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## Original Article

## Immigration and dispersal are key determinants of cultural diversity in a songbird population

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Socially learned signals and behaviors are found throughout the animal kingdom and often show striking variation within species over space and time. However, the extent to which this cultural diversity is generated by demographic factors such as immigration and dispersal has proved difficult to investigate and remains largely untested in a natural setting. Focusing on 14 different local neighborhoods within a wild population of great tits *Parus major*, we examined the relationship between individual movements over a 7-year period and patterns of cultural diversity at a neighborhood level, assessed using 2 indices: Song repertoire size and repertoire novelty, measured at the neighborhood (but not individual) level. We found that the repertoire size of a neighborhood is positively correlated with its levels of immigration, but that repertoire novelty is constrained by dispersal and geographic proximity among neighborhoods, both of which promote song sharing. In parallel, we show that the acoustic structure of some songs changes subtly over distance, in line with the view that learning errors can lead to the establishment of novel social traits (cultural differentiation). Our findings demonstrate that spatial variation in cultural diversity in animal societies can partly be explained as the outcome of dispersal and immigration transferring traits between neighborhoods and also suggest that trait transmission declines in fidelity over distance.

**Key words:** birdsong, cultural evolution, dispersal, great tit, immigration, repertoire.

## INTRODUCTION

Socially learned behaviors, such as tool use, predator avoidance strategies, and complex vocal communication, have been demonstrated in a wide range of animals from insects to mammals (reviewed in Janik and Slater 2000; Brown and Laland 2003; Leadbeater and Chittka 2007; Rapaport and Brown 2008). These findings have established that culturally transmitted traits once believed to be uniquely human attributes (Laland and Janik 2006) are widespread phenomena. They have also highlighted the extensive cultural variation found within many animal societies, from the richness of distinctive dialects in saddlebacks (Jenkins 1978) to the complex differences in behavioral patterns among populations of chimpanzees (Whiten et al. 1999). It is now widely appreciated that the cultural traits of animals vary geographically within animal species (Marler and Tamura 1964; Nottebohm 1969; Nelson 1998; Podos and Warren 2007; Krützen et al. 2011) and change

over time (Harbison et al. 1999; Derryberry 2009; but see Nelson et al. 2004). Cultural transmission, and the potential for generating cultural diversity, is made possible by social learning (van Schaik 2010). However, although social learning processes have been extensively studied (Beecher and Brenowitz 2005; Galef and Laland 2005 for reviews), few empirical studies have considered other drivers of the spatial and temporal variation affecting learning and hence cultural diversity (for exceptions, Nelson and Marler 1994; Slabbekoorn et al. 2003; Rivera-Gutierrez et al. 2010). Thus, we still know remarkably little about the mechanisms underlying patterns of cultural diversity in noncaptive populations.

Some of the most common factors hypothesized to drive cultural variation are purely spatial (i.e., distance), whereas others are behavioral or demographic, such as dispersal, immigration, and population size (Boesch and Tomasello 1998; Nelson 2000; Ellers and Slabbekoorn 2003; Nunn et al. 2009). When viewed across space, it is generally assumed that variation in cultural traits is positively related to geographic isolation: The greater the distance between communities, the fewer cultural traits they will share (Ellers and

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Slabbekoorn 2003; Podos and Warren 2007; Nunn et al. 2009). The extent to which this relationship is mediated by other factors is much less clear. For example, dispersal and immigration may vary independently of distance and are proposed to influence cultural diversity by allowing traits to spread within and between populations (Ellers and Slabbekoorn 2003; Nunn et al. 2009). In addition, the transfer of traits may be further influenced by learning, as copying errors is one of the mechanisms that can lead to novel traits, a process first described by Slater (1986) and later termed “cultural differentiation” (Lynch 1996; Whiten et al. 2001). This can operate in tandem with a dispersal mechanism (i.e., after individuals switch from one location to another) or alternatively by a more gradual diffusion across the population as static neighbors copy each other’s traits. Finally, population size is thought to influence cultural diversity by determining the number of potential tutors and hence sources of novel cultural traits (Williams and Slater 1990; Nunn et al. 2009).

Assessing these hypotheses has proved difficult for a number of reasons. First, many previous studies have focused on transmission of behavioral traits between animals in captivity (Laland and Williams 1997; Funabiki and Funabiki 2008) or else in primates (Whiten 2011) where the results are difficult to interpret given the nuance and complexity of social traits. Second, in natural (noncaptive) settings, the distance between communities is generally used as a proxy for dispersal, despite the fact that distance is only one of many factors influencing the transfer of traits between groups of individuals (reviewed in Clobert et al. 2009) and can be an unsuitable proxy for dispersal (Greenwood et al. 1979). Third, even when dispersal and immigration are measured, data are rarely collected over the longer time frames (i.e., years or decades) relevant to cultural transmission. Fourth, patterns are often quantified over large spatial scales or across physical barriers that limit the movements of animals, making it difficult to rule out the influence of genetic or biogeographic factors in shaping cultural traits (Laland and Janik 2006). These difficulties may explain why previous studies in animals have produced such mixed results, with the transmission of behavioral traits showing effects of geographic isolation (Miyasato and Baker 1999; Krützen et al. 2011) and dispersal (Searcy et al. 2002; Rivera-Gutierrez et al. 2010) in some studies, but not in others (Wright and Wilkinson 2001; Petruskova et al. 2010; Can wei et al. 2011; Laiolo 2011). Thus, our understanding of the key processes shaping spatial and temporal patterns of cultural diversity is limited, particularly in natural landscapes.

