

Evolution driven by differential dispersal within a wild bird population

Dany Garant¹, Loeske E.B. Kruuk², Teddy A. Wilkin¹, Robin H. McCleery¹ & Ben C. Sheldon¹

¹Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

²Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, UK

Evolutionary theory predicts that local population divergence will depend on the balance between the diversifying effect of selection and the homogenizing effect of gene flow^{1–3}. However, spatial variation in the expression of genetic variation will also generate differential evolutionary responses. Furthermore, if dispersal is non-random it may actually reinforce, rather than counteract, evolutionary differentiation. Here we document the evolution of differences in body mass within a population of great tits, *Parus major*, inhabiting a single continuous woodland, over a 36-year period. We show that genetic variance for nestling body mass is spatially variable, that this generates different potential responses to selection, and that this diversifying effect is reinforced by non-random dispersal. Matching the patterns of variation, selection and evolution with population ecological data, we argue that the small-scale differentiation is driven by density-related differences in habitat quality affecting settlement decisions. Our data show that when gene flow is not homogeneous, evolutionary differentiation can be rapid and can occur over surprisingly small spatial scales. Our findings have important implications for questions of the scale of adaptation and speciation, and challenge the usual treatment of dispersal as a force opposing evolutionary differentiation.

Theoretically, adaptive population divergence depends on the balance between diversifying natural selection and homogenizing gene flow, with one force opposing the other^{4,5}. Variability in habitat quality can generate different selection pressures and can thus result in phenotypic divergence⁶ and potentially even sympatric speciation^{7,8}, as will differences in the genetic architecture of phenotypic traits and hence any evolutionary response to natural selection. So far, however, there have been very few documented examples of these processes from wild populations in natural environments. In addition, whereas most models of evolution under spatially variable selection assume that dispersal is random, this need not be the case, especially when there is an interaction between phenotype and habitat quality^{9,10} such as might result from social dominance of large over small individuals¹¹. Theoretically, differential dispersal could then act to reinforce differentiation generated by the response to diversifying selection. However, it is unclear whether these processes do in fact operate in this way in natural populations.

We examined spatial variation in the selection and evolution of fledgling mass as documented during a long-term study of a population of individually marked great tits (*Parus major*) at Wytham, Oxfordshire, UK (51°47' N, 1°20' W), from 1965 to 2000. Fledgling mass is an excellent model trait because it is subject to positive directional selection^{12,13} (see Fig. 1), can be easily measured on large samples of relatives, and shows moderate heritability in this and other species of birds^{13–15}. In this population, great tits show natal dispersal behaviour only, with very little breeding dispersal outside the area in which they settle as first-time breeders¹⁶, which facilitates the assessment of dispersal patterns of individuals.

Wytham is a heterogeneous woodland, arbitrarily divided into

nine sectors that show different habitat characteristics¹⁷. A close examination of phenotypic and genotypic (estimated by individual breeding values¹⁸) trends for fledgling mass over our 36-year study period revealed highly significant spatio-temporal heterogeneity among the eight sectors of the woodland studied for the whole period (sector-by-year interaction: phenotype, $\chi^2_{(7)} = 40.79$, $P < 0.001$; genotype, $\chi^2_{(7)} = 116.78$, $P < 0.001$). More detailed analyses reveal strikingly different patterns depending on sector, with a strong spatial organization of the pattern observed among sectors (Fig. 2a). Specifically, sectors in the eastern part of the wood (Marley Wood and Marley Plantation, henceforth referred to as east; see Fig. 2a) showed the same general trend, whereas sectors in the northern part of the wood (Extra, Great Wood and Common Piece, henceforth called north; see Fig. 2a) showed a different tendency. The remaining sectors, located in the central part of the wood, showed an intermediate response (Fig. 2a) and will not be discussed in the remaining analyses. These sectors receive substantial immigration from both east and north (see Supplementary Information) and are therefore expected to behave in an intermediate fashion. An analysis based on individual nest boxes (which had the same location for the entire study period), without any reference to sector, confirmed the general pattern of clustering into east and north blocks (Fig. 2b). We therefore sought to explain the differences between the areas (east and north) with the most contrasting patterns.

Birds in the eastern part of the wood showed a decrease in mean phenotype (Fig. 3a) and breeding value (Fig. 3b) over time. In contrast, birds from the northern part of the wood showed no temporal trend in their mean phenotype (Fig. 3a) but a highly significant increase in their breeding value over time (Fig. 3b). Consequently, the two parts of the population showed significantly different patterns of divergence in both phenotype (difference between slopes = 0.019 ± 0.0081 , $t_{67} = 2.35$, $P = 0.022$; estimates are presented throughout with their standard errors, s.e.m.) and underlying genotype (difference between slopes = 0.0089 ± 0.0012 , $t_{67} = 7.32$, $P < 0.001$). Linear mixed modelling, controlling for non-independence of chicks from a brood, confirmed these significant differences between areas over time (phenotypes,

