishing between them might lead great tits to use heterospecific ISI more in the form of density than breeding performance when making dispersal decisions.

Keywords Breeding-habitat selection · Habitat copying · Heterospecifics · Species coexistence · Social information

Introduction

In community ecology, sympatric species sharing ecological requirements have been usually considered as competitors. The coexistence of species with overlapping resource use has been shown to negatively affect fitness in many animal species (Brown and Davidson 1977; Minot 1981; Gustafsson 1987; Wedin and Tilman 1993; Schmidt and Whelan 1998; Cooper et al. 2007). Consequently, theory predicts heterospecific avoidance during habitat selection to avoid competition (Stamps 1991).

In this context, recent experimental evidence suggests the potential use of heterospecific location or abundance as valuable information in breeding-habitat selection (Mönkkönen et al. 1990; Elmberg et al. 1997; Forsman et al. 1998), as well as in foraging-patch selection (see for instance Whiting and Greef 1999, Nieh et al. 2004, and Silverman et al. 2004). Indeed, in breeding-habitat selection, organisms that rely on the location of heterospecifics to settle in a breeding area have been shown to achieve direct fitness benefits (Forsman et al. 2002; see however Forsman et al. 2007). Also, the use of

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information inadvertently produced by the foraging success of heterospecific fishes (*Gasterosteus* sp.) as a source of heterospecific inadvertent social information (ISI sensu Danchin et al. 2004) has been demonstrated in a foraging context (Coolen et al. 2003). Furthermore, Seppänen and Forsman (2007) have recently demonstrated in a well-designed experiment that individuals from one species may acquire arbitrary preference of competing informant species for such a trait as a symbol attached to nest sites. Their results show the importance of interspecific social learning in species coexistence. Finally, the heterospecific habitat copying hypothesis (Parejo et al. 2005) states that individuals of one species, to assess local habitat quality, may use information inadvertently produced by the breeding performance of individuals of other species. This hypothesis, which broadens the habitat copying hypothesis (Wagner and Danchin 2003) to heterospecifics, states that whenever individuals share ecological needs, they may inadvertently produce valuable information to members of the other species. It is the fact that heterospecifics as well as conspecifics are competitors that makes their performance a valuable source of information about habitat suitability. Therefore, competitors may also be envisaged as potentially beneficial neighbours. Heterospecific habitat copying may thus provide another mechanism, among many others, explaining species coexistence.

Heterospecific information may be secondary because it is rather indirect relative to conspecific or other more direct information (Parejo et al. 2005). Indeed, conspecific information likely reveals habitat quality more accurately than heterospecific information because an individual's ecological needs are likely to overlap much more with conspecifics than heterospecifics. However, conspecifics could be, under certain circumstances, suboptimal sources of information compared to heterospecifics (Seppänen et al. 2007). In particular, using heterospecifics as a source of information could reduce intraspecific competition whenever a resource is limiting, and heterospecifics would not compete as severely for that resource (Seppänen et al. 2007). Moreover, in most natural communities, heterospecifics are more abundant than conspecifics and thus more likely to be used as a source of information. Consequently, population density of both con- and heterospecifics may be a factor revealing the suitability of con- and heterospecific cues for habitat selection. Recent theoretical models suggest that conspecific and heterospecific attraction may be most beneficial at moderate population densities (Mönkkönen et al. 1999; Fletcher 2006). Furthermore, Fletcher (2007) has recently demonstrated that, in a bird species, the least flycatcher *Empidonax minimus*, social attraction to con- and heterospecifics (American redstart *Setophaga ruticilla*) is more effective at intermediate population densities.

Heterospecifics are likely to produce ISI through their location and performance. The use of these two types of information among conspecifics is claimed to be widespread in breeding-site choice of many animal taxa (e.g., Deutsch and Nefdt 1992, Stamps 1987, Danchin et al. 1998, Reed et al. 1999, Doligez et al. 2002, le Galliard et al. 2003, and Parejo et al. 2007a). ISI is highly valuable to indicate local habitat quality for two reasons. First, such information is easier to gather than independently evaluating all habitat characteristics influencing habitat quality such as the amount and quality of food sources, predation pressure, and micro-climate conditions (Boulinier and Danchin 1997). Second, it is reliable because it is not produced intentionally. For instance, individuals are selected to perform as well as possible rather than to inform others, and thus they are unlikely to falsify their performance (Danchin et al. 2004).

In this study, we experimentally test whether the manipulated reproductive success of blue tits (*Cyanistes caeruleus*; see Parejo et al. 2007a) is used as heterospecific ISI in breeding habitat decisions by sympatric great tits (*Parus major*). This study constitutes the first experimental test of the heterospecific habitat copying hypothesis because, until now, only some correlative evidence in other bird species has supported this hypothesis (Parejo et al. 2005). In the blue tit, correlative evidence suggests that settlement decisions are related to cues produced by conspecifics (Parejo et al. 2007b). Moreover, an experimental manipulation of the reproductive success demonstrated that blue tits use conspecific ISI in their dispersal decisions (Parejo et al. 2007a). In these two cases, results were independent from the local reproductive success of the great tit, indicating that blue tits do not use great tits to gain information. However, both blue and great tits might serve as heterospecific sources of information for the other species because they share ecological requirements and are thus competitors (Dhondt 1989). In our study system, 53.3% of the occupied nest boxes were used by blue tits versus 42.7% by great tits. With such relative densities, great tits have about the same probabilities of acquiring information on breeding-habitat quality through conspecifics as heterospecifics. Furthermore, the two species share requirements (nest boxes and diet) and show a high overlap in their breeding phenology. Thus, heterospecific ISI is likely to be used by these species.