Here we assess the relative roles of spatial and demographic factors on cultural diversity in a free-ranging population of a songbird, the great tit *Parus major*. This species provides an ideal system for studying cultural evolution because males develop a repertoire of 1–8 song types by copying from conspecific individuals throughout their life, although mostly in the first year after birth, after which they set up their first territory (McGregor and Krebs 1982a). Moreover, song types can be easily measured and classified using standard techniques with acoustic analysis software, providing 2 well-established indices of cultural diversity: Song repertoire size and repertoire novelty (Krebs et al. 1978, 1981; McGregor and Krebs 1982a). We focused on arbitrarily selected study plots (hereafter termed “neighborhoods”) containing variably sized samples of individuals. Song repertoire size and repertoire novelty were calculated at the level of these neighborhoods using a cumulative score from all males present because we were not able to identify individuals reliably in the field. We then calculated distance between neighborhoods, neighborhood size, dispersal among neighborhoods, and immigration from outside the study site using

data averaged across 7 years (2004–2010) of a long-term study of individually identified birds. Seven years is 3.8 times the average generation time of our study species (Bouwhuis et al. 2009), and our data set therefore provides information about the dynamics of the study population over 3–4 generations.

Using these field data, we assessed the effects of demographic and spatial factors on song repertoires within and between neighborhoods. If spatial factors are important determinants of cultural diversity, we predicted a decline in dispersal and thus song sharing with distance between neighborhoods. Similarly, if demographic factors are important determinants of cultural diversity, we predicted that larger and more novel repertoires (i.e., higher cultural diversity) would be associated with more populous neighborhoods and those attracting larger numbers of immigrants. This follows from the logic that a larger cumulative repertoire would be generated by a greater number of individuals and also that individuals dispersing from natal territories outside the study area would be more likely to introduce novel song types. Because great tits learn many of their songs in their natal neighborhood (McGregor and Krebs 1982a), rarely if ever adding to their song repertoire during adulthood (Rivera-Gutierrez et al. 2011), dispersing individuals of any age are likely to transmit songs to their breeding neighborhood. We therefore also predicted that dispersal between study neighborhoods will promote song sharing and that this in turn will result in less novel repertoires (i.e., lower cultural diversity) when comparing those neighborhoods. Finally, if the spatial component of cultural diversity is influenced by cultural differentiation (i.e., copying errors between individuals), and the number of copying events between 2 neighborhoods increases with geographic distance, then we predict a negative effect of distance on trait similarity (in this case comparing within song types).

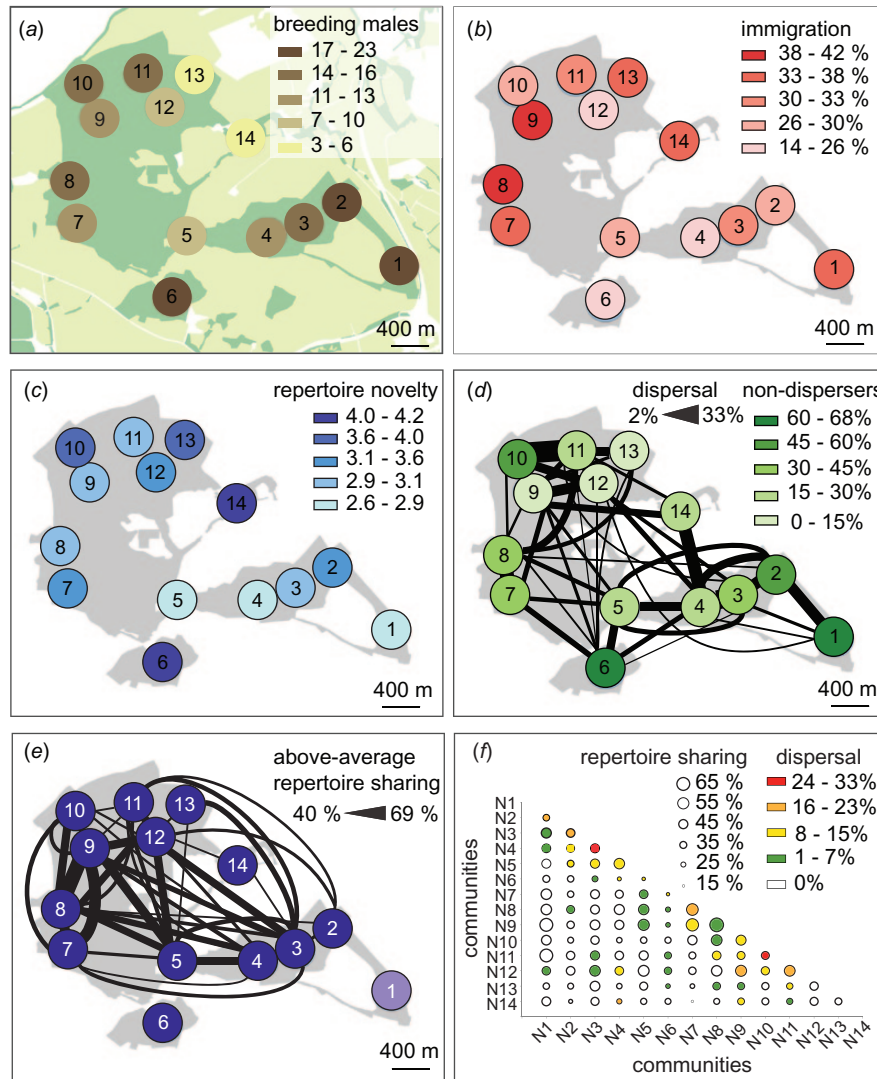
## METHODS

### Study population

The study was carried out in Wytham Woods, Oxfordshire, UK (51°46′, 1°20′W), a continuous 380-ha deciduous woodland surrounded by farmland (see Gibson 1988 for a full description). Because of the logistical challenges of recording song repertoires from the entire population of great tits in Wytham Woods (347 breeding pairs in 2010), we focused on 14 plots, or “neighborhoods,” of 12.6 ha (circular plots with a radius of 200 m). We emphasize that the term “neighborhood” here represents a small group of arbitrarily selected individuals that interact with each other in these 12.6-ha study plots, but can also potentially interact with birds outside the neighborhood, depending on their position within the plot. We ensured that neighborhoods were evenly spread out across the entire woodland so as to represent habitats of various degrees of isolation (e.g., well inside the woods or surrounded on several sides by open fields), and far apart enough so as not to contain overlapping territories (Figure 1a). The choice of the neighborhoods was not influenced by the number of great tits breeding in the area. Neighborhoods are denoted by  $N_i$  where  $i$  is the number assigned to the neighborhood. In total, the neighborhoods encompass approximately 50% of woodland area at Wytham Woods, and approximately 50% of the breeding adults of the total population present at the study site (179 breeding pairs out of 347).