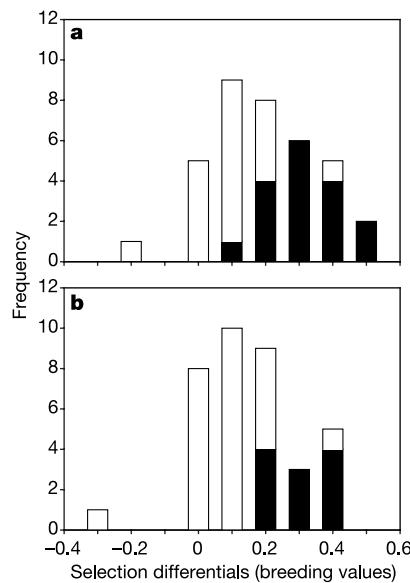


Figure 1 Distribution of standardized directional selection differentials for great tits for each year from 1965 to 2000 in Wytham¹³. **a**, Fledgling mass phenotype; **b**, fledgling mass breeding values. The shaded proportions of each bars indicate selection differentials significantly ($P < 0.05$) different from zero in individual years.

0.0185 ± 0.0031 , $\chi^2_{(1)} = 34.90$, $P < 0.001$; breeding values, 0.0085 ± 0.0008 , $\chi^2_{(1)} = 102.27$, $P < 0.001$; see also Supplementary Information). As a result, the population in the eastern part of the wood, which was composed of birds with the highest average fledging mass phenotype and breeding value at the beginning of the study period, is now composed of the smallest birds.

Different patterns of evolution might be caused by different patterns of selection, differing responses to selection, differences in dispersal, or a combination of these processes. Nestling fledging mass was under significant directional selection for survival in both areas (selection intensity: east, 0.140 ± 0.032 , $\chi^2_{(1)} = 27.91$, $P < 0.001$; north, 0.179 ± 0.023 , $\chi^2_{(1)} = 85.42$, $P < 0.001$) and

the same was true for the breeding values for this character (east, 0.077 ± 0.032 , $\chi^2_{(1)} = 8.48$, $P = 0.004$; north, 0.128 ± 0.023 , $\chi^2_{(1)} = 36.46$, $P < 0.001$). The intensity of directional selection did not differ between areas (phenotype, $t_{24917} = 0.99$, $P = 0.322$; breeding value, $t_{24917} = 1.30$, $P = 0.194$).

The response to selection depends on the amount of additive genetic variance expressed; a given character can express differing quantities of genetic variance in different environments¹⁹. In birds, size-related heritabilities are generally higher under favourable environmental conditions than under poorer conditions, in which a smaller component of additive genetic variance is commonly observed¹⁹. In our study population we found significantly greater

