# Breeding dispersal of Great Tits *Parus major* in a homogeneous habitat: effects of sex, age, and mating status

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We studied patterns of breeding dispersal of adult Great Tits *Parus major* in a homogeneous habitat (extensive orange plantations) in eastern Spain. Data included 482 movements of known individuals gathered during 11 years. Most birds (67%) did not change territory between seasons. Dispersal propensity was independent of sex, and decreased with age at least up to the sixth year of life. Of birds that changed territory, 92% moved less than 200 m. Young females dispersed significantly farther than adult males, while values for young males and adult females were intermediate. About two thirds of the birds kept the same mate in consecutive years. Both males and females that changed mate dispersed more often than faithful individuals, and females, but not males, dispersed also farther after mate change. Most individuals changed mate because of the death of their partner. The probability of dispersal was similar for widows and divorcees of either sex. However, distances moved by widowed females were longer than those of widowed males or divorced males or females. We discuss these results within the context of breeding dispersal in passerines. Results generally agree with the ideas that (1) females disperse more than males; (2) dispersal tendency decreases with age; and (3) dispersal is more frequent after mate change. However, the interactions among sex, age and mating status, as well as characteristics of the habitat, modulate these general trends, so that dispersal patterns could vary both within and between populations of the same species.

Key words: Dispersal patterns, divorce, mate change, *Parus major*, sex-biased dispersal, territory change, widowing

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## INTRODUCTION

Dispersal is a fundamental process in the life of all organisms, since it might affect the two major components of fitness: fecundity and survival (e.g. Clobert *et al.* 2001a, Bullock *et al.* 2002). Two broad types of dispersal, with different causes and consequences, are usually considered: natal dispersal ('the movement between the natal area or social group and the area or social group where breeding first takes place') and breeding dispersal ('the movement between two successive breeding

areas or social groups') (Clobert *et al.* 2001b, see also Kenward *et al.* (2002) for a more complex nomenclature).

Several patterns of breeding dispersal have been described for birds (Greenwood & Harvey 1982, Clarke *et al.* 1997, Newton 2001a). For example, dispersal is generally more frequent and/or distances moved are longer (1) in females (vs. males), (2) in young birds (vs. older ones), and (3) after mate change. These patterns show, however, abundant exceptions which are not easily predictable from the characteristics of the species involved, so it does not seem to be appropriate to assume them to hold for any species. Some examples follow.

In a first review, Greenwood (1980, Greenwood & Harvey 1982) found that, among birds, females use to disperse more than males. Later reviews (e.g. Clarke *et al.* 1997) confirmed this pattern, though it is not universal, nor is it constant within species or even between subsets of the population (e.g. widowed and divorced individuals). Clarke *et al.* (1997: p. 435) explicitly said "... for many species it is inappropriate to consider a sex bias in dispersal to be a species constant."

A clear pattern of decreasing dispersal with increasing age has been found in long-lived birds (reviewed in Newton 2001a), apparently related to benefits of site-familiarity through life. Evidence for short-lived passerines is, however, less clear. For example, Payne & Payne (1993) found that young male Indigo Buntings *Passerina cyanea* disperse more frequently than adults, but this pattern was not significant for females. Montalvo & Potti (1992) found that young female Pied Flycatchers *Ficedula hypoleuca* disperse further than older ones, a pattern not found in males. Moreover, whether young birds disperse more than adults depend on the habitat characteristics (e.g. Foppen & Reijnen 1994). So, again, a context-dependent age-biased dispersal could be expected to occur within a species.

Finally, although a trend to disperse more frequently and further after mate change has been described (Newton 2001a), this pattern is not always found in both sexes. For example, Morton (1997) found that female Mountain White-Crowned Sparrows *Zonotrichia leucophrys oriantha* which changed mate dispersed farther than those that keep the same mate, but this was not found for males. More difficult to compare are those studies that include the causes of mate change (divorce vs. widowing). Both differences in dispersal patterns between divorced and widowed birds (Harvey *et al.* 1979) and between sexes among divorced (Harvey *et al.* 1979, Desrochers & Magrath 1993, Saitou 2002) or widowed birds (Harvey *et al.* 1984) have been found.

Methodological problems could in part contribute to differences in the patterns found, such as difficulties in following birds dispersing outside the study area (e.g. Nathan 2001), the parameter actually studied (proportion of birds dispersing or distance moved; e.g. Clarke *et al.* 1997), the use of exact age or age classes (e.g. juveniles vs. adults), and the use of different categories of birds according to their mating status, not always comparable between studies. Interactions in dispersal propensity or distances among sex, age and mating status have arisen when they have been looked for (e.g. Harvey *et al.* 1979, Montalvo & Potti 1992, Morton 1997, Saitou 2002), so including all these factors in the analysis of dispersal seems necessary. Dispersal patterns might also be affected by the heterogeneity or fragmentation of the habitat (e.g. Foppen & Reijnen 1994, Matthysen 2002, Dale *et al.* 2005).