The local reproductive success of blue tits in 1year at the scale of patches (patch reproductive success, i.e., mean number of fledged chicks per patch) was manipulated via brood-size manipulations. Patches were either (1) manipulated to decrease the mean reproductive success of blue tits (treatment D), (2) unmanipulated (unmanipulated control), (3) manipulated by cross-fostering chicks between nests within patches of the same treatment, thus leaving blue tit patch reproductive success unchanged (manipulated control), or (4) manipulated to increase the local mean reproductive success of blue tits (treatment I). This manipulation of the quantity of juvenile blue tits produced in our study patches altered the quality of juveniles (mean body condition), generating a negative relation between the quantity and quality of fledglings (Parejo et al. 2007a) and thus allowing us to disentangle the role of these two cues (quality and quantity) in breeding-habitat selection. We expect manipulation to influence dispersal decisions in great tits. As number and condition of chicks in each nest are usually positively related, it is logical to assume that the most reliable estimate of quality must result from the use of the two cues simultaneously. If this is the case, we expect a preference of great tits for control (unmanipulated and manipulated control) over manipulated patches (D and I treatments). Alternatively, we might deduce that the correlation offers individuals with the possibility of estimating quality by the use of either of the two cues. In this case, we would expect a preference for both I and D patches relative to control patches (both unmanipulated and manipulated control). Finally, individuals might use only one of the two cues. If they rely on fledging number, for instance, we would expect a preference for I over the control (both unmanipulated and manipulated control) over D patches.

Materials and methods

Study system and methodology

The experiment was conducted during the spring of 2003 and its effects observed during the spring of 2004 in a 500-ha portion of a mixed deciduous forest of the Parc Régional de la Forêt d’Orient in central France (Aube, 48°17′ N, 4°17′ E). The study area was divided in patches of 8.14 ± 0.90ha each (mean ± SD, Fig. 1). Patches were separated by paths at least 3m wide. In the study area, there were 759 nest boxes evenly distributed over 31 patches, resulting in patches containing an average of 24.48 ± 0.52 nest boxes each (mean ± SD, Fig. 1). Further details may be found in Parejo et al. (2007a). Blue and great tits commonly used such nest boxes. There were empty boxes in all patches during the study period because nest boxes were provided in excess.

The blue and great tits are small, short-lived territorial hole-nesting passerines common in European woodlands (Cramp and Perrins 1993). In the study area, they are mostly sedentary (winter recaptures regularly occur). The mean size of the first clutch was 11.31 eggs (range = 5–17, $N = 228$) and 10.4 eggs (range = 5–14, $N = 161$) for blue and great tits, respectively. In both species, only the female incubates the eggs and broods the young, whereas both sexes feed and clean them. The nestling periods last 16–20days and 16–22days in blue and great tits, respectively (Cramp and Perrins 1993).

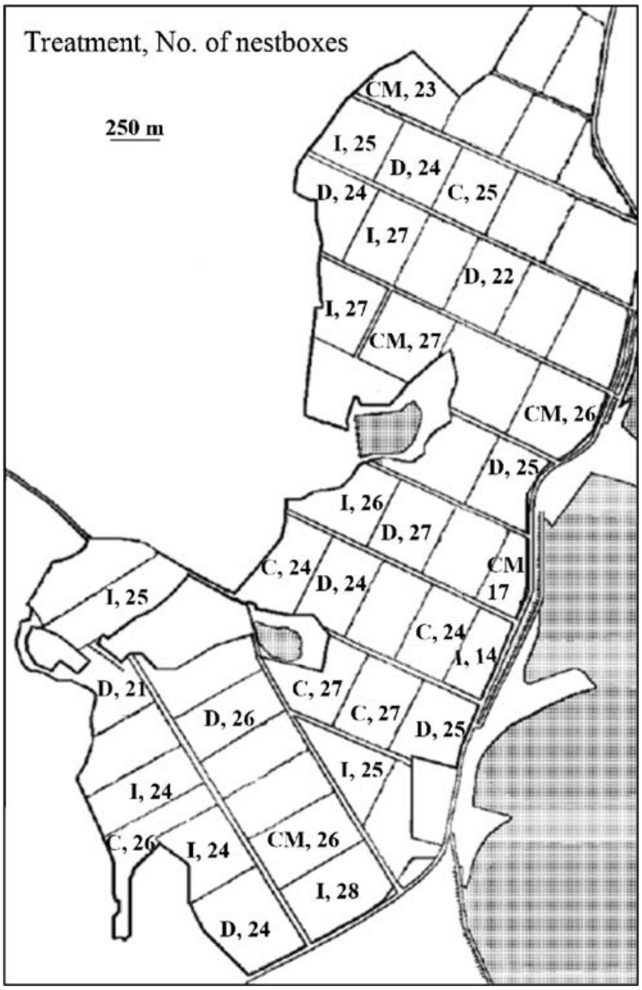

Fig. 1 Map of the study area with the 31 nestbox patches. Numbers within patches indicate the treatment and the number of nest boxes present in each patch. Patches with no data for the number of nest boxes are wooded patches with no nest boxes. The *gray area* indicates water, and the non-delimitated *white area* indicates cultivated fields. Experimental treatments are *D* decreased patches, *C* unmanipulated control patches, *CM* manipulated control patches, and *I* increased patches