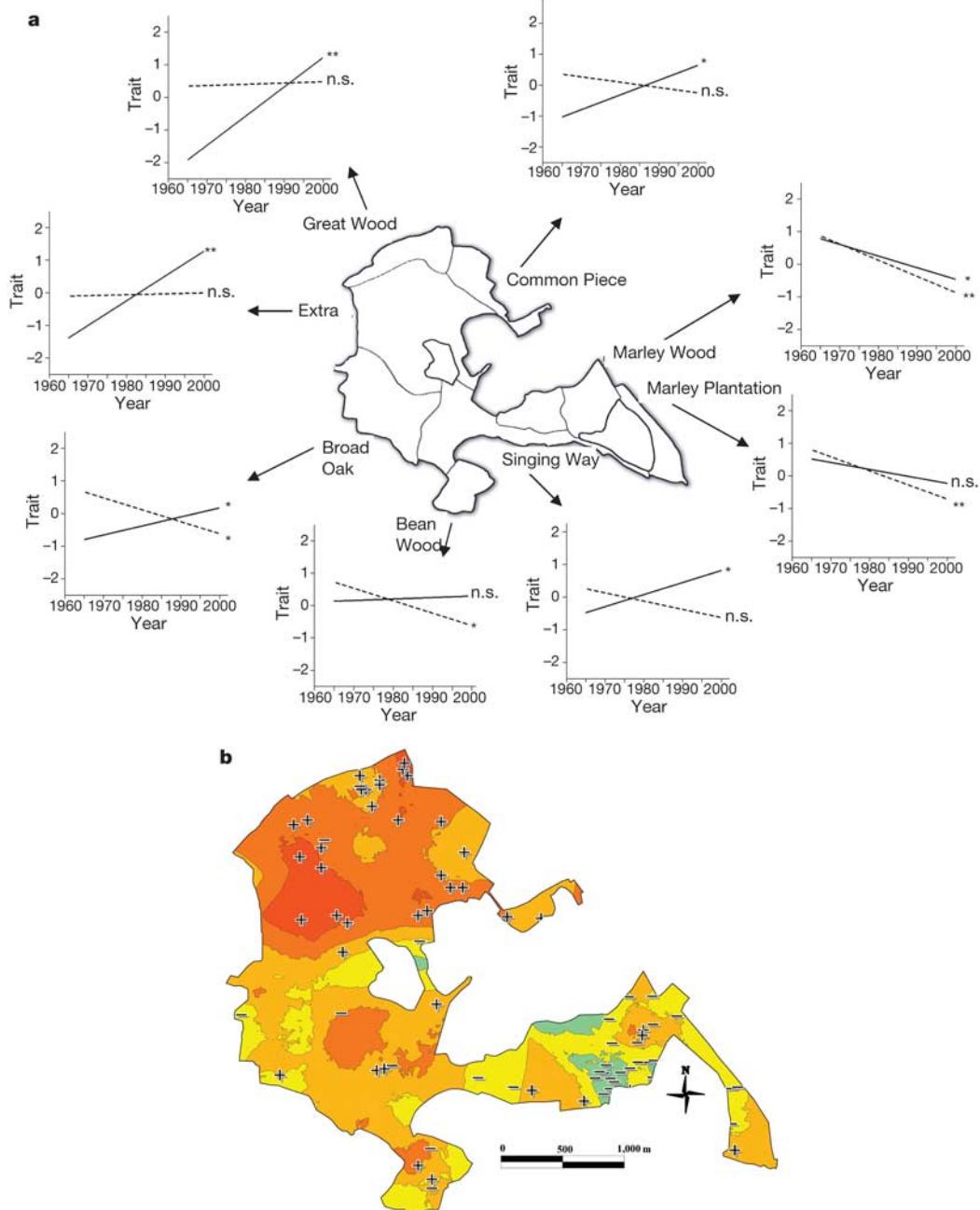


Figure 2 Within-population differences in great tit fledgling mass trends from 1965 to 2000. **a**, Temporal patterns of variation for each sector of Wytham at phenotypic (dashed lines) and genotypic (solid lines) levels. Significance: n.s., not significant; one asterisk, $P < 0.05$; two asterisks, $P < 0.01$, referring to trends over time. **b**, Temporal changes in the genotypic component (estimated breeding value) of fledgling mass

analysed at the level of individual nest boxes. Colours indicate local trends over time: red, increase; green, decrease. Plus signs, individual nest boxes that showed a significant increase; minus signs, individual nest boxes that showed a significant decrease.

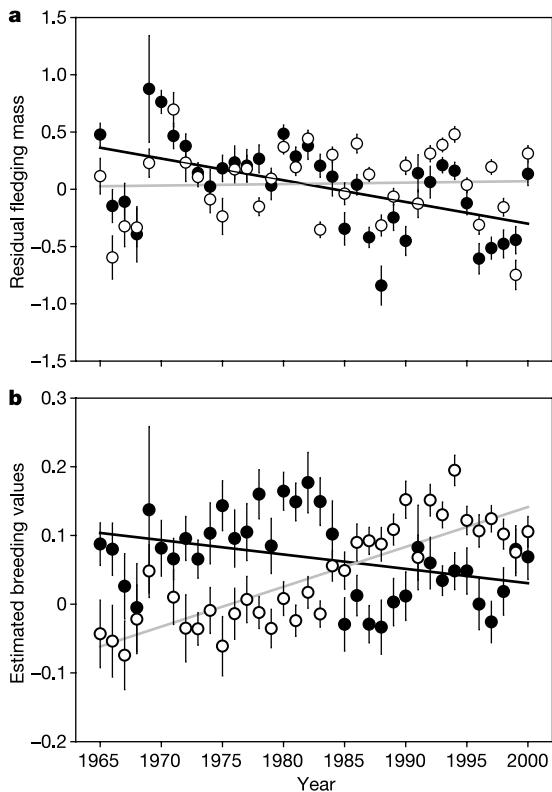


Figure 3 Temporal trends in fledgling mass of great tit nestlings born within the eastern and northern parts of Wytham from 1965 to 2000. Mean residual fledgling mass (**a**) and breeding values (**b**) (values are means \pm 95% confidence intervals). Nestlings born in the north (grey line and open circles) showed no change in their phenotype ($b = 0.00024 \pm 0.00611$, $t_{33} = 0.04$, $P = 0.969$) but a highly significant increase in their breeding value over the study period ($b = 0.00633 \pm 0.00078$, $t_{33} = 8.11$, $P < 0.001$; weighted by annual sample size). Birds born in the east (black line, filled circles) showed a significant decrease at both levels (phenotype, $b = -0.01870 \pm 0.00514$ g yr $^{-1}$, $t_{34} = -3.64$, $P < 0.001$; breeding values, $b = -0.00255 \pm 0.00094$, $t_{34} = -2.73$, $P = 0.010$). The difference between the slopes is significant for both measures (see the text).

additive genetic variance in the north than in the east, which translated into a significantly higher heritability of fledgling mass in this area (see Table 1). As a consequence, the expected response to selection was greater in the northern part of the wood than in the east. Using the simplest approach, in which the response to selection (R) is the product of selection and heritability of a character, scaled by generation time ($R = h^2 S / \text{number of generations}$), with a generation time of 1.97 years in the east and 1.83 years in the north, the expected response in the east ($+0.0141$ g yr $^{-1}$) is less than half that in the north ($+0.0287$ g yr $^{-1}$). Thus, this difference between areas in the expected response to selection, generated by variable levels of additive genetic variance, could contribute to the pattern of phenotypic differentiation observed between areas.