### Song sampling

Songs were recorded April–June 2010, from dawn (05h00) to midday (12h00). To stimulate singing by resident males, a high-quality



**Figure 1**

Location of 14 study plots (“neighborhoods”; circles) in Wytham Woods in relation to (a) extent of woodland habitat and population density, (b) immigration, (c) repertoire novelty, (d) dispersal, and (e) repertoire sharing. In (a), dark green represents woodland, whereas fields are in light green. The number of breeding males in each neighborhood is indicated with different shades of brown: The darker the brown the higher the population density in the neighborhood. In (b), the mean annual proportion of immigrant male great tits in the total breeding population of each neighborhood in 2004–2010 (i.e., mean immigration) is shown with different colors indicating different levels of immigration: The darker the red the higher the level of immigration. In (c), repertoire novelty of each neighborhood in 2010 is shown, where different colors indicate different levels of repertoire novelty: The darker the blue the higher the novelty of the repertoire. In (d), the different shades of green of each neighborhood represent the proportion of birds which did not disperse from this neighborhood (averaged across all years, 2004–2010), whereas black lines show the proportion of dispersal between neighborhoods (the thicker the line, the higher the dispersal between the neighborhoods). When no dispersal occurred between 2 neighborhoods, no line is shown. In (e), the black lines indicate the proportion of song types shared between neighborhoods. For clarity, only the values above average are shown, and N1 is excluded. (f) Matrix representing the relationship between dispersal and repertoire sharing. Each pair of neighborhoods (one plotted on the x axis, another on the y axis) is represented by a circle with diameter proportional to the level of repertoire sharing between the 2 neighborhoods. Colored circles indicate that dispersal occurred between 2 neighborhoods; white circles indicate lack of dispersal.

recording of typical great tit song was broadcast at natural volume (~70 dB at 10 m) for ~10 s using an Ipod mp3 player and an Adasta travel loudspeaker. Great tits are known to respond to the song of a conspecific by singing a similar song (Krebs et al. 1981). However, this is more likely to happen when the bird is familiar with the singing individual (Falls et al. 1982). Therefore, to minimize any bias due to possible song matching, for playback we used 1 song type recorded from 1 single bird in Surrey, England, >100 km from the study area. Any bias introduced by song matching was also

minimized by ensuring that all birds recorded from all neighborhoods had received the same playback cut. Therefore, even if the absolute number of song types recorded per neighborhood might have been decreased by the use of playback, the relative number of song types between neighborhoods, which is important for the purposes of our analysis, will not have been affected. In nearly all cases, only 1 male at a time responded to playback, so opportunities to match neighbors’ songs were very limited. Vocal responses by residents were recorded with a Sennheiser ME66-K3U directional gun

microphone and a portable Edirol R-09 Digital recorder (settings: wav format, 16-bit acquisition, sampling frequency 44.1 kHz). Time of recording and location of singing birds were recorded using a Garmin GPSMAP 60CSx device. To sample the entire neighborhood, playback and recording were first conducted at the center of the neighborhood, then repeated at 50-m intervals on a spiral, until reaching the border of the neighborhood 200 m away. Despite our efforts to sample thoroughly every area of each neighborhood, it is impossible to be certain that we have recorded every individual male present, particularly as individuals were not identifiable in the field. A total of ~10 h was spent in each neighborhood during the course of at least 4 mornings (9 h 54 min  $\pm$  7 min per neighborhood over a total of 4.9  $\pm$  0.2 mornings per neighborhood). The final data set contained 374 songs (26.4  $\pm$  1.4 songs per neighborhood). Each song recording contained a single song type.

### Measures of cultural diversity

The cultural diversity of a neighborhood of songbirds can be quantified in terms of repertoire size, that is, the total number of distinct song types produced by all members of the neighborhood altogether (Rivera-Gutierrez et al. 2010). Note that we define neighborhood repertoire size as the number of distinct song types produced by the entire population occurring within the neighborhood, rather than mean repertoire size averaged across individuals. Many studies use repertoire size as the sole measure of cultural diversity (Nicholson et al. 2007; Franco and Slabbekoorn 2009). However, because this is likely to underestimate the extent of cultural diversity within a neighborhood (Gil and Gahr 2002), we also use a metric of “repertoire novelty” (also termed “rare songs” (McGregor and Krebs 1982a) or “new songs” (Franco and Slabbekoorn 2009)); that is, the number of songs exclusively sung in a particular neighborhood.

### Acoustic analyses and song classification

A great tit song is a succession of strophes, each composed of a repetition of syllables of a few notes (1–6 notes in our data). We used Raven Pro Software (Bioacoustics research program, Cornell Lab of Ornithology, USA) to process the recordings with a sample rate of 22050 Hz and generate broadband spectrograms (bandwidth = 323 Hz, FFT = 1024). The signal below 60–70 dB (depending on recording quality) was removed, to remove any noise and reverberation. We used the spectrograms to classify the songs into song types visually, on the basis of the shape, frequency of notes, and number of notes per syllable, following methods described in McGregor and Krebs (1982a) (Supplementary Figure S1). We identified 62 different song types, 29 of which had been recorded on several occasions.

The visual classification of songs into song types has been employed widely by previous studies (McGregor and Krebs 1982a; Rivera-Gutierrez et al. 2010). However, as this approach can be subjective and lead to inaccuracy (Williams and Slater 1991), we used computer-based methods to validate and improve our classification. To achieve this, standard acoustic parameters were measured with Raven Pro. For each note of a syllable, we measured maximum and minimum frequencies, peak frequency, bandwidth, duration, internote interval, and intersyllable interval (Supplementary Figure S1). Each measure was taken for 6 syllables, and the mean was calculated. In addition, we recorded parameters for the whole song: Maximum and minimum frequencies, bandwidth, frequency and bandwidth changes (the difference between the peak frequency or

the bandwidth of the first and last note of a phrase), number of notes per syllables and pace.