As both species are cavity nesters, sharing nest boxes in the same forests, and feed mainly on arboreal arthropods, they can be considered to have overlapping ecology.

The nest boxes were checked regularly from nest building (early April) to fledging during each breeding season to determine reproductive parameters and compute emigration and immigration rates. Adults were captured, measured, and ringed in the nest boxes when chicks were from 8 to 13days old or identified during incubation and chicks ringed around 13days old. Measurements taken were body mass (measured with a Pesola spring balance with a precision of 0.1g) and tarsus length (measured with a sliding calliper to the nearest 0.1mm). In the 2003 breeding season, we captured 101 adult great tits, which represented 54.9% of the breeders that raised chicks until the age of

8 days, and we marked 837 chicks, which constituted 100% of the chicks that survived until the ringing age. From these marked individuals, only 49 (28 adults and 21 juveniles) were recaptured breeding in 2004. In that year, we captured 41.9% of the breeding adults (with 8-day-old chicks). The mortality rate for this species is high, for instance in Britain, mortality ranged from 0.56 to 0.60 (Clobert et al. 1988). Therefore, the low apparent local return rate may be a consequence of the high-mortality rate together with our relatively low capture rate of adults. However, as the adult capture effort in 2003, measured as the probability of each breeder to be captured, did not differ among treatments (logistic regression model: treatment effect, $\chi_3^2 = 4.80$, $P = 0.19$, $N = 210$), we can consider observed patterns as representative of the whole population. Dispersal distance between nest boxes used in the two consecutive years was estimated from the Universal Transverse Mercator coordinate of each nest box determined by the Global Positioning System. Position was recorded only when the estimated error was <5m.

Emigration was quantified by two variables: dispersal probability between patches in the two consecutive years as a binary variable (resident versus emigrant) and actual dispersal distance between subsequent nest boxes. Despite that data on individual dispersal distance could be skewed if many individuals dispersed very far and hence outside of our study system, we considered this measure in our emigration analyses because (1) the study area was a large (500ha), quite-isolated forest patch. Thus, dispersal seems far more likely to occur inside than outside the study area, and (2) even if some birds dispersed far away, it is important to understand dispersal within our large study system to understand its local population dynamics.

The immigration rate was computed as the ratio of the number of immigrants into a patch (number of breeders in the patch minus the faithful breeders) to the number of nest boxes that were available to great tits (nest boxes not previously occupied by insects or small mammals). Another estimate was the observed number of immigrants. These two estimates of immigration are likely to quantify different aspects of the immigration process. Indeed, while the number of immigrants is likely to estimate the attractiveness of a patch, the immigration rate quantifies the relative attractiveness of a patch by accounting for patch occupancy.

Population density for each tit species was computed for each patch as the proportion of nest boxes occupied by great or blue tits. This was realistic because patches had approximately the same dimensions and nest box density. Whenever patch dimension varied, nest box density varied proportionately (Fig. 1). The proportion of occupied nest boxes by blue tits ranged from 0.11 to 0.54 (mean = 0.31) and by great tits from 0.04 to 0.36 (mean = 0.17).

A nestbox was considered to be occupied when egg-laying began; only first clutches were included in these analyses.

Manipulation of blue tit reproductive success

Blue tits breeding success was manipulated at the patch scale by removing three 2-day-old nestlings from nests of the D treatment plots to nests (matched by hatching dates) of patches of the I treatment in 2003. In addition, nestlings were cross-fostered between pairs of nests of patches assigned to the manipulated control treatment. At the beginning of 2003, each patch was randomly assigned to one of the following treatments: (1) patches with decreased patch reproductive success of blue tits (D, $N = 10$ patches), in which the success of 51% ($\overline{X}$) of the 49 existing blue tit nests was reduced by removing three chicks; (2) unmanipulated control patches ($N = 6$ patches), in which no manipulation was performed and the natural blue tits' patch reproductive success remained unchanged; (3) manipulated control patches ($N = 5$ patches), in which 38% ($\overline{X}$) of the 21 blue tit nests had three chicks cross-fostered (both nests belonged to patches of the manipulated control treatment). This manipulation thus did not lead to any change in the blue tits' patch reproductive success. (4) Patches with increased patch reproductive success (I, $N = 10$ patches), in which the success of 49% ($\overline{X}$) of the 51 existing blue tits nests was enlarged. All patches thus included non-manipulated nests.