In spite of being an intensively studied species, breeding dispersal patterns of Great Tits *Parus major* have been the subject of very few studies. To find papers devoted to breeding dispersal we have to go back to studies made in the late seventies by Harvey *et al.* (1979), or earlier (e.g. Kluijver 1951). Nonetheless, some information on dispersal distances and causes related to it have been recently made available by Saitou (2002), Van de Casteele *et al.* (2003), Pampus *et al.* (2005) and Tinbergen (2005) in the context of other studies. Apart from the fact that some of the aspects studied in one population are unlikely to be extended to others (e.g. Clarke *et al.* 1997), some basic topics, as the possible effects of age on dispersal, have not been dealt with to date.

**Figure 1.** View of the study area in Sagunto (Valencia, Spain) with extensive orange plantations (photo J. Andreu).

Our aim was to describe the patterns of breeding dispersal of Great Tits in a homogeneous habitat, in relation to sex, age and mating status. We tried to overcome some of the problems discussed above, considering both proportion of bird dispersing and distances moved, including both exact ages of the birds (up to 6 years old) and age classes (juveniles and adults), and clearly separating the possible mating status categories (faithful, divorced and widowed individuals).

## METHODS

Data used here were collected during a long-term study on the breeding ecology of Great Tits in eastern Spain (e.g. Monrós *et al.* 2002, Barba *et al.* 2004). The study area was located within extensive orange plantations in Sagunto (Valencia, Spain; Fig. 1), and the only obvious heterogeneity was by the different age of the trees on each grove. Nestboxes were available each year from late February to the end of the breeding activities, by mid July. Usually, nestboxes were placed in the

same tree each year, but there were some changes caused by removal of some trees to plant new ones. 105 nestboxes were available in an area of 85 ha in 1992, and some nestboxes were added in the following years, totalling 120 in 1998. The area was enlarged to 110 ha, and 30 more nestboxes were placed, in 1999 (Fig. 2). The study area was surrounded by similar habitat (orange plantations).

The position of each nestbox was recorded using a GPS. Distances between all nestboxes available one year and the next, were estimated from UTM coordinates. From these, we computed a matrix of potential dispersal distances each year. For each year, we computed the minimum distance between each nestbox and the nearest nestbox next year, being the mean of the annual means 61.08 m (SD = 2.99; range 57–68 m). On average, the occupation rate was 74% (ranging from 46%, the first year of the study, to 90%).

Core data for this study were collected between 1992 and 2002 (i.e. the last dispersal event considered was that of birds breeding in 2001 and 2002). An exception was made for

**Figure 2.** Map of the study area showing the distribution of the nestboxes in 2000. We show, for this particular year, the distribution of 'core' and 'border' nestboxes.

analyses concerning the mating status of the birds (widows or divorcees). For these, the last dispersal event considered was that of birds breeding in 1999 and 2000; we then used information from 2001 and 2003 breeding seasons to confirm whether the birds were alive in 2000. We assumed that, if a bird which bred in 1999 was not captured as breeder between 2000 and 2003, it was dead before the 2000 breeding season. Data include 482 dispersal events where the breeding places of individuals in two consecutive breeding seasons were known (including the occupation of the same nestbox in consecutive years, where dispersal distance equals zero). Individuals involved in experiments were excluded.

All the birds used in this study were individually ringed or were ringed at their first capture. All the birds were captured during feeding nestlings, and after capture sex and age were recorded. We captured an average of 59% (range 48–70%) of breeding birds in normal years (only 6% were captured the first year and only 26% in 2002, due to large-scale desertion of first clutches after heavy rains). Over 95% of the breeding birds that had nestlings were caught each year. We grouped the birds into 'young' (first-year breeders) and 'adults', based on plumage characteristics. Four individuals could not be assigned to either of these categories, so they were not used in analyses involving age

classes. For birds that were ringed as nestling, fledgling or as first-year breeders, the exact age could be determined, which was subsequently used in some of the analyses.

Breeding dispersal data were treated in two ways which might underlie independent decisions by the birds (e.g. Clarke *et al.* 1997, Forero *et al.* 1999). First, they were treated as a categorical variable, considering whether the bird had changed its breeding place between years or not. Average Great Tit density in the study area was 0.98 (SD = 0.15, range 0.86–1.16, except the first year which was 0.58) pairs/ha, so we assumed 'territories' to have about 50 m radius. Thus, we assumed that a bird changed territory if it moved more than 50 m, and these birds are referred hereafter as those actually 'dispersing'. Movements shorter than 50 m generally involved the re-occupation of the same nestbox at the same site (i.e. dispersal distance = 0), but 'short movements' also occurred when the nestbox had been moved from its previous place to the nearest available site after cutting off or severe pruning of the tree where it was placed.

Second, the actual distance between two consecutive places could be measured from UTM coordinates. In this paper, 'breeding dispersal distance' is defined as the linear distance between first clutches of two consecutive years. Second or

repeat clutches were relatively rare in our population (e.g. Barba *et al.* 1995) and were not included in the analyses. We only performed analyses using actual distances for birds that changed territory, i.e. those moving more than 50 m.

We checked whether dispersal distances were related to annual densities in both years involved in each dispersal event. None of the linear regressions performed were significant (for the 'starting year': $r = 0.21$, $F_{1, 8} = 0.36$, $P = 0.57$; for the 'finishing year': $r = 0.29$, $F_{1, 8} = 0.74$, $P = 0.41$). Therefore, we did not take into account annual differences in densities in the analyses performed.