Although expected responses to selection thus differed depending

on the areas under study, these differences would seem likely to be swamped by gene flow, given that, on average, 62% of the breeding birds in a given area are born outside that area (see Supplementary Information), and they would not in any case explain the decline observed in the east. However, we also found marked evidence for differential dispersal, both within the study population and in terms of birds immigrating to the study area, both of which act to reinforce the different expected responses to selection documented above. Specifically, birds born in the central part of the wood showed non-random natal dispersal patterns (Fig. 4a), with birds emigrating to the north showing no change in mean phenotype over time (adult body mass from 1978 to 2000, $b = 0.0183 \pm 0.0116$, $t_{21} = 1.58$, $P = 0.130$), whereas birds emigrating to the east showed a significant decline in their body mass ($b = -0.0494 \pm 0.0123$, $t_{18} = -4.01$, $P < 0.001$); the difference between areas was significant (see Fig. 4a). This pattern of non-random dispersal was also present when analysing the phenotypic trends for birds immigrating to the wood but born outside Wytham (see Fig. 4b) (adult body mass from 1974 to 2000: east, $b = -0.0507 \pm 0.0084$, $t_{22} = -6.08$, $P < 0.001$; north, $b = -0.0161 \pm 0.0062$, $t_{23} = -2.58$, $P = 0.017$); the difference between areas was again significant (Fig. 4b). This pattern is unlikely to have been caused by the influence of the environment on adult mass of birds after settlement, because the change from fledgling to adult mass (for birds from the central area, measured as nestlings) did not differ between areas over time (see Fig. 4c). The pattern therefore reflects differential distribution according to mass before settlement. A within-family comparison, restricted to broods in which one or more offspring immigrated to each of the north and east areas (267 nestlings from 114 families), confirmed the dependence of dispersal on phenotype (Fig. 4d). Within families, heavier offspring showed an increasing tendency over time to settle in the north of the wood. Settlement of birds is therefore markedly non-random, is dependent on phenotype, and contributes to the within-population differentiation.

The collection of long-term data on population dynamics from this study population indicates the ecological mechanism responsible for local differentiation. Specifically, our results indicate that the north has become the preferred habitat over time. In a previous study, we showed that density-dependent processes are important determinants of the uncoupling between genotypic and phenotypic trends in fledgling mass over time in this population¹³. Higher density had a detrimental effect on mean fledgling mass, leading to a larger negative environmental deviation of the phenotype from its genotypic value at the population level (that is, birds were lighter than expected)¹³. However, although the number of nest boxes and their locations were kept constant throughout the study period, breeding density varied both spatially and temporally within the study population (Fig. 5) and it is therefore a potentially important factor at a local scale within this population. Average local breeding density in the east was more than twice that in the north (mean occupied nest-box Theissen polygon area \pm SD: east = $4,253 \pm 1,225$ m 2 , north = $10,097 \pm 2,187$ m 2 , paired t -test comparing annual values, $t_{28} = 13.71$, $P < 0.001$; see Fig. 5), indicating higher pressures on the habitat in the east than in the north. However, overall population density increased over the study period¹³, and we found a significant decrease in mean polygon

Table 1 Components of phenotypic variance in great tit fledgling mass (g) and resulting heritability in contrasting areas of Wytham Woods

	N (nestlings)	Trait mean (s.d.)	Additive genetic variance (s.e.m.)	Environmental variance (s.e.m.)	Phenotypic variance	h^2 (s.e.m.)
East	9,237	18.7 (1.5)	0.220 (0.036)	0.884 (0.066)	1.104	0.199 (0.031)
North	15,682	18.8 (1.4)	0.315 (0.027)	0.756 (0.046)	1.071	0.294 (0.024)
P			0.035	0.113		0.015

Significance (P) of the differences between areas is based on a t -test; environmental variance is defined as the sum of brood, year and residual variance.