Statistical analyses

Analyses were performed using SAS statistical software (SAS 2001 Institute, Cary, NC, USA).

As in Parejo et al. (2007a), the effect of the treatment at the level of the patch on fledging quality and quantity was investigated by means of a linear mixed model (Mixed SAS procedure). In this analysis, we tested the effect of the treatment on chick body condition, introducing chick weight as the dependent variable, chick tarsus length and brood age as predictors, and the treatment as a factor. The nest was introduced as a random effect in this analysis because chicks from the same nest are not independent. The effect of the treatment on fledging quantity was analysed by a one-way analysis of variance (ANOVA; GLM SAS procedure) in which the number of fledglings per nest was the dependent variable and the treatment the factor.

The effect of the experimental manipulation of the blue tits' performance information on the great tits' emigration process was studied by performing (1) generalized linear mixed models with logit link function and binomial distribution (Glimmix SAS procedure), in which the probability of each great tit to emigrate from a patch between years 2003 and 2004 was the dependent variable; and (2) linear mixed models (Mixed SAS procedure), in which the log-transformed dispersal distance for each individual was the dependent variable. In these analyses, the sex of the individual was introduced as a factor to account for the fact that sex is known to affect dispersal decisions (Greenwood 1980), and blue and great tit densities (arcsin transformed) as predictors to take into account population density (of both con- and heterospecifics) as one of the factors affecting animal dispersal decisions (see review in Clobert et al. 2001). In addition, we introduced the mean patch reproductive success (mean number of fledged chick per patch) of great tits in the models to address the possible influence of conspecific performance information. Finally, the patch was introduced as a random effect nested within the treatment to take into account the possible non-independence of individuals from the same patch.

The effects of the treatment on both the great tits' individual emigration probability and dispersal distance were studied separately for juveniles and adults because factors affecting natal and breeding dispersal are likely to differ (Clobert et al. 2001). For juveniles, determinants of dispersal probability could not be analysed because, among recaptured juveniles, only one recruited in its natal patch. When analysing the dispersal of juveniles, the low sample size did not allow us to perform the statistical analysis with the patch nested within the treatment as a random effect. Therefore, to account for this possible non-independence of data, we performed two different analyses of covariance (GLM SAS procedure): one with all the dispersal events and the other one with one random dispersal event per patch. Although the dispersal of adults and chicks from the same nests may not be statistically independent events, we considered them independent in the emigration analysis because all the 49 individuals recaptured in 2004 came from 44 different nests and, except for two individuals that were faithful to both mate and nest in the two subsequent years, no bird coming from a specific nest, either adults or juveniles, went to the same nest as its partner, offspring, siblings, or parents.

General linear models and generalized linear mixed models (GLM and Glimmix SAS procedures) were used to test for the effect of the experimental treatment on the immigration rate and on the number of immigrants to a patch. The experimental treatment was introduced in the model as a factor, and blue and great tit densities (arcsine transformed), as well as mean patch reproductive success of great tits as co-variables. Analysis of the number of immigrants was performed with log-link function and Poisson error, using the SAS macro-GLIMMIX.

Significance level was set at $\alpha = 0.05$. The best-fit model for analyses was determined using Akaike's information criterion as an estimate of the improvement in fit for the addition of variables (Burnham and Anderson 2002). Because the number of data points in the models divided by K (the number of parameters in the model) is always less than 40, AIC was corrected for small sample sizes (known as AICc) following Burnham and Anderson (2002). The model with the lowest value of AICc is the most parsimonious one and therefore the model selected. The Akaike weights give the relative support that a given model has from the data compared with the other models in the set (all information in Burnham and Anderson 2002). Only the five top-ranked candidate models are reported.

Our results were qualified by calculating power with the G-Power program version 3.0.5, assuming $\alpha = 0.05$ and the thresholds suggested by Cohen (1992) for differences or changes in means of 0.2, 0.5, and 0.8 for respectively small, medium, and large effect sizes.

Results

Manipulation of blue tit reproductive success

The experimental manipulation affected mean chick body condition of blue tits (Fig. 2a, modified from Parejo et al. 2007a; Fig. 2a) once the effect of chick age and the random effect of the nest were controlled. Mean body condition of blue tit chicks was higher in D patches than in I patches and in nests in control patches that had, in general, chicks of intermediate condition (Fig. 2a), although in unmanipulated control patches (NMC in Fig. 2), chick quality was almost as high as in D patches. Mean chick body condition, however, did not differ between the two types of control patches. The experimental manipulation also affected the mean fledgling number per breeding blue tit pair per patch (i.e., patch reproductive success; Fig. 2b, modified from Parejo et al. 2007a; Fig. 2b): The mean number of fledglings was higher in I patches and lower in D patches compared to the control patches (Fig. 2b). The mean number of fledglings did not differ between the two types of control patches. Data from the two control treatments (C) were combined for subsequent analyses because neither the mean body condition nor the mean number of fledglings per patch differed between these two treatments.

Furthermore, our experiment produced a negative relationship between the mean body condition and mean number of fledglings of blue tits that does not exist under natural conditions in the population, given that we found no relationship between these two variables in blue tit unmanipulated nests after controlling for chick age, chick tarsus length, and the random effect of the nest (see Parejo et al. 2007a).