To test the accuracy of our visual classification, we performed a principal component analysis (PCA) followed by a cross-validated discriminant function analysis (DFA) (Supplementary Table S1; Supplementary Figure S2). The results revealed low support for some of our classifications so we split 4 song types into 2–3 different song types, resulting in a final total of 67 song types. A new DFA validated 75.6% of our final classification, above acceptable thresholds used in previous studies (e.g., >70%; Parsons and Jones 2000; Seddon and Tobias 2007). The details of the PCA and DFA can be found in the Supplementary Material.

To assess whether our song sample was representative of the total repertoire, we plotted repertoire size against recording time for each neighborhood. The curves reached asymptotes for 11 neighborhoods (Supplementary Figure S3), suggesting that we have captured a large proportion of the songs produced within each neighborhood. In the 3 remaining neighborhoods, 1 or 2 new songs (out of a total repertoire of 12–14 song types) were recorded during the last hour of recording; we still included these neighborhoods in our analysis because despite these new song types, the rate of collection of new songs was declining steeply. The diversity of song types obtained corresponds to the usual number found in previous studies of great tits: Although individual repertoires in this species can contain up to 8 song types, individuals in our study area have been shown, after extensive recording, to have repertoires of up to 6 songs only, and 3.1 songs on average (McGregor and Krebs 1982a).

### Repertoire sharing

The average total repertoire size of a neighborhood was 12.6  $\pm$  2.0 song types (mean  $\pm$  SD), with a minimum repertoire size of 8 and a maximum of 15. Following Rivera-Gutierrez et al. (2010), we defined and calculated repertoire sharing as the proportion of song types shared by 2 neighborhoods, using the formula:

$$\text{Repertoire sharing} = 2 * \frac{\text{Number of song types shared by } N_i \text{ and } N_j \text{ between } N_i \text{ and } N_j}{\text{Repertoire size } (N_i) + \text{repertoire size } (N_j)}$$

### Repertoire novelty

We assigned a value between 1 and 6 to each song type depending on its rarity, that is, the number of neighborhoods in which it had been recorded (Supplementary Table S2). For each neighborhood, we then calculated the “novelty” of its repertoire, defined as:

$$\text{Repertoire novelty} = \frac{\sum \text{Value of each song type in the repertoire}}{\text{Repertoire size}}$$

The possible range of repertoire novelty value for a neighborhood was therefore 1 (all song types of the neighborhood recorded in 12 or more neighborhoods) to 6 (all song types of the neighborhood unique to this neighborhood). The variation in repertoire novelty between neighborhoods is presented in Figure 1c. We only found a weak relationship between the rarity of a song type (number of neighborhoods where it was recorded) and its rarity in terms of number of songs (proportion of songs in the neighborhood which belong to this song type) (Pearson correlation coefficient = 0.314,  $P = 0.070$ ,  $n = 34$ ). Thus, the frequency of occurrence of a given song type within a neighborhood does not predict how common it is in other neighborhoods.



## Fidelity of transmission of song types

To investigate the impact of distance (as a proxy for number of transmissions, see below) on the acoustic structure of great tit songs in our population, for each song type we calculated the Euclidean distance in acoustic space between all pairs of samples of this song type, using the principal components obtained from the PCA described above. The distance between pairs of songs was calculated using the GPS coordinates of the location where each song was recorded. We limited analyses to the 9 song types for which we had at least 15 recordings.

## Predictors of cultural diversity

Neighborhood size, immigration, and dispersal data were collected as part of a long-term study of the population carried out by collaborators (Edward Grey Institute, University of Oxford) in 2004–2010. The values and variability of these variables in each neighborhood are presented in [Supplementary Figure S4](#). Whereas the values varied between neighborhoods, they remained consistent and repeatable between years within each neighborhood (see [Supplementary Information](#)).

### Immigration

Following the general methods described by Gosler (1993), nest-boxes were monitored and 15-day-old chicks and unbanded adults were fitted with a unique metal leg bands supplied by the British Trust for Ornithology. Unbanded adults were aged and sexed based on plumage (Svensson 1984). Immigrants were identified as adult birds which had not previously been banded as nestlings in Wytham Woods and which consequently had immigrated from outside the woods. This allowed us to estimate the level of immigration by male birds for each neighborhood. We defined immigration as the proportion of immigrant males in the total breeding male population of a neighborhood. We found that on average, between 2004 and 2010,  $30.5 \pm 1.8\%$  of the breeding males were immigrants, and  $22.2 \pm 1.5\%$  were new immigrants (i.e., breeding in Wytham Woods for the first time). The proportion of breeding immigrants in a neighborhood varied from 13.8% to 41.6% (Figure 1b). Out of the 283 birds immigrating into our neighborhoods between 2004 and 2010, approximately 30% bred for more than 1 year, yet only in 1 instance did an immigrant bird change neighborhood after its first breeding attempt. The “internal” component of immigration (dispersal of immigrants within the woodland) is therefore negligible.

### Neighborhood size

We estimated the number of breeding males in the neighborhood from the number of breeding attempts in nest-boxes. On average, between 2004 and 2010, there were  $13.6 \pm 0.65$  breeding attempts in each neighborhood (range: 3–25), including an average of  $12.8 \pm 1.4$  breeding attempts per neighborhood in 2010 (range: 3–23). This is likely to be a slight overestimate as it includes repeat clutches (these generally occurred after a failed first clutch, as second broods are rare after a successful first brood). We included breeding attempts occurring less than 50 m outside the neighborhood boundary, as this is the average radius of great tit territories in Wytham Woods (Krebs 1971), and thus, these birds may have been recorded singing within the neighborhood. Although the boundary of each neighborhood was arbitrarily defined and may not reflect the actual partitioning of the great tits in social groups, the population size of each neighborhood is a valuable measure of the density of breeding males and therefore of singing interactions.