We also tried to detect whether there was a 'border effect' in our data, i.e. whether dispersal distances differed between boxes placed at different distances from the boundary of the study area. To do this, we divided the study area into two subareas, a 'core' and a 'border' subarea. To achieve similar group sizes, the border subarea included all the nestboxes within 75 m from the border ($n = 128$), while the core subarea included 116 nestboxes. The total was higher than the number of nestboxes placed in any single year since we used the accumulated map of nestbox locations over the study years; an example is shown in Fig. 2 for year 2000. We found no significant differences in dispersal distances from core ($n = 76$) or border ($n = 86$) nestboxes (Mann-Whitney $U = 2778$, $P = 0.10$).

It was not possible to transform the data on dispersal distances to achieve normality, so parametric tests were not adequate for our data and we used non-parametric tests throughout. The effects of different factors on the probability of dispersal were analysed with stepwise logistic regressions (backwards procedure). We give the statistics (Wald) of the variables finally included in the model, or indicate $P > 0.05$ if no variable was included. Effects of different factors on the distances moved were analysed with Mann-Whitney or Kruskal-Wallis tests. *A posteriori* tests performed after significant Kruskal-Wallis tests were done by multiple comparisons between treatments (e.g. Siegel & Castellan 1989), and were considered significant if $P < 0.05$. To have an idea of the possible importance of interactions between factors on the distances moved, we repeated the analyses using ANOVAs. None of these results were significant, and are not presented.

A potential problem in long-term studies is pseudoreplication – the non-independence of dispersal data of the same individual in different years. We approached this problem in two different ways. First, we repeated all the analyses including a single randomly selected observation from each individual ($n = 301$ dispersal events instead of 482), and none of the results changed (except the comparisons between widowed and divorced birds for which sample sizes were too small to perform sensible analyses). Second (though data were not normally distributed and therefore the approach was not strictly correct), we performed hierarchical models to test for differences in dispersal distances among sexes and age classes. Sex and age (juveniles, adults) were included as factors and individual (random effect) as a nested factor within age and sex. Sample sizes in this analysis were 130 different individuals and 160 dispersal events. The effect of the individual was not significant ($F_{19,138} = 0.65$, $P = 0.92$), so using different dispersal events from the same individual probably would not bias the results.

## RESULTS

### Change of territory between consecutive breeding seasons

Out of 482 dispersal events studied, 323 (67%) did not involve a change of territory between consecutive breeding seasons. Therefore, Great Tits of the population of Sagunto tended to stay in a territory once they bred in it. The probability of changing territory was independent of sex (males: 30%, $n = 208$; females 35%, $n = 270$), but young birds moved more frequently than adults (39%, $n = 147$, vs. 30%, $n = 331$; logistic regression, with sex, age and their interaction as factors in the initial model, Wald = 4.72, $df = 1$, $P = 0.03$). Results were the same using only birds for which the exact age was known ($n = 328$ dispersal

events), since only age entered the model (Wald = 7.45, $df = 1$, $P = 0.006$). The probability of changing territory decreased with age, at least up to the sixth year of life (Fig. 3).

### Dispersal distances

Among dispersal events implying change of territory, 92% of the cases were shorter than 200 m (medians were between 69 and 100 m in different



**Figure 3.** Decrease of the probability of breeding dispersal with age in Great Tits in Spanish orange groves ($y = 1/(1 + e^{0.179+0.275x})$, $P = 0.006$). Sample sizes are indicated.

years; Table 1). For all the study years these values were significantly lower than the potential distances considering all the nestboxes available (medians between 560 and 912 m; Table 1).

There were significant differences in dispersal distances (medians) among sex and age classes (Kruskal-Wallis, $\chi^2 = 8.24$, $df = 3$, $P = 0.041$; Fig. 4). *A posteriori* analyses showed that young females dispersed significantly farther than adult males while young males and adult females dispersed at intermediate distances and did not differ significantly from any of the other categories.

Lumping both sexes, we found no significant differences of dispersal distance among birds of different ages (Kruskal-Wallis, $\chi^2 = 3.65$, $df = 3$, $P = 0.30$, $n = 106$). There was no trend with age (Spearman rank correlation, $r_S = -0.049$, $P = 0.62$, $n = 106$). Sample sizes were too small to test both sexes separately.
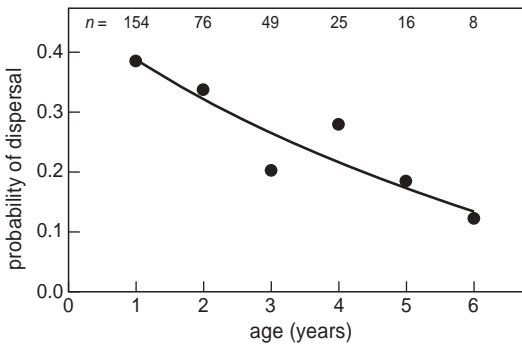
### Effect of mate change

Among individuals whose mate was known in two consecutive years, about two thirds kept the same mate (68% for males, $n = 119$; 63% for females, $n = 209$). Among these faithful pairs, 74% did not change territory and 20% moved to the neighbouring territory.

**Table 1.** Comparison between actual distances dispersed by adult Great Tits and potential distances available in a nest box study in Spanish orange groves. Potential distance is between each nestbox occupied by a bird which dispersed and all the nestboxes placed the following year. The number of movements reflects the number of dispersal events implying a change of territory (i.e. longer than 50 m).