Effect of the manipulation of blue tit reproductive success on great tit emigration

We found an effect of the age (juvenile versus adult) of the individual in 2003 on emigration probability (logistic

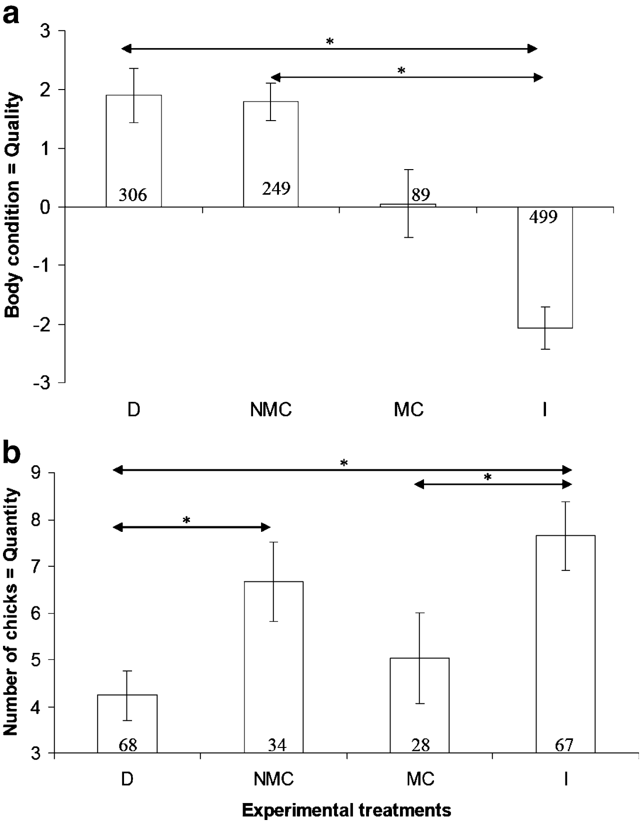

Fig. 2 Effect of the experimental manipulation of PI in 2003 on **a** mean chick body condition and **b** mean number of chicks per nest. *Error bars* are standard error. Chick body condition is computed as the residuals of the general linear mixed model performed analysing the effect of tarsus length, chick age at capture, and the random effect of the nest on chick mass. *Numbers inside bars* are sample sizes of individuals (*top panel*) and nests (*bottom panel*). Only significant pairwise differences are shown, with *arrows* designating pairs and asterisks indicating significant differences. Neither mean chick body condition (P=0.54) nor mean number of chicks (P=0.21) differed between the two types of control patches. Experimental treatments are *D* decreased patches, *NMC* control patches, *CM* manipulated control patches, and *I* increased patches. *P<0.05. Modified from Parejo et al. (2007a)

regression model: $\chi^2_1 = 21.77$, $p < 0.0001$, $n = 49$ individuals) and on dispersal distance (ANOVA: $F_{1,41} = 62.89$, $P < 0.0001$, $n = 43$ individuals). We thus performed separate analyses for each age class.

The most parsimonious model to explain adult great tit emigration probability between 2003 and 2004 retained blue and great tit densities and the patch treatment (Table 1). However, neither blue tit density ($F_{1,23} = 1.54$, $P = 0.23$, $n = 28$ individuals) nor great tit density ($F_{1,23} = 2.25$, $P = 0.15$, $n = 28$ individuals) proved to be related to adult emigration probability. The patch treatment did not affect the adult emigration probability either ($F_{2,23} = 0.30$, $P = 0.74$, $n = 28$ individuals, Fig. 3a). A model including great tit density and the treatment showed the same Akaike weights, although in this case, none of the explanatory variables (great tit density: $F_{1,24}$=0.78, P=0.39; treatment effect: $F_{2,24}$=0.35, P=0.71, n=28 individuals) were significant in the model either.

The most parsimonious model explaining adult dispersal distance of great tits included heterospecific population density (Table 1). The two variables, adult great tit dispersal distance and heterospecific population density, were negatively related ($F_{1,20}$=8.16, P=0.01, regression coefficient=−1.39, n=22 individuals). Adult dispersal distance did not differ among experimental patch treatments (Fig. 3b) because models in which treatment, great tit density, patch effect (nested within the treatment effect), or sex effects were added had considerably lower Akaike weights than did the selected one (Table 1).

The dispersal distance of juvenile great tits did not differ according to the manipulation performed at the patch scale (Table 1). The selected model to explain the dispersal distance of juveniles included blue tit density when we analysed all data and sex when using only one datum per patch (Table 1). However, neither blue tit density ($F_{1,19}$= 1.31, P=0.27, n=21 individuals) in the first analysis nor sex of the individual ($F_{1,10}$=4.93, P=0.05, n=12 individuals) in the second were related to juvenile dispersal distance. Models in which the treatment effect was added had lower Akaike weights (Table 1).