### Dispersal

We calculated dispersal between 2 neighborhoods as the proportion of birds hatching in 1 neighborhood and breeding at least once in the other:

$$\text{Dispersal}(i, j) = \frac{D(i \rightarrow j) + D(j \rightarrow i)}{D_{\text{total}}(i) + D_{\text{total}}(j)}$$

where  $D(i \rightarrow j)$  is the number of dispersers emigrating from neighborhood  $i$  to neighborhood  $j$  and  $D_{\text{total}}(i)$  is the total number of dispersers moving from neighborhood  $i$  to another part of the woodland over a 7-year period (2004–2010). The range of dispersal scores is 0 (indicating that neighborhoods  $i$  and  $j$  did not exchange a single individual) to 1 (indicating that all dispersers from neighborhood  $i$  dispersed to neighborhood  $j$ , while all dispersers from neighborhood  $j$  dispersed to neighborhood  $i$ ). A high dispersal score between 2 neighborhoods indicates a high proportion of dispersers from 1 neighborhood in the other, but it does not necessarily imply that movements are reciprocal. Note that in our calculations, as with neighborhood size, we also included individuals breeding <50 m outside of the border of the neighborhood. Nearly all dispersal movements between different neighborhoods occurred early in an individual's life, before their first breeding attempt (360 out of 361 natal dispersers). We found that on average  $66.6 \pm 5.4\%$  of each year's recruits dispersed to a location outside their natal neighborhood (range: 31.8–92.8%), with an average (straight line) dispersal distance of  $464 \pm 27$  m. This approximately equates to the distance between N10 and N11, whereas the largest dispersal distance between 2 neighborhoods was 2400 m between N1 and N12 (see Figure 1). These values are similar to those found previously in this population (Szulkin and Sheldon 2008).

### Distance

We calculated “direct” and “habitat” distance between the borders of each neighborhood using Google Earth. Direct distance was the shortest distance irrespective of habitat (i.e., including open habitats); habitat distance was the shortest distance through suitable habitat (i.e., woodland). The mean  $\pm$  SEM direct distance was  $1600 \pm 77$  m (range: 403–3640 m), whereas the mean habitat distance was  $2026 \pm 116$  m (403–4794 m).

## Analytical approach

Prior to all analyses (including PCA described above), we log-transformed or square root-transformed all acoustic variables as well as immigration to avoid problems of data nonlinearity and to ensure residuals were normally distributed.

We first investigated the effects of demography on cultural diversity by testing the effects of dispersal, immigration, and neighborhood size on repertoire size and repertoire novelty. All pairwise variables (e.g., dispersal and repertoire sharing) were averaged across neighborhoods. Because our sample size is relatively small and our predictors may be correlated with each other, we did not run full models including all predictors but tested the effect of each predictor on our 2 dependent variables individually (i.e., 6 different models). To test the effect of our 3 predictors on repertoire size, we used generalized linear models (GLMs), whereas we used general linear models (LMs) to test the effect of the same predictors on repertoire novelty. A GLM approach was necessary in the models of repertoire size because this variable is count data with a dispersion parameter different from 1, meaning that it was necessary to apply

a quasi-Poisson distribution with a log link function. The effect of neighborhood size (defined as the number of males breeding in a neighborhood) on our 2 dependent variables was nonsignificant (and in a negative direction). Thus, we did not control for neighborhood size in the 4 remaining individual models.

The results of these tests led us to conduct 2 additional tests: First, we were surprised to find a lack of effect of both neighborhood size and immigration on repertoire novelty because mechanisms of song learning and song sharing in great tits would suggest that these effects are very likely. Therefore, we tested the effect of the interaction between neighborhood size and immigration on repertoire novelty (LM). Second, when plotting the data while testing the effect of dispersal on repertoire novelty (LM), we noticed an obvious outlier which was likely to weaken the strength of any potential effect. We tested and confirmed with a Grubb's test that this point was an outlier and ran the LM a second time, this time excluding the outlier; this significantly increased the strength of the effect we had previously found.

To investigate the effect of dispersal and distance on repertoire sharing, we performed Mantel tests on the matrices of distance, dispersal, and repertoire sharing among neighborhoods (symmetrical matrices with a nil diagonal). We used Mantel tests because they calculate the correlation between 2 matrices while taking into account the nonindependence of the data using random permutations of rows and columns in one of the matrices. In all Mantel tests, we used 9999 permutations. To evaluate the relative effects of distance metrics on repertoire sharing, we ran a general linear mixed model (GLMM) in which repertoire sharing was the dependent variable; direct distance, habitat distance, and dispersal were fixed effects; and neighborhood identity was the random effect.

Finally, we used the same Mantel test approach described above to determine whether acoustic similarity between songs of the same type (calculated as the inverse of the Euclidean distance between them in acoustic space) was influenced by distance between neighborhoods.

All data were checked for spatial autocorrelation by plotting spatial correlograms (plots of Moran's I coefficient  $\pm$  standard deviation, up to the 7th nearest neighborhood) for all 6 variables (neighborhood size, repertoire size, repertoire novelty, repertoire sharing, dispersal, and immigration) (Supplementary Figure S5). None of the variables showed any significant spatial autocorrelation

at any spatial scale. Means are given as  $\pm 1$  standard error, except when specifically mentioned.