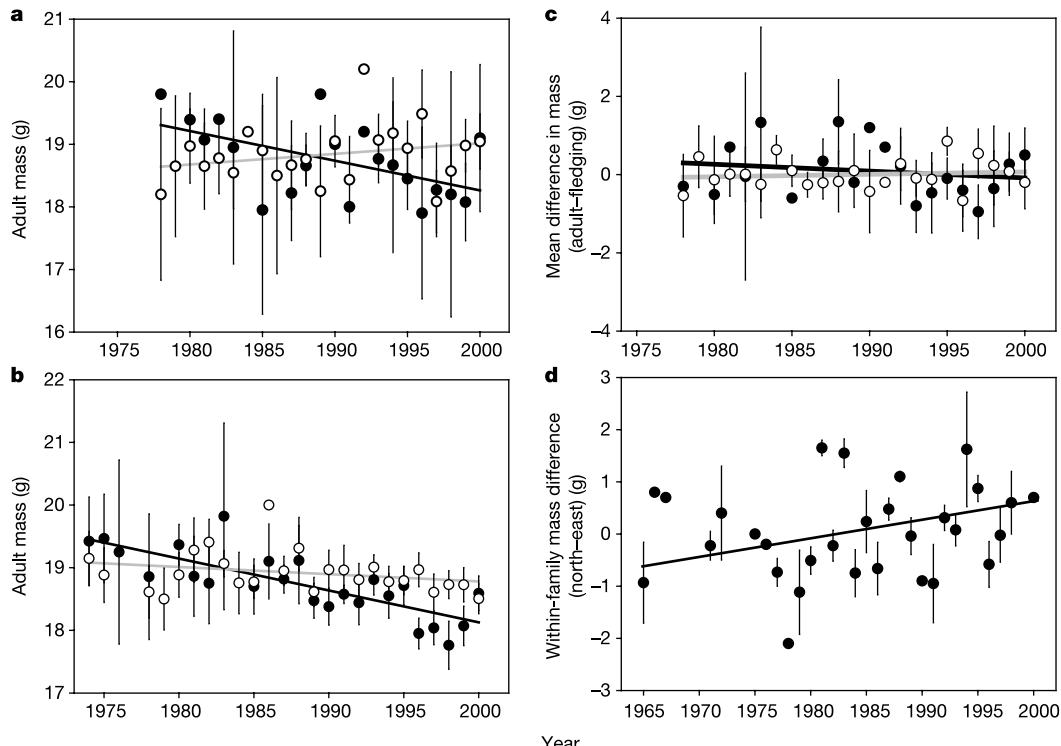


Figure 4 Mean adult mass of great tits immigrating to the eastern and northern parts of Wytham. The distribution of phenotypes with respect to time and area is non-random, because birds settling in the east (black line, filled circles) showed a much greater change in mass over time than birds settling in the north (grey line, open circles) (values are means \pm 95% confidence intervals). **a, b**, The difference between the slopes is significant for both birds originating from the central part of the wood (0.0676 ± 0.0176 , $t_{39} = 3.84$, $P < 0.001$) (**a**) and birds originating from outside the woodland (0.0347 ± 0.0104 , $t_{45} = 3.33$, $P = 0.002$) (**b**). **c**, Difference between adult and fledging masses for central emigrants settling in the east (black line, filled circles) or the

north (grey line, open circles) of Wytham. The difference between areas over time is not significant (0.0093 ± 0.0233 , $t_{39} = 0.40$, $P = 0.692$), indicating that the area of settlement does not influence the adult mass difference observed in **a**. **d**, Mean difference in fledging mass of great tits from the same family settling into the east and north parts of Wytham. The distribution of phenotypes changed over time, with the difference in mass between individuals settling in the two areas changing from being negative to positive over the study period. The difference between areas over time is significant (linear mixed model controlling for brood identity: 0.0311 ± 0.0127 , $\chi^2_{(1)} = 6.01$, $P = 0.014$).

area over time in the north ($-156.5 \pm 35.5 \text{ m}^2 \text{ yr}^{-1}$, $t_{27} = -4.41$, $P < 0.001$), with no significant change in the east ($-34.4 \pm 24.6 \text{ m}^2 \text{ yr}^{-1}$, $t_{28} = -1.40$, $P = 0.173$; significant difference between the two trends; $b = 122.2 \pm 42.8 \text{ m}^2 \text{ yr}^{-1}$, $t_{55} = 2.85$, $P = 0.006$). The temporal difference between the two areas might indicate an effect of preferential settlement in higher-quality (lower-density) habitat, a suggestion reinforced by the phenotype-dependent dispersal, which is consistent with larger, heavier, individuals being able to settle in preferred habitats. We tested whether habitat preference was linked with an increase in fitness. We first found that the survival of chicks to recruitment did not differ significantly between areas throughout the study period (difference = 0.0029 ± 0.0040 , $\chi^2_{(1)} = 0.52$, $P = 0.470$), but that survival was greater on average in the north (east = 9.8%, north = 10.8%, standard error of difference = 0.4%, $\chi^2_{(1)} = 6.05$, $P = 0.014$). Further analyses of adult components of fitness showed that lifetime reproductive success was higher (difference = $+0.182 \pm 0.047$ recruits, $t_{4243} = 3.92$, $P < 0.001$) and had increased significantly more over time in the north than in the east (difference = $+0.012 \pm 0.005$ recruits yr^{-1} of birth, $t_{4243} = 2.41$, $P = 0.016$). Thus, estimates of fitness components corroborate the suggestion that habitat quality differences drive differential dispersal and hence population differentiation. Other ecological mechanisms might have a role in the change in habitat quality, but these have not been quantified. Moreover, it is likely that many of these mechanisms would be correlated with the difference in density (for example, interspecific competition or food availability).