Effect of the manipulation of blue tit reproductive success on great tit immigration

Great tit local immigration rate from 2003 to 2004 did not differ among treatments (Fig. 3c). The most parsimonious model to explain great tit local immigration rate included conspecific local density, which was positively related ($F_{1,28}$=54.29, P<0.0001, regression coefficient= 0.57, n=31 patches), and heterospecific density, which was negatively related ($F_{1,28}$=6.74, P=0.01, regression coefficient=−0.24, n=31 individuals; Table 1). Nevertheless, it should be taken into account that the great tit immigration rate was not independent of the conspecific local density because the former was estimated as the number of immigrants into a patch (number of breeders in the patch minus the faithful breeders)/number of nest boxes not previously occupied by insects or small mammals, while the latter was the number of faithful breeders.

The number of great tit immigrants did not differ among treatments (Fig. 3c). The most relevant model positively related the number of immigrants to local heterospecific density in 2003 ($F_{1,29}$=14.23, P=0.001, regression coefficient=1.80, n=31 patches, Table 1). The model in which

Table 1 Models for the factors determining emigration and immigration of great tits

Model	Factors	*K*	Deviance	AICc	ΔAICc	Akaike weight
Adult dispersal probability						
1	**BT density, GT density, treatment**	**5**	**30.98**	**121.1**	**0.00**	**0.08**
2	GT density, Treatment	4	34.36	121.2	0.10	0.08
3	Sex, GT density, Treatment	5	34.08	121.5	0.40	0.07
4	Sex, BT density, Treatment	5	32.83	121.8	0.70	0.06
5	BT density, Treatment	4	32.86	121.9	0.80	0.06
Adult dispersal distance						
1	**BT density**	**3**	**3.35**	**27.5**	**0.00**	**0.25**
2	BT density, GT density	4	3.31	28.8	1.30	0.13
3	BT density, patch (treatment)	4	3.35	28.9	1.40	0.13
4	BT density, treatment	4	3.05	29.3	1.80	0.10
5	Sex, BT density	4	3.34	29.9	2.40	0.08
Juvenile dispersal distance (all individuals considered)						
1	**BT density**	**3**	**1.33**	**9.0**	**0.00**	**0.22**
2	BT density, treatment	4	1.04	10.1	1.10	0.13
3	GT density	3	1.36	10.8	1.80	0.09
4	BT density, GT density	4	1.30	11.0	2.00	0.08
5	Sex	3	1.32	11.7	2.70	0.06
Juvenile dispersal distance (only one individual per patch considered)						
1	**Sex**	**3**	**0.61**	**7.7**	**0.00**	**0.12**
2	Sex, Treatment	4	0.36	7.9	0.20	0.11
3	Sex, BT density	4	0.61	8.1	0.40	0.10
4	Sex, BT density, treatment	5	0.34	8.7	1.00	0.07
5	BT density	3	0.91	8.7	1.00	0.07
Local immigration rate						
1	**BT density, GT density**	**4**	**0.22**	**−47.8**	**0.00**	**0.71**
2	GT density	3	0.27	−45.8	2.00	0.26
3	BT density, GT density, GT patch RS	5	0.20	−40.0	7.80	0.01
4	BT density, GT density, treatment	5	0.20	−39.1	8.70	0.01
5	GT density, treatment	4	0.25	−37.7	10.1	0.00
Number of immigrants						
1	**BT density**	**3**	**35.67**	**51.0**	**0.00**	**0.51**
2	BT density, GT density	4	35.46	52.1	1.1	0.30
3	BT density, treatment	4	35.59	54.8	3.8	0.08
4	BT density, GT density, treatment	5	35.37	56.4	5.4	0.03
5	BT density, GT patch RS	4	34.84	57.3	6.3	0.02

The independent variables considered were the sex, the manipulated (patch reproductive success of blue tits = treatment) and unmanipulated inadvertent social information (density of blue and great tits, patch reproductive success of great tit), and the patch nested inside the treatment as a random factor. For each case, only the five top-ranked models are shown. The selected model is in bold type. *K* is the number of estimated parameters. *BT* blue tit, *GT* great tit, *RS* reproductive success.

treatment effect was added had much lower Akaike weights (Table 1).

Discussion

The experimental manipulation that we performed to modify blue tit patch reproductive success, as one of the forms of ISI, was successful and affected blue tit dispersal decisions (Parejo et al. 2007a). However, our results suggest that great tits do not use the heterospecific breeding performance in their dispersal decisions.

There are several potential explanations for the lack of evidence of the use of heterospecific breeding performance by great tits:

1. An experimental design including all possible combinations of quality and quantity of fledglings (high quality–high quantity, high quality–low quantity, low quality–high quantity, and low quality–low quantity) could be thought