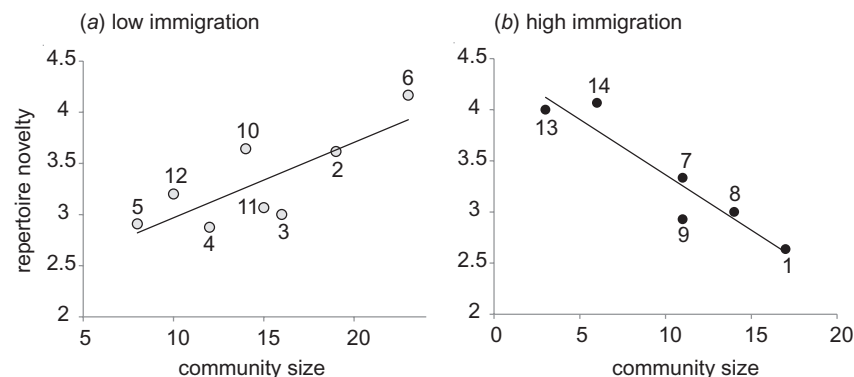
## RESULTS

### Effects of demography on cultural diversity

When testing the effect of neighborhood size (i.e., number of breeding males), dispersal, and immigration on repertoire size and repertoire novelty, we found no effect of neighborhood size on either variable (repertoire size: GLM, parameter estimate =  $-0.007 \pm 0.008$ ,  $t_{12} = -0.94$ ,  $P = 0.37$ ; repertoire novelty: LM, parameter estimate =  $-0.007 \pm 0.027$ ,  $F_{1,12} = 0.06$ ,  $P = 0.81$ ). These results ran contrary to our predictions, suggesting that the number of males present in a population has little influence on total repertoire size within that population. We note that the effects were extremely weak, and the sign of the slopes was negative; thus, we found no evidence that positive associations between neighborhood size and repertoire size or novelty needed to be controlled in other models.

We found a significant positive effect of the proportion of immigrants in a neighborhood on repertoire size (GLM, parameter estimate =  $0.82 \pm 0.37$ ,  $t_{12} = 2.229$ ,  $P = 0.04$ ) but no effect on repertoire novelty (LM, parameter estimate =  $0.35 \pm 1.24$ ,  $F_{1,12} = 0.08$ ,  $P = 0.78$ ). However, additional analysis revealed a strong effect of the interaction between neighborhood size and immigration on repertoire novelty (LM, parameter estimate =  $-1.66 \pm 0.27$ ,  $F_{1,10} = 36.48$ ,  $P < 0.001$ ). In other words, neighborhood size affects repertoire novelty differently depending on the proportion of immigrants in the neighborhood (Figure 2). This is made clear by the finding that, in the 8 neighborhoods with below-average levels of immigration, neighborhood size had a positive effect on repertoire novelty (parameter estimate =  $0.07 \pm 0.02$ ,  $t_6 = 3.09$ ,  $P = 0.02$ ), whereas in the 6 neighborhoods with above-average levels of immigration, the effect was negative (parameter estimate =  $-0.11 \pm 0.02$ ,  $t_4 = -5.46$ ,  $P = 0.005$ ). We did not find any correlation between immigration rates and neighborhood size (LM, parameter estimate =  $-0.003 \pm 0.006$ ,  $t_{12} = -0.55$ ,  $P = 0.59$ ).

When testing the effect of dispersal on repertoire size and novelty, we found no effect on repertoire size (GLM, parameter estimate =  $-2.93 \pm 2.69$ ,  $t_{12} = -1.089$ ,  $P = 0.30$ ) but a weak negative effect on repertoire novelty (LM, parameter



**Figure 2**

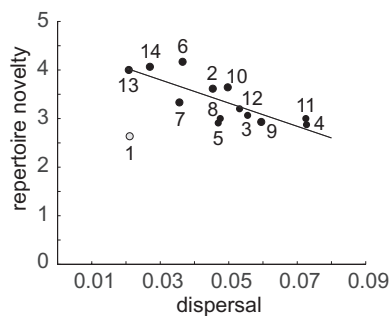
Relationship between neighborhood size (number of breeding males in a neighborhood) and repertoire novelty (a number between 0 and 6, related to the proportion of rare song types in a neighborhood) for different levels of immigration. (a) Neighborhoods with below-average levels of immigration (regression slope  $B = 0.07$ ,  $r = 0.78$ ,  $n = 8$ ); (b) neighborhoods with above-average levels of immigration (regression slope  $B = -0.11$ ,  $r = 0.94$ ,  $n = 6$ ). Data points are labeled by neighborhoods to illustrate geographical proximity.

estimate =  $-14.30 \pm 7.58$ ,  $F_{1,12} = 3.56$ ,  $P = 0.08$ ). We note that these analyses include an outlier neighborhood, as confirmed by a Grubb's test ( $G = 1.3724$ ,  $P < 0.001$ ). This neighborhood (N1) was the most isolated plot at the study site, with particularly low levels of dispersal and repertoire novelty, presumably due to its remote location and the fact that it is almost entirely bordered by fields (Figure 1). When we removed this outlier, the effect of dispersal on repertoire novelty became strongly significant (parameter estimate =  $-23.93 \pm 5.70$ ,  $F_{1,11} = 17.63$ ,  $P = 0.001$ ; Figure 3).

### Effects of dispersal and distance on song sharing and cultural diversity

On average,  $39.9 \pm 1.2\%$  of song types were shared between pairs of neighborhoods (range: 14.8–69.2%) (see Supplementary Materials for details). Song sharing was negatively correlated with both direct (Mantel test: correlation coefficient = 0.26,  $P = 0.027$ ) and habitat (correlation coefficient = 0.29,  $P = 0.016$ ) distance. Thus, the greater the proximity between 2 neighborhoods, the more they shared song types (Figure 1d–f). This pattern may be caused either by the restricted local distribution of song types leading to more sharing between neighborhoods separated by small distances or else by the transfer of songs between neighborhoods by dispersing individuals.

Focusing on the role of dispersal, we found that song type sharing was positively correlated with dispersal events between neighborhoods (Mantel test: correlation coefficient = 0.22,  $P = 0.048$ ). This offers a potential explanation for the spatial pattern of shared song types because dispersal was negatively correlated with both direct and habitat distance ( $P < 0.0001$ ); that is, closer neighborhoods experienced more dispersal (see Figure 1a). To test whether dispersal was important in predicting song type sharing, we included both distance and dispersal in a mixed model framework. The results revealed that dispersal explains song type sharing independently of distance (GLMM: dispersal:  $F_{1,27.3} = 12.18$ ,  $P = 0.002$ ; habitat distance:  $F_{1,39.3} = 9.14$ ,  $P = 0.004$ ; direct distance:  $F_{1,35.5} = 7.37$ ,  $P = 0.01$ ). This is illustrated most clearly in Figure 1f where repertoire sharing is positively correlated with the number of reciprocal dispersal events (the exception being neighborhood N1).