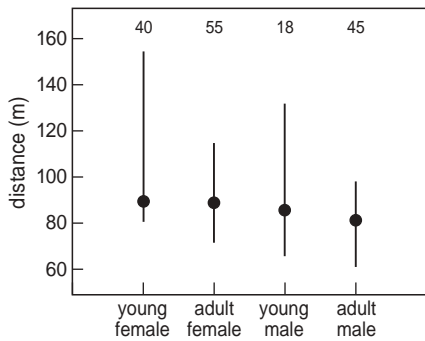| Year | Number of movements | Potential median (m) | Observed median (m) | $U$ | $P$ |
|---|---|---|---|---|---|
| 92-93 | 3 | 912.0 | 89.9 | 50.5 | 0.008 |
| 93-94 | 21 | 647.0 | 69.3 | 1915 | < 0.001 |
| 94-95 | 21 | 602.1 | 91.1 | 2575.5 | < 0.001 |
| 95-96 | 9 | 598.1 | 82.3 | 318.5 | < 0.001 |
| 96-97 | 7 | 580.9 | 87.1 | 178.5 | < 0.001 |
| 97-98 | 16 | 559.5 | 86.2 | 898.5 | < 0.001 |
| 98-99 | 21 | 697.6 | 87.7 | 4505.5 | < 0.001 |
| 99-00 | 29 | 697.2 | 99.5 | 5855 | < 0.001 |
| 00-01 | 15 | 629.3 | 72.6 | 981.5 | < 0.001 |
| 01-02 | 19 | 678.1 | 93.1 | 1653 | < 0.001 |

**Figure 4.** Dispersal distances in relation to sex and age class of Great Tits in Spanish orange groves. Medians, 25% and 75% percentiles, and sample sizes are given. Differences between young females and adult males were significant ($P < 0.05$).



**Figure 5.** Dispersal distances of female Great Tits in relation to mate fidelity.

Birds changing mate more often changed territory than faithful ones (45%, $n = 164$, vs. 36%, $n = 178$; logistic regression, Wald = 14.26, $df = 1$, $P < 0.001$), and juveniles more often than adults (41%, $n = 142$, vs. 31%, $n = 262$; logistic regression, Wald = 4.08, $df = 1$, $P = 0.04$), but neither sex, nor interactions between these factors affected the probability of territory change. However, we found sex differences in the distances moved by dispersers. Thus, females that had a new mate moved significantly longer distances (median = 98.8 m, $n = 45$) than faithful individuals (median = 82.9 m, $n = 32$; Fig. 5), while males changing mate (median = 83.7 m, $n = 30$) did not differ from either females changing mate or faithful individuals (Kruskal-Wallis, $\chi^2 = 8.19$, $df = 2$, $P = 0.017$, followed by *a posteriori* multiple comparisons).

**Widowed and divorced birds**
Most individuals changed mate because of the death of its previous one (69% of cases for males, 76% for females). The probability of territory change was not significantly affected by mating status (divorcees: 46%, $n = 35$; widows: 42%, $n = 92$), sex, age class, or interactions between these factors (logistic regression, $P > 0.05$).
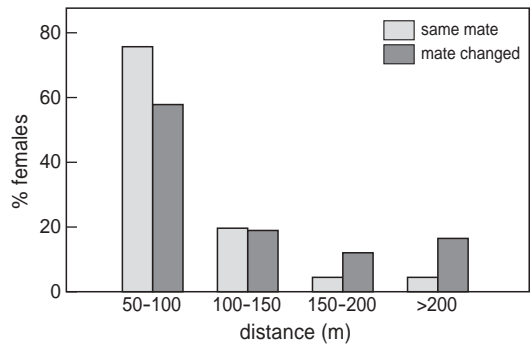
Concerning distances, medians were similar for divorced and widowed females (99.5 m, $n = 7$, vs. 99.6 m, $n = 26$; Mann-Whitney $U = 86$, $P = 0.83$) and males (89.9 m, $n = 9$, vs. 74.6 m, $n = 14$; $U = 51$, $P = 0.43$). Distances were also similar between divorced males (89.9 m, $n = 9$) and females (99.5 m, $n = 7$; $U = 26$, $P = 0.56$). However, widowed females dispersed larger distances (median = 99.6 m, $n = 26$) than males (74.6 m, $n = 14$; Mann-Whitney $U = 92$, $P = 0.015$).

## DISCUSSION

**Dispersal propensity and distances**
Great Tits in Sagunto rarely moved large distances and, even among movements implying change of territory, 92% were shorter than 200 m. These distances are obviously restricted to those that could be detected within the study area, and some individuals might have moved outside. Overall, however, most of the movements detected were far shorter than those possible even within the study area, and no significant differences in dispersal distances were detected between birds breeding in the border and in the core of the study area. Thus,

we believe that results presented here adequately describe the breeding dispersal pattern of the studied population, with the exception of the few relatively long dispersal events which might have gone undetected.