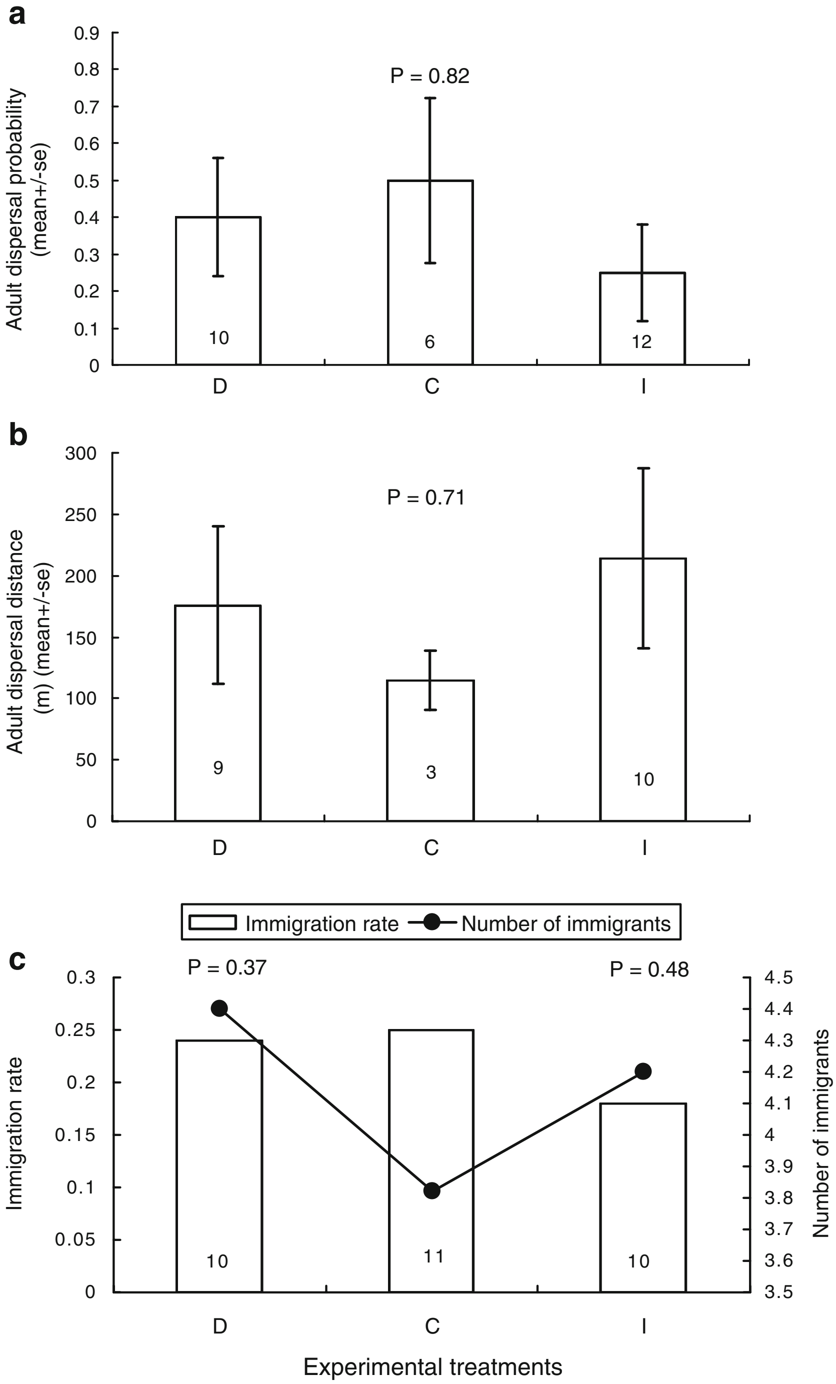

Fig. 3 Effect of experimental manipulation of blue tits' performance in 2003 on the dispersal probability of adult great tits in 2004 (*top panel*), the dispersal distance of adult great tits in 2004 (*middle panel*), and the immigration rate and the number of immigrants to the patches in year 2004 (*bottom panel*). *Numbers inside bars* are sample sizes (individuals in the top and middle panels and patches in the bottom panel). *P* values are provided for the treatment effect. Experimental treatments: *D* decreased patches, *C* control patches, *I* increased patches

to be more suitable than the approach used here. That design would generate overlapping predictions for each of the combinations, while our design generates two predictions that separate each combination between quality and quantity of fledglings. Therefore, our experimental design seems to be simpler than and, at least, as valid as the other design to test the working hypothesis.

2. Another explanation relates to time constraints because the gathering of performance based information may occur only during the short time during which heterospecific breeding performance is available (i.e., at the end of the nestling period), and synchrony is likely to be lower among heterospecifics than among conspecifics.
3. Alternatively, in that system, it may well be that costs of interspecific competition exceed the benefits of acquiring information from heterospecifics. In our study area, tit breeding density is not very high (mean number of breeding pairs of tits/ha = 1.5), although other nest box studies have reported density-dependent effects at similar or lower breeding density (e.g., Wilkin

et al. 2006). In any case, if competition diminishes the value of the information, it would lead to heterospecific avoidance, but for resident great tits, we found exactly the opposite pattern because they appeared to prefer patches with high blue tit densities.