**Figure 3**

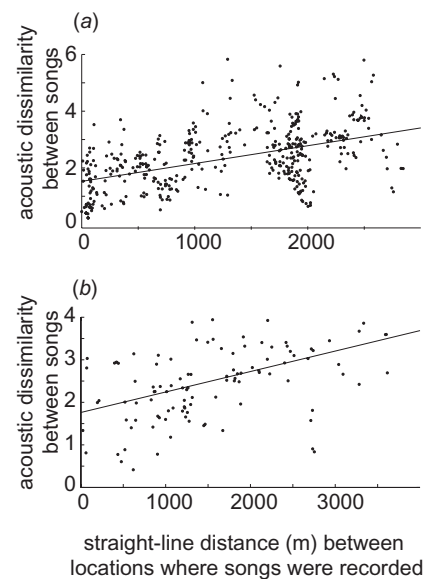
Relationship between repertoire novelty (a number between 0 and 6, related to the proportion of rare song types in a neighborhood) and dispersal (proportion of birds dispersing from one neighborhood to another, averaged over 7 years, 2004–2010); regression line (regression slope  $B = -23.93$ ,  $r = 0.79$ ,  $n = 13$ ) excludes 1 outlier (open circle; neighborhood N1). Data points are labeled by neighborhoods to illustrate geographical proximity.

### Effects of distance on fidelity of song transmission

We found that in 7 (77%) of 9 song types, there were no significant effects of distance on acoustic structure: The acoustic similarity of songs between neighborhoods did not depend on the distance between those neighborhoods (Supplementary Table S3). However, for song types E and M, the correlation was positive and highly significant (Mantel tests, E: correlation coefficient = 0.50,  $P < 0.001$ ; M: correlation coefficient = 0.45,  $P = 0.001$ ; Figure 4). Thus, for song types E and M, the further apart 2 examples were recorded, the more dissimilar they were. This pattern held when controlling for multiple comparisons (Bonferroni correction, adjusted  $P$  value = 0.006; see Supplementary Information, Supplementary Figure S6). We emphasize that visual and DFA classifications for E and M were in agreement, so it is unlikely that our result is due to misclassification. Moreover, plots of acoustic distance against geographic distance revealed that out of the 25 song types for which we had collected a minimum of 3 samples across multiple neighborhoods, 9 (including E and M) were strikingly clustered in neighborhoods (Supplementary Figure S7), suggesting that the decrease of acoustic similarity over distance was more widespread than suggested by the Mantel tests, but undetected at our sampling levels.

### DISCUSSION

We have made use of data from a long-term field study to assess the role of individual movements over time in shaping patterns of cultural variation in great tits. Our results provide the clearest evidence to date that both dispersal and immigration influence cultural diversity. Specifically, we have shown that immigration is associated with an increase in repertoire size, whereas dispersal is associated with a decrease in repertoire novelty. We also present evidence that song sharing increases with dispersal and decreases



**Figure 4**

Relationship between geographic distance (shortest distance between the locations where 2 samples of the same song type were recorded) and acoustic dissimilarity (i.e., Euclidean distance in acoustic space) for song types E (a) and M (b) (E: regression slope  $B = 0.50$ ,  $r = 0.5$ ,  $t = 6.0$ ,  $P < 0.001$ ,  $n = 29$  recordings; M: regression slope  $B = 0.45$ ,  $r = 0.45$ ,  $t = 3.76$ ,  $P = 0.001$ ,  $n = 15$  recordings). All statistics are from Mantel tests.

with isolation (i.e., distance between neighborhoods). These findings shed light on the role of individual movements across space as fundamental drivers of cultural evolution.

### Dispersal, immigration, and geographic isolation

The influence of dispersal on patterns of cultural diversity in songbirds has been investigated indirectly by previous empirical and theoretical studies, largely by examining the sharing of traits among neighborhoods (Searcy et al. 2002; Ellers and Slabbekoorn 2003). The most common variant of this framework focuses on natural or anthropogenic barriers likely to prevent the study organisms to disperse freely (Baker and Mewaldt 1978; Rivera-Gutierrez et al. 2010). In such cases, positive relationships have been detected between dispersal and song sharing, supporting the prediction that song sharing is constrained by physical barriers (Laiolo and Tella 2007; Rivera-Gutierrez et al. 2010).

The present study builds on these previous approaches in 2 ways: First by evaluating the implications of dispersal on direct measures of cultural diversity and cultural novelty in neighborhoods, and second by considering cultural transmission in continuous habitat. The focus on continuous landscapes allows us to consider long-term patterns of individual movement among neighborhoods and to use distance as a proxy for dispersal, without having to control for the complicating effects of barriers. Our results support the findings of previous studies by showing that dispersal promotes song sharing among neighborhoods. By demonstrating this effect in continuous habitat, we establish that a fundamental mechanism driving spatial patterns of cultural diversity involves the dispersal decisions of individuals, rather than the constraints of physical barriers.

Another factor thought to shape cultural evolution is population size, with most studies concluding that the size of the pool of potential tutors determines cultural diversity (Laiolo and Tella 2007; Lind and Lindfors 2010). In this study, cultural diversity (i.e., repertoire size) was not affected by the number of breeding males present in a neighborhood but instead was positively related to rates of immigration over time (regardless of population size or density). One possible explanation of this result in our system is that immigrants originate from outside the study population, and these individuals presumably introduce novel songs to neighborhoods, in accordance with theoretical models (Nunn et al. 2009). We conclude that, for cultural diversity, it is not so much the absolute number of potential tutors that is important, but their source. However, it is also possible that our result reflects a false negative and that weak effects of neighborhood size on cultural diversity remained undetected in this study.