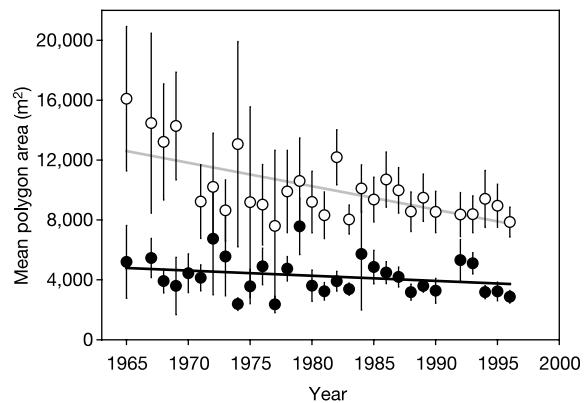


Figure 5 Mean polygon area (m^2) of breeding pairs of great tits in north (grey line, open circles) and east (black line, filled circles) areas over the study period (values are means \pm 95% confidence intervals). This measure is inversely related to the breeding density experienced by breeding birds.

Here we have demonstrated significant evolutionary differentiation within a single population over small spatial and temporal scales. This differentiation results from the joint effects of differences in the expression of genetic variation and in dispersal, both potentially driven by variation in habitat quality. To put the patterns revealed here in context, the mean distance between breeding locations in the east and north populations is 3,720 m; the mean

natal dispersal distance of great tits in this population is 674 m for males (median 532 m) and 911 m for females (median 771 m)²⁰. The documented divergence here now amounts to 0.39 phenotypic standard deviations of fledging mass (change in haldanes: $h_{p(1.29)} = 0.02$), over a 36-year period (equivalent to 19 generations) and the average within-year quantitative genetic variation between areas (measured with Q_{st} on breeding value differences²¹) for the population between 1995 and 2000 is estimated to be 0.020 (95% confidence interval 0.003–0.037). These differences demonstrate that marked evolutionary differentiation is possible at small spatial and temporal scales within populations²², even in the absence of differences in selective regime²³. Our findings have important implications for future studies of local adaptation and speciation, and underline the importance of integrating knowledge about fine-scale environmental heterogeneity into such studies. □

Methods

Study species and data collection

We used data obtained from the long-term study of the great-tit population in Wytham Woods, Oxford, UK^{13,24}. All breeding attempts are monitored from the date of egg laying until all nestlings had fledged. At 15 days old (hatch day = 1), nestlings were weighed (to the nearest 0.1 g) and marked with individually numbered aluminium rings. At the same time, their parents were captured and their identity was checked, which allowed us to build pedigrees for the quantitative genetic analysis (see ref. 13 for further details). Here we used data from 1965 to 2000 because nest box locations were kept constant from 1964, and because we were able to correct for the effect of laying date, clutch size and egg weight for these years (see ref. 13). In all the analyses on fledging mass we therefore used the residual mass from a general linear model including laying date, clutch size and egg weight as variables. Second clutches and repeat clutches laid after failure of the first clutch were removed from the data set¹³. Thus, data were available for 4,856 breeding attempts involving 37,337 nestlings. To evaluate phenotypic trends of immigrants (from inside and outside) we used uncorrected adult mass (for birds caught in May); however, this was available for a more limited number of years (from 1974 to 2000 for birds from outside Wytham, $N = 1,185$; from 1978 to 2000 for birds from inside Wytham, $N = 217$). Linear regressions of annual means were weighted by the number of individuals in a given year in all cross-sectional analyses.

Quantitative genetic analyses

Variance components of fledging mass and individual breeding values were estimated through a mixed-model restricted-maximum likelihood (REML) estimation procedure with the software packages VCE4 (ref. 25) and PEST²⁶. We used the pedigree information to fit an individual 'animal model'¹⁸, in which year of birth was included as a random effect to account for temporal heterogeneity in environmental effects on the phenotype. The brood identity was also fitted as a random effect to account for common-environment and maternal effects specific to the individual brood. Best linear unbiased predictors of individual breeding values were then quantified from pedigree information by using REML estimates of variance components with the software package PEST. Change in estimated breeding values over different generations reflects changes in the genetic composition of the population. Because a lack of pedigree connectedness could introduce a form of gene-environment covariance, we calculated the proportion of individuals reproducing in either east or north (the areas with most contrasting changes in phenotype and genotype, and most separated in space) that had parents reproducing in the opposite habitat. We found that 9.2% of offspring reproduced in the habitat opposite to that of their parents (that is changed from north to east or vice versa within a generation). We also found that 72% of birds reproduced in the same habitat as their parents, but because each generation comprises two parents and given that we have a mean of six generations (excluding nestling generation) per individual in our pedigree, the probability that a lineage of the mean length is composed entirely of birds born in a given area is $(0.72^{26})^{-1} = 0.72^{63} = 1 \times 10^{-9}$.

Selection analyses

Selection intensity (i)¹ was estimated with linear regressions, for relative survival (within each area separately) on both standardized (zero mean, unit variance, within each area) phenotypic and breeding values of the body mass. Statistical significance of the standardized selection differentials was estimated with logistic regression²⁷. Here we used a logistic regression model with fixed (phenotype or genotypic values) and random effects that allowed us to take into account the non-independence of fledglings within nest boxes by including brood identity as a random effect in the model (a generalized linear mixed model, GLMM, with binomial error; implemented in Genstat version 7.1 (ref. 28)). The significance of body mass (or breeding value) as a predictor of survival ($0 =$ died, $1 =$ survived) was assessed from the Wald statistic, which is distributed as $\chi^2_{(1)}$. Differences in chick survival between areas were tested by using a GLMM (with binomial error distribution) including area (east or north) and year (continuous) and their interactions as fixed effects and brood identity as a random effect. The association between area and adult lifetime reproductive success (LRS) (for adults born between 1965 and 1998; $N = 4,243$) was also tested by using a GLMM (with Poisson error distribution)

including adult status (immigrant or resident), area (east or north) and year of birth (continuous) and their interactions as fixed effects, and including year of birth as a random effect to account for cohort-specific variation (an analysis of adult LRS that also included adult mass as a covariate ($N = 2,607$) gave similar results).