Another way of looking at breeding dispersal is to check the number of territories moved by dispersing birds. This takes into account differences in territory size in different habitats, making results easier to compare between populations. Considering a mean territory radius of 50 m, 67% of the dispersal events in Sagunto did not involve a change of territory between consecutive breeding seasons. Moreover, among Great Tits which kept the same mate in consecutive years, 74% moved less than one average territory width in Sagunto, as compared to 80% in an English population (Harvey *et al.* 1979), and 87% in a Japanese one (Saitou 2002). Tinbergen (2005) also estimated that the mean distance moved by Great Tits in his studied population was in the order of one territory size. Similar results were reported by Kluijver (1951). The close similarity of these figures, given the very different habitat types, points to a very general pattern of breeding dispersal, i.e. birds tend to return to the same territory, or close to it. This result is not surprising, since there is a marked tendency in many species of moving only one or very few territories between years (e.g. Pärt & Gustafsson 1989, Montalvo & Potti 1992, Desrochers & Magrath 1993, Foppen & Reijnen 1994). The advantages of knowing the breeding place, especially in relation to food location and potential enemies, are frequently invoked to explain breeding site fidelity (e.g. Schieck & Hannon 1989, Gauthier 1990).

### Age and dispersal

The probability of changing territory decreased more or less linearly at least up to the sixth year of life in Great Tits. This was true for both males and females. These results generally agree with the idea of a development of site fidelity with age, so frequently found in long-lived species (Newton 2001a). Evidence from short-lived passerines, considering individuals of known age, are much

scarcer, though all pointed to a progressive decrease of dispersal propensity and/or distance with age (e.g. Shulter & Clark 2003, Winkler *et al.* 2004, Dale *et al.* 2005). Other studies made categorical analyses, so their ability to detect trends was limited. Given these results, studies considering only two age classes (juveniles and adults) are very limited to draw conclusions, and their ability to detect differences would depend on the slope of the curve. Our results on Great Tits, and those of the above-mentioned studies, suggest that a progressive decrease in dispersal tendency (or an increase in site fidelity) with age could also be the general pattern in small passerines. But more studies considering exact ages are needed to first confirm this pattern and then compare the shapes of the curves among populations and species.

Whether using exact ages or age classes (see e.g. Pärt & Gustafsson 1989, Montalvo & Potti 1992, Payne & Payne 1993, Morton 1997, Winkler *et al.* 2004), the general trend observed is that juveniles disperse more frequently and/or farther than adults. A possible explanation for this behaviour is that juveniles first established in vacant territories, which are probably of bad quality, and move to better ones when they are older and are able to defend them. As the bird gets older, the matching between its own 'quality' and the quality of its territory becomes better, so finding a better, available territory in the vicinity would be more difficult. This was argued by Newton & Marquiss (1982; see also Newton 2001b) for the Sparrowhawk *Accipiter nisus*, and a similar argument has been proposed for some passerines thereafter (e.g. Foppen & Reijnen 1994 and references therein).

A different question is how far dispersing individuals move. Considering two age classes, we detected an interaction between age and sex, young females dispersing farther than adult males. We discuss this finding in the following section.

### Sex and dispersal

We found no sex differences in dispersal propensity, i.e. the probability of changing breeding place is similar for both sexes, and this is true across age classes and mating categories. However, once a

bird moves, females do it farther than males. This generally agrees with the most frequent pattern found in birds, a female-biased dispersal (Clarke *et al.* 1997). But looking at the details of our study, this assertion needs to be fine-tuned. First, both the age of the bird and its mating status are factors interacting with sex in determining dispersal patterns, and they have not been taken into account in many studies. Second, as pointed out by Clarke *et al.* (1997), the selection of the parameter to be measured (dispersal propensity or dispersal distance) might affect the conclusion, and many studies only considered one of them. Thus, the lack of sex differences in dispersal found in many studies (review in Clarke *et al.* 1997) could be at least partly a consequence of pooling different subgroups of individuals, or measuring one or the other dispersal parameter. In our study, no sex differences in dispersal propensity were found, while sex differences in dispersal distances were found when also considering the age and the mating status of the birds.

Considering the interaction between age class and sex, our results showed only small differences between age-sex categories in distances moved, and significant differences were only found between young females and adult males. Overall, both this result, and the general trend (see Fig. 4), agree with the expected results for this monogamous territorial species (Greenwood 1980), where males are more attached to the breeding places they defend. This is superimposed on the trend of increasing philopatry with age discussed in the previous section.

Blondel *et al.* (2000) argued that higher female dispersal distances of Corsican Blue Tits *Parus caeruleus*, which were a consequence of the high divorce rates, ultimately resulted from habitat heterogeneity. Thus, females moved leaving behind a bad territory to look for a better one, while males were more attached to their territory. The opposite might be argued for our relatively homogeneous habitat as far as females concerns. Males would keep their territory, and females would have little scope to improve the quality of the territory by moving elsewhere. This would explain both the lack of sex differences in dispersal propensity, and the small distances moved by dispersing females, probably looking only for the nearest available breeding site.

## Mate faithfulness and dispersal

Individuals changing mate more often changed territory than faithful ones, independently of sex. This is not surprising, because of pairs split up, by definition they cannot stay in the same territory. In line with our earlier data, juveniles also dispersed more often than adults, with no interaction between age and sex. Considering the distances moved by dispersing individuals, females changing mate dispersed farther than faithful ones, while no differences in dispersal distances were found among males. This is consistent with the territorial system of this species, where males defend a territory and attract females, and with the above discussion on the low propensity of females to change territory. Direct comparisons of these results cannot be made with other Great Tit populations, since birds 'changing mate' (independently of the cause) were not considered. Nevertheless, information available (Table 2) strongly suggests that birds changing mate disperse more often and/or farther than faithful ones.