4. Another possibility is that the overlap in resource use between these two species is not great enough to make the information from heterospecifics valuable. However, the two species have been shown to compete during the breeding season (Dhondt 1989) as well as during the winter (Hogstad 1989). Moreover, great tits seem to use information on heterospecific density.
5. Alternatively to the last possibility is the fact that the two study species are residents and non-hoarding tits, and thus, they tend to be equally informed on habitat quality, this diminishing the probabilities of heterospecific information use. The use of information produced by heterospecifics has been suggested to be more likely in situations in which individuals of one species have less accurate information on local habitat quality than the other species (Seppänen et al. 2007).
6. Nevertheless, it is possible that heterospecific habitat copying was not detected simply because that strategy is beneficial only under some environmental circumstances. Our study covered only 2 years, and thus it may be that the use of heterospecific performance information was not advantageous at that moment. Therefore, more multiple-year studies would be needed to elucidate the environmental parameters that influence the role of information on con- and heterospecific breeding performance in breeding habitat choice.
7. Finally, our sample size might not have been large enough to allow us to detect statistically significant differences among treatments in great tit individual dispersal decisions. Indeed, power calculations for our analyses revealed a low power (ranging from 0.11 to 0.14) to detect low effect sizes (0.20), a moderate power (ranging from 0.48 to 0.65) to detect medium (0.50) effect sizes, and a high power (ranging from 0.88 to 0.97) for large effect sizes (0.80). This allows us to conclude that the experimental manipulation of heterospecific performance information does not exert a large effect and probably not a medium effect either on great tit dispersal decisions. Subtle effects of our experiment, however, may be unnoticeable with our sample sizes.

Adult great tit emigration and immigration decisions correlated with information on con- as well as heterospecific abundance, which may constitute other potential sources of ISI. Conspecific and heterospecific attraction have been shown in many animals, either as the main mechanism explaining habitat selection (e.g., Forsman et al. 2002, Nocera et al. 2006, and Fletcher 2007) or as one more among all the mechanisms used in a population (e.g., Doligez et al. 2004 and Parejo et al. 2007a). However, in the literature, apart from the widely accepted use of neighbours as indirect measures of habitat quality (Forsman et al. 2002; Fletcher 2007), other possible mechanisms have been proposed to explain con- and/or heterospecific attraction, such as increased mating success and positive density dependence effects (i.e., the Allee effect; Stamps 1988).

Adult great tits dispersal distance negatively related to blue tit density. Meanwhile, the immigration rate in 2004 was positively related to patch-specific conspecific density in 2003 and the number of immigrants to patch-specific heterospecific density. Although the result concerning immigration rate might be affected by the relationship between immigration rate and conspecific local density, the fact that the three analyses indicate the same strengthens the results. Furthermore, great tit immigration rate was negatively related to local heterospecific density in 2003, which may simply be a result of competition. All together, these results suggest that (1) great tits may be influenced by heterospecifics in dispersal decisions but (2) appear to consider conspecifics also in settlement decisions. These results are not surprising if we bear in mind that information availability for emigrants and immigrants may differ greatly (Doligez et al. 2002). Indeed, only local breeders, i.e., emigrants and birds immigrating from immediate vicinity, have access to information about a given breeding patch throughout the breeding season. For many immigrants, the time available to gather information on future breeding patches is limited to the period after breeding, which may constrain immigrants in gathering information on the easiest cues, which are extracted from conspecifics.

The use of information produced by con- or heterospecific density rather than performance may result from the longer time availability of the former. Local population density may be evaluated all year long, including at the beginning of the following season, while information on breeding performance may be assessed only during a short time at the end of each reproductive season (Boulinier et al. 1996). Consequently, habitat selection based on density is likely to be a more ubiquitous strategy in resident birds such as the great tits as they spend much of the year in the reproductive habitat. Similar studies on the collared flycatcher (*Ficedula albicollis*) suggest that conspecific density likely constitutes a valuable source of information even in migratory species (Doligez et al. 2004).

None of the variables analysed seems to affect juvenile dispersal decisions. Although the use of information produced by the breeding performance of neighbours is particularly expected in juveniles because they cannot rely on their own reproductive success (Danchin et al. 1998), juveniles may be unable to gather this kind of information due to time constraints (Doligez et al. 2004; Nocera et al.

2006; Parejo et al. 2007a). Similarly, our results suggest that ISI taken from local population density is probably less influential in great tit juveniles, as their dispersal decisions were not associated to con- and/or heterospecific density.

Great tits in our population seemed not to rely on conspecific breeding performance. However, as this variable was not manipulated in our study, we cannot conclude definitively that great tits do not use it, only that their dispersal decisions seem to be more influenced by con- and heterospecific density as sources of ISI.

In conclusion, our study reveals that great tits might use interspecific ISI more in the form of density than actual breeding performance. When making habitat selection decisions, great tits did not appear to respond to the manipulated blue tit reproductive success, either to the number or to the condition of fledglings, but seemed to be influenced by heterospecific density. The basis of this may reside in the difficulty in distinguishing between these two tightly intertwined forms of information, density, and breeding performance. As we manipulated only heterospecific breeding performance and not heterospecific density, our only firm conclusion is that heterospecific breeding performance is not the main cue used by great tits when selecting a breeding habitat and that it is apparently less influential than heterospecific density. As habitat copying may be defined as breeding habitat selection based on ISI (Wagner and Danchin 2003, Danchin et al. 2004), and great tits seem to rely on heterospecific density as a form of ISI, we may conclude that great tits might be using a heterospecific habitat copying strategy.

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