Mapping

Average temporal changes in genotypic (breeding values) component of the fledging mass within each nest box (for which data were available for at least two years) were mapped (Fig. 2b) using inverse distance weighting interpolation. This method uses a moving average to interpolate pixel values and estimate local trends between spatially discontinuous and highly variable data. Each pixel value is calculated by averaging the weighted sums of all data points within a user-defined search area, such that points farther away influence the pixel value less than those that are close (decay exponent = 2). In this case, the radii of the search area and the display area were four times the average point density (413 m).

Density and definition of mean polygon area

To estimate the local breeding density experienced by each pair of great tits, Theissen polygons²⁹ were formed around each occupied nest box and their areas were calculated. Nest boxes were considered occupied if a confirmed breeding attempt was made by a pair of either great tits or blue tits (*Parus caeruleus*). We used data on both species (available from 1965 to 1996) because they compete for the same nest boxes and for food^{17,30}. In this case, Theissen polygons contain all points closer to a given nest box than to any other nest box, such that polygon boundaries are equidistant between occupied nest boxes. The area of each polygon is inversely related to the interspecific breeding density experienced by the breeding pair.

Received 2 July; accepted 21 September 2004; doi:10.1038/nature03051.

- Endler, J. A. *Natural Selection in the Wild* (Princeton Univ. Press, Princeton, New Jersey, 1986).
- Endler, J. A. *Geographic Variation, Speciation, and Clines* (Princeton Univ. Press, Princeton, New Jersey, 1977).
- Slatkin, M. Gene flow and the geographic structure of natural populations. *Science* **236**, 787–792 (1987).
- Felsenstein, J. The theoretical population genetics of variable selection and migration. *Annu. Rev. Genet.* **10**, 253–280 (1976).
- García-Ramos, G. & Kirkpatrick, M. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* **51**, 21–28 (1997).
- Smith, T. B., Wayne, R. K., Girmen, D. J. & Bruford, M. W. A role for ecotones in generating rainforest biodiversity. *Science* **276**, 1855–1857 (1997).
- Hendry, A. P., Day, T. & Taylor, E. B. Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. *Evolution* **55**, 459–466 (2001).
- Doebeli, M. & Dieckmann, U. Speciation along environmental gradients. *Nature* **421**, 259–264 (2003).
- Barton, N. H. in *Dispersal* (eds Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D.) 329–340 (Oxford Univ. Press, 2001).
- Verhulst, S., Perrins, C. M. & Ridlington, R. Natal dispersal of great tits in a patchy environment. *Ecology* **78**, 864–872 (1997).
- Braillet, C. et al. Two blue tit *Parus caeruleus* populations from Corsica differ in social dominance. *J. Avian Biol.* **33**, 446–450 (2002).
- Naef-Daenzer, B., Widmer, F. & Nuber, M. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *J. Anim. Ecol.* **70**, 730–738 (2001).
- Garant, D., Kruuk, L. E. B., McCleery, R. H. & Sheldon, B. C. Evolution in a changing environment: a case study with great tit fledgling mass. *Am. Nat.* **164**, E115–E129 (2004).
- Merilä, J., Kruuk, L. E. B. & Sheldon, B. C. Cryptic evolution in a wild bird population. *Nature* **412**, 76–79 (2001).
- Jensen, H. et al. Sexual variation in heritability and genetic correlations of morphological traits in house sparrow (*Passer domesticus*). *J. Evol. Biol.* **16**, 1296–1307 (2003).
- Harvey, P. H., Greenwood, P. J. & Perrins, C. M. Breeding area fidelity of Great tits (*Parus major*). *J. Anim. Ecol.* **48**, 305–313 (1979).
- Minot, E. O. & Perrins, C. M. Interspecific interference competition—nest sites for blue and great tits. *J. Anim. Ecol.* **55**, 331–350 (1986).
- Lynch, M. & Walsh, B. *Genetics and Analysis of Quantitative Traits* (Sinauer, Sunderland, Massachusetts, 1998).
- Hoffman, A. A. & Merilä, J. Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.* **14**, 96–101 (1999).
- van der Jeugd, H. P. & McCleery, R. Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *J. Evol. Biol.* **15**, 380–387 (2002).
- Spitze, K. Population structure in *Daphnia obtusa*: Quantitative genetic and allozymic variation. *Genetics* **135**, 367–374 (1993).
- Blondel, J., Dias, P. C., Perret, P., Maistre, M. & Lambrechts, M. M. Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. *Science* **285**, 1399–1402 (1999).
- Postma, E. & van Noordwijk, A. J. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature* doi:10.1038/nature03083 (this issue).
- Perrins, C. M. Population fluctuations and clutch size in the great tit, *Parus major* L. *J. Anim. Ecol.* **34**, 601–647 (1965).
- Neumaier, A. & Groeneveld, E. Restricted maximum likelihood estimation of covariances in sparse linear models. *Genet. Sel. Evol.* **30**, 3–26 (1998).
- Groeneveld, E., Kovac, M., Wang, T. L. & Fernando, R. L. Computing algorithms in a general purpose BLUP package for multivariate prediction and estimation. *Arch. Anim. Breed.* **35**, 399–412 (1992).
- Fairbairn, D. J. & Preziosi, R. F. Sexual selection and the evolution of sexual size dimorphism in the water strider, *Aquarius remigis*. *Evolution* **50**, 1549–1559 (1996).
- VSN International, *Genstat* version 7.1 (VSN International, Oxford, 2003).
- Rhynsburger, D. Analytic delineation of Theissen polygons. *Geogr. Anal.* **5**, 133–144 (1973).