We are aware of only two studies in other passerines explicitly comparing dispersal behaviour between birds changing mate or not (Table 2). As far as comparison allows, results on both Indigo Buntings and Mountain White-Crowned Sparrows are similar to those found by us in Great Tits. On the one hand, faithful female Indigo Buntings dispersed less frequently than those changing mate (no data are available for males). On the other hand, distances moved by female sparrows changing mate were higher than those moved by faithful ones, while no differences were found for males.

Summarizing, evidence available for passerines suggests that both sexes are more prone to change territory after mate change. Sexes differ, however, when dispersal distances are considered, since females changing mate move farther than males. This pattern is better understood when the cause of

**Table 2.** Effects of mating status on dispersal propensity and distance in passerines. F: females; M: males; F+M: females and males analysed together. MR: Mate Retention (breeding with the same mate in two consecutive years); MC: Mate Change (breeding with different mate in two consecutive years whatever the cause (widowing or divorce); W: Widow (re-mating between consecutive years due the death of the mate); D: Divorce (re-mating between consecutive years while the former mate is still alive); CT: Change of Territory; NT: No change of Territory; n.s.: not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.t.: no statistical test performed; (+): no a posteriori comparisons performed after detection of significant differences among categories.

| | Proportion/ Distance | Results | | Species | Reference |
|---|---|---|---|---|---|
| $F_{MR}$ vs. $F_{MC}$ | Proportion | $F_{MR} < F_{MC}$ | *** | *Passerina cyanea* | Payne & Payne 1993 |
| | Distance | $F_{MR} < F_{MC}$ | *** | *Zonotrichia leucophrys oriantha* | Morton 1997 |
| $M_{MR}$ vs. $M_{MC}$ | Distance | $M_{MR} = F_{MC}$ | n.s. | *Zonotrichia leucophrys oriantha* | Morton 1997 |
| $F+M_{MR}$ vs. $F+M_W$ | Distance | $F+M_{MR} < F+M_W$ | * | *Ficedula hypoleuca* | Montalvo & Potti 1992 |
| $F+M_{MR}$ vs. $F+M_D$ | Proportion | $F+M_{MR} < F+M_D$ | *** | *Parus caeruleus* | Blondel *et al.* 2000 |
| | Proportion | $F+M_{MR} < F+M_D$ | *** | *Parus major* | Saitou 2002 |
| | Distance | $F+M_{MR} < F+M_D$ | * | *Ficedula hypoleuca* | Montalvo & Potti 1992 |
| $F_{MR}$ vs. $F_W$ vs. $F_D$ | Distance | $F_{MR} < F_W = F_D$ | ***(+) | *Parus caeruleus* | Pampus *et al.* 2005 |
| | Distance | $F_{MR} < F_W = F_D$ | **(+) | *Parus major* | Pampus *et al.* 2005 |
| | Distance | $F_{MR} = F_W = F_D$ | n.s. | *Parus major* | Van de Casteele *et al.* 2003 |
| $M_{MR}$ vs. $M_W$ vs. $M_D$ | Distance | $M_{MR} = M_W = M_D$ | n.s. | *Parus caeruleus* | Pampus *et al.* 2005 |
| | Distance | $M_{MR} < M_W = M_D$ | **(+) | *Parus major* | Pampus *et al.* 2005 |
| | Distance | $M_{MR} = M_W = M_D$ | n.s. | *Parus major* | Van de Casteele *et al.* 2003 |
| $F_{MR}$ vs. $F_W$ | Distance | $F_{MR} = F_W$ | n.s. | *Parus major* | Harvey *et al.* 1979 |
| $M_{MR}$ vs. $M_W$ | Distance | $M_{MR} = M_W$ | n.s. | *Parus major* | Harvey *et al.* 1979 |
| $F_{MR}$ vs. $M_D$ vs. $F_D$ | Distance | $F_{MR} = M_D < F_D$ | *** | *Parus caeruleus* | Blondel *et al.* 2000 |
| $F_{MR}$ vs. $F_D$ | Distance | $F_{MR} = F_D$ | n.s. | *Ficedula albicollis* | Pärt & Gustafsson 1989 |
| | Distance | $F_{MR} < F_D$ | * | *Ficedula hypoleuca* | Harvey *et al.* 1984 |
| | Distance | $F_{MR} < F_D$ | *** | *Turdus merula* | Desrochers & Magrath 1993 |
| $M_{MR}$ vs. $M_D$ | Distance | $M_{MR} = M_D$ | n.s. | *Ficedula albicollis* | Pärt & Gustafsson 1989 |
| | Distance | $M_{MR} = M_D$ | n.s. | *Ficedula hypoleuca* | Harvey *et al.* 1984 |
| | Distance | $M_{MR} < M_D$ | *** | *Turdus merula* | Desrochers & Magrath 1993 |
| | Distance | $M_{MR} < M_D$ | * | *Parus caeruleus* | Blondel *et al.* 2000 |
| $F+M_W$ vs. $F+M_D$ | Distance | $F+M_W = F+M_D$ | n.s. | *Parus caeruleus* | Pampus *et al.* 2005 |
| | Distance | $F+M_W = F+M_D$ | n.s. | *Parus major* | Pampus *et al.* 2005 |
| $F_W$ vs. $F_D$ | Distance | $F_W = F_D$ | n.s. | *Ficedula hypoleuca* | Montalvo & Potti 1992 |
| | Distance | $F_W = F_D$ | n.s. | *Ficedula albicollis* | Pärt & Gustafsson 1989 |
| $M_W$ vs. $M_D$ | Distance | $M_W = M_D$ | n.s. | *Ficedula hypoleuca* | Montalvo & Potti 1992 |
| | Distance | $M_W = M_D$ | n.s. | *Ficedula albicollis* | Pärt & Gustafsson 1989 |
| $F_{W\,CT}$ vs. $F_{W\,NT}$ | Proportion | $F_{W\,CT} > F_{W\,NT}$ | * | *Wilsonia citrina* | Howlett & Stutchbury 2003 |
| $M_{W\,CT}$ vs. $M_{W\,NT}$ | Proportion | $M_{W\,CT} = M_{W\,NT}$ | n.s | *Wilsonia citrina* | Howlett & Stutchbury 2003 |
| $F_W$ vs. $M_W$ | Proportion | $F_W = M_W$ | n.s | *Acanthiza pusilla* | Green et al. 2004 |
| | Proportion | $F_W = M_W$ | n.s | *Parus major* | Harvey et al. 1979 |
| | Proportion | $F_W > M_W$ | *** | *Tyranus tyranus* | Murphy 1996 |
| | Distance | $F_W > M_W$ | * | *Ficedula hypoleuca* | Harvey et al. 1984 |
| | Distance | $F_W = M_W$ | n.s | *Ficedula hypoleuca* | Montalvo & Potti 1992 |
| | Distance | $F_W = M_W$ | n.s | *Parus major* | Harvey et al. 1979 |
| | Distance | $F_W = M_W$ | n.s | *Turdus merula* | Desrochers & Magrath 1993 |