Conversely, we found a significant effect of the interaction between neighborhood size and immigration on repertoire novelty. Specifically, at low levels of immigration, neighborhood size was positively related to repertoire novelty, whereas at higher level of immigration, neighborhood size was negatively related with repertoire novelty. One possible reason for this outcome is that birds immigrating into a particular neighborhood may derive from a single origin, such as a neighboring hedgerow or woodlot, thus introducing song types from a similar source repertoire. Thus, in neighborhoods with a high proportion of immigrants, large populations are more likely to contain multiple immigrants from the same area, which may reduce cultural innovation as determined by our measure of repertoire novelty. In other words, the songs of immigrants will not be unique in these cases simply because they are swamped by those of other immigrants. Further studies addressing this question would be helpful, particularly as our

sample size is quite small for testing the effect of 3 predictors at once.

We found that geographically isolated neighborhoods had lower levels of natal dispersal and shared fewer song types with other neighborhoods. Habitat distance was a better predictor of dispersal than direct distance, presumably because woodland birds rarely travel through unsuitable habitat (Desrochers and Hannon 1997). Cultural exchanges are thus more frequent between neighborhoods separated by several kilometers of woodland (e.g., N3 and N11) than between neighborhoods on opposite sides of a 500-m-wide field (e.g., N5 and N6; Figure 1a). This underscores the need to consider the spatial distribution of suitable environments and potential barriers when trying to understand patterns of cultural diversity (Laiolo and Tella 2007; Rivera-Gutierrez et al. 2010).

When we compared the effects of distance and dispersal on repertoire sharing, we found that dispersal was the strongest predictor. This confirms that dispersal is not simply determined by distance but also reflects the decisions of individuals to move between sites, likely driven by preferences for a certain area or neighborhood based on variables such as habitat quality, population density, breeding opportunities, and risk of inbreeding (Greenwood et al. 1978; Clobert et al. 2009). Taken together, our findings demonstrate that a combination of distance and dispersal behavior can help to predict patterns of cultural diversity, even in relatively small areas of continuous habitat. We emphasize that this finding may be particularly relevant to closed-ended learners and species such as great tits, which, although sometimes thought to be open-ended learners, tend to acquire most of their songs during the first few months of life (McGregor and Krebs 1982a; Rivera-Gutierrez et al. 2011). The outcome is likely to be shifted radically in truly open-ended learners, which can abandon obsolete signals and learn local signals after dispersing into a neighborhood, altering patterns of cultural variation (Baker and Mewaldt 1978).

A potential limitation of our study is that cultural variation was estimated on a shorter time frame than demographic variation. Specifically, songs were collected in a single year, whereas demographic variables such as population density, dispersal, and immigration were averaged over a 7-year period. Further experiments are required to record measures of demography and song diversity over similar timescales and thus to investigate in more detail how year-to-year changes in population dynamics affect cultural diversity. This approach would allow finer-scaled comparisons, for example, between annual immigration and short-term changes in local repertoire, potentially revealing that patterns of cultural variation are shaped by other factors, such as mortality rate. However, our use of song data from a single year seems unlikely to explain the finding that dispersal and immigration play key roles in the development and maintenance of cultural diversity, particularly as a previous study of the same population over 10 years showed that repertoire size and sharing were consistent across years, even when population size varied (McGregor and Krebs 1989).

### Cultural differentiation

Cultural differentiation is the process by which cultural traits undergo modification during transmission because of copying errors (Jenkins 1978; Lynch 1996). The main implication of this idea is that signal design may vary spatially without any need for dispersal and immigration. We found 2 strands of evidence consistent with cultural differentiation: First, a strong correlation between song divergence and geographic distance for 2 song types, E and M (Supplementary Table S3; Figure 4), and second, clustering of



signal properties within neighborhoods for >35% of song types (Supplementary Figure S7). These patterns of gradation and clustering are unlikely to reflect acoustic adaptation to habitat, as habitat structure is fairly uniform across the study site (Gibson 1988). Moreover, we show that some complex song types remain similar at multiple points across the study site, contrary to the predictions of the acoustic adaptation hypothesis. Thus, we conclude that the fidelity of transmission between individuals may influence variation in signal design.

Although cultural differentiation is known to be an important determinant of cultural diversity in primates (Whiten et al. 2001), our findings suggest that the process may be more widespread in vertebrates. They also suggest that mechanisms of cultural evolution may not apply consistently across signal types, a finding reported in other songbirds. For example, in chestnut-sided warblers *Dendroica pensylvanica*, song types associated with male–male conflict have high turnover (rates of change) across space, whereas songs involved in mate attraction are more stereotyped (Byers et al. 2010). All great tit song types appear to be used in both territory defense and mate choice (Krebs et al. 1978; McGregor and Krebs 1982b). It is not known whether these functions are mediated separately by different song types, but it is conceivable that songs used for territory defense benefit from stereotypy (Krebs et al. 1981), whereas songs used to court females benefit from variability, simply because females often prefer songs “slightly different from their father’s” (McGregor and Krebs 1982b). Further studies testing the functional significance of signal types, and the relationship between function and spatial variation, are needed to explore this possibility.

## CONCLUSION

Our study highlights the importance of demography, and especially of factors linked to the movements of individuals, in generating spatial variation in cultural traits within a single population of great tits. We have shown that immigration from outside the population and dispersal across the population are strong predictors of cultural variation. In this system, cultural diversity is reduced by the movement of individuals spreading cultural traits among neighborhoods and promoted by novel sources of tutors (immigrants). We also present evidence that cultural differentiation, involving cultural trait transfer with copying errors among static territorial individuals, offers a separate mechanism with a diversifying effect on cultural diversity. We conclude that demographic factors are key components shaping the cultural landscape of animals, with the movement of individuals playing an integral role. Understanding how these processes play out across time and space is crucial to understanding the development and maintenance of cultural diversity.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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