**Table 2.** Continued

| | Proportion/ Distance | Results | | Species | Reference |
|---|---|---|---|---|---|
| $F_{D\,CT}$ vs. $F_{D\,NT}$ | Proportion | $F_{D\,CT} > F_{D\,NT}$ | ** | *Wilsonia citrina* | Howlett & Stutchbury 2003 |
| $F_{D\,CT}$ vs. $M_{D\,NT}$ | Proportion | $F_{D\,CT} > M_{D\,NT}$ | * | *Wilsonia citrina* | Howlett & Stutchbury 2003 |
| $F_D$ vs. $M_D$ | Proportion | $F_D > M_D$ | * | *Acanthiza pusilla* | Green *et al.* 2004 |
| | Proportion | $F_D > M_D$ | *** | *Parus major* | Saitou 2002 |
| | Proportion | $F_D = M_D$ | n.s. | *Tyranus tyranus* | Murphy 1996 |
| | Distance | $F_D > M_D$ | * | *Ficedula hypoleuca* | Harvey *et al.* 1984 |
| | Distance | $F_D = M_D$ | n.s. | *Ficedula hypoleuca* | Montalvo & Potti 1992 |
| | Distance | $F_D > M_D$ | ** | *Parus major* | Harvey *et al.* 1979 |
| | Distance | $F_D > M_D$ | n.t. | *Parus major* | Saitou 2002 |
| | Distance | $F_D = M_D$ | n.s. | *Turdus merula* | Desrochers & Magrath 1993 |

mate change (divorce or widowing) is considered, as we do in the next section. We will see that, in our study population, widowed females, and not divorcees, were mainly responsible for this pattern.

**Divorce, widowing and dispersal**

Most studies dealing with the effect of mate change on dispersal consider whether the change of mate is caused by divorce or death of the previous mate. However, each study has analysed data in a different way (Table 2), so it is difficult to compare them and extract general conclusions.

The origin of mate change (widowing or divorce) had no significant effect on within-sex breeding dispersal patterns found in Sagunto: dispersal was similar for divorced and widowed females and for divorced and widowed males. The same general result was obtained by Van de Casteele *et al.* (2003) in Great Tits, Pampus *et al.* (2005) in Great and Blue Tits, Montalvo & Potti (1992) in Pied Flycatchers, and Pärt & Gustafsson (1989) in Collared Flycatchers *Ficedula albicollis* (see Table 2 for details). Therefore, evidence available suggests that the cause of mate change does not affect the within-sex dispersal pattern after changing mate.

Among widows, we found no differences in dispersal propensity between sexes, but widow females dispersed farther than males. For Great Tits, Harvey *et al.* (1979) reported similar results in relation to dispersal propensity but did not find sex differences in dispersal distances. Considering other species (Table 2), the result most frequently found is the lack of differences between sexes but, in case of differences, widowed females dispersed farther than males. Our results fit within this general pattern.

For divorcees, the pattern found in Sagunto differs somewhat from that reported for other Great Tit populations. Harvey *et al.* (1979) and Saitou (2002) found sex differences in dispersal among divorcees, divorced females dispersing more frequently and farther than males, while we did not find differences in Sagunto. The general trend for other species (Table 2) is similar to that found for widows: in the case of differences, females are the ones dispersing more often and/or farther.

Assuming that the patterns of mate choice are similar in the three Great Tit populations for which data are available, differences should be sought for in the habitat characteristics. This would influence

the relative importance of having a good territory or a good mate. In a homogeneous habitat, as in orange groves, the quality of the mate would be expected to have relatively more weight. Hence, any member of the pair which might be 'unhappy' with the other would be more prone to move and look for a better one. This would explain why either male or female divorcees stay in (or move from) their previous territory, obviously assuming that either sex has the choice of divorce; see e.g. Ens *et al.* (1993). This would be more difficult if habitat heterogeneity is greater, and defending a territory is important *per se*, as might happen in more heterogeneous habitats. In this case, males (the ones defending the territory) would be less prone to abandon it, even if the female is of lower 'quality' than preferred. In a study on Blue Tits in a heterogeneous habitat, Blondel *et al.* (2000) showed that divorced females dispersed farther than divorced males, and females significantly improved their breeding site after moving, while males did not; the improvement in breeding site was related to a better breeding performance.

A methodological reason could also contribute to the differences found between our population and others. We captured birds when feeding nestlings, so pairs that fail early in the nesting cycle were rarely identified. Since divorce rate is higher after breeding failure (e.g. Greenwood & Harvey 1982), our sample of divorcees could be biased to those that divorced after successful breeding or after loosing the brood at a late stage. Whether this would affect the dispersal patterns differentially for males and females is unknown to us, and we are not aware of any study covering this aspect.

On the other hand, if one of the pair members dies in a homogeneous habitat (Sagunto), the male would tend to keep the territory, while the female would tend to look for another male elsewhere. In a heterogeneous habitat, females would also tend to stay in good territories and accept the incoming male. Residence status (resident vs. non-resident) could complicate this pattern in the Japanese population (see Saitou 2002).

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## SAMENVATTING

Veel vogels maken een nest op de plek waar ze het vorig jaar hebben gebroed. Dat is begrijpelijk gezien de kennis van de lokale situatie die over de jaren opgebouwd wordt. Toch kan het in bepaalde situaties gunstig zijn om juist niet in de buurt van het vorige nest te broeden. Onze kennis over plaatskeuze van het nest van het ene op het andere jaar is nog zeer onvolledig. De onderhavige

studie had als doel patronen hierin bij Koolmezen *Parus major* te beschrijven. De studie onderzocht dispersie – de keuze van een nieuw territorium van het ene op het andere jaar – van volwassen Koolmezen in een gebied bestaande uit uitgestrekte sinaasappelplantages in het oosten van Spanje. Het gebied was betrekkelijk homogeen, waardoor territoria vermoedelijk weinig in kwaliteit verschilden, zodat de noodzaak om tussen jaren te verhuizen in beginsel gering was. Het studiegebied besloeg 85–110 ha, waarbinnen maximaal 150 nestkasten hingen. Het merendeel hiervan was bezet. Vogels werden gevangen, en vervolgens geringd, tijdens het voeren van de jongen. Zo werden over een periode van 11 jaren 482 waarnemingen verzameld over de plaatskeuze van geringde vogels tussen opeenvolgende jaren. De meeste vogels (67%) vestigden zich van het ene op het andere jaar in hetzelfde territorium, waarbij de afstand tussen de opeenvolgende broedpogingen minder dan 50 m was. De kans dat een vogel een ander territorium opzocht, nam af naarmate de vogels ouder werden. Dat gold zowel voor mannetjes als voor vrouwtjes. Vogels die zich in een ander territorium vestigden, verplaatsten zich over een geringe afstand: 92% verhuisde over een afstand van minder dan 200 m. Jonge vrouwtjes (één jaar oud) verplaatsten zich over grotere afstanden dan volwassen mannetjes. Voor jonge mannetjes en volwassen vrouwtjes werden intermediaire afstanden gemeten.

Ongeveer twee derde van de vogels was tussen opeenvolgende jaren met dezelfde partner gepaard, althans voor zover deze nog in leven was. Mannetjes en vrouwtjes met een nieuwe partner vestigden zich beide vaker elders dan vogels met dezelfde partner. Bovendien was de dispersie-afstand groter na het aangaan van een nieuwe paarband, hoewel dit niet voor mannetjes gold. Kiezen van een nieuwe partner volgde meestal op de dood van de vorige, maar in 24–31% van de gevallen leefde de partner van het vorig jaar nog en was er dus sprake van een 'scheiding'. De kans op dispersie was voor gescheiden vogels gelijk aan vogels die hun partner hadden overleefd. De verplaatste afstanden waren echter voor weduwen groter dan voor weduwnaars of gescheiden vogels. De waarnemingen aan Koolmezen blijken goed overeen te komen met trends bij andere zangvogels: (1) vrouwtjes verplaatsen zich meer dan mannetjes; (2) de kans om zich te verplaatsen neemt af met de leeftijd; (3) dispersie komt meer voor na het kiezen van een nieuwe partner. Maar er zijn vele uitzonderingen. Er is meer onderzoek nodig om te begrijpen hoe factoren als sekse, leeftijd, partnerkeuze alsmede habitatkenmerken precies op elkaar inwerken en zo verschillen in patronen van dispersie binnen en tussen populaties van dezelfde soort teweegbrengen. (CB)