30. Minot, E. O. Effects of interspecific competition for food in breeding blue and great tits. *J. Anim. Ecol.* **50**, 375–385 (1981).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We are grateful to A. Charmantier, A. G. Gosler, J. L. Quinn and C. M. Perrins for comments on the manuscript and to the many people who collected data during the long-term tit study in Wytham. D.G. was financially supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Postdoctoral Research Fellowship, and by a Biotechnology and Biological Sciences Research Council (BBSRC) grant to B.C.S. and L.E.B.K., who are both Royal Society University Research Fellows; T.A.W. was funded by a studentship from the BBSRC.

Authors' contributions D.G. conducted analyses and discovered the original pattern, and drafted the manuscript together with B.C.S., who also provided overall guidance, and L.E.B.K., who also advised over quantitative genetic analyses. T.A.W. conducted spatial analyses. R.H.M.C. maintained the long-term database.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to D.G. (dany.garant@zool.ox.ac.uk).

Gene flow maintains a large genetic difference in clutch size at a small spatial scale

Erik Postma & Arie J. van Noordwijk

Netherlands Institute of Ecology (NIOO-KNAW), Centre for Terrestrial Ecology, PO Box 40, 6666 ZG Heteren, The Netherlands

Understanding the capacity of natural populations to adapt to their local environment is a central topic in evolutionary biology. Phenotypic differences between populations may have a genetic basis, but showing that they reflect different adaptive optima requires the quantification of both gene flow and selection^{1–3}. Good empirical data are rare⁴. Using data on a spatially structured island population of great tits (*Parus major*), we show here that a persistent difference in mean clutch size between two subpopulations only a few kilometres apart has a major genetic component. We also show that immigrants from outside the island carry genes for large clutches. But gene flow into one subpopulation is low, as a result of a low immigration rate together with strong selection against immigrant genes. This has allowed for adaptation to the island environment and the maintenance of small clutches. In the other area, however, higher gene flow prevents local adaptation and maintains larger clutches. We show that the observed small-scale genetic difference in clutch size is not due to divergent selection on the island, but to different levels of gene flow from outside the island. Our findings illustrate the large effect of immigration on the evolution of local adaptations and on genetic population structure.

Gene flow plays a crucial role in the evolution of natural populations^{2,3}. Although its role may be beneficial (by counteracting the negative effects of genetic drift and inbreeding on genetic variation^{5,6}), its role in constraining evolution by homogenizing the gene pool gains most attention^{1,7}. In spite of a wealth of theoretical studies showing that gene flow counteracts genetic differentiation, and thus the evolution of local adaptations, good empirical evidence is scarce, particularly for quantitative traits in spatially structured populations⁴. Those empirical studies that addressed the impact of gene flow on the evolution of local adaptations have focused on only some aspects, and investigated,

for example, the performance of populations inhabiting two different environments^{8,9}, or the effect of immigration into a single population^{10–12}. Furthermore, in the majority of studies assumptions had to be made regarding the genetic component in the phenotypic variation observed, or levels of selection and gene flow were not quantified (but see ref. 13).

A fascinating case of phenotypic variation at a small spatial scale can be found on the island of Vlieland in the Netherlands (Fig. 1a), where over the period 1975–95 females that bred in the western part of the island laid 1.15 ± 0.14 eggs more than females that bred in the eastern part (paired *t*-test: $t_{20} = 8.55$, $P < 0.001$), which is 0.91 s.d. of the average within-area and within-year distribution (Fig. 1b). Here we analyse what proportion of this persistent difference can be attributed to genetic variation, and then investigate the roles of immigration and several components of selection in maintaining this difference.

The classic approach to test for local adaptations, and genetic differences in general, is a common garden or other transplant experiment. Although such experiments are relatively easy to perform in a laboratory setting^{14,15}, or in sessile organisms in the wild¹⁶, they are not feasible for the majority of wild animals (but see refs 13, 17). However, about 10% of the females born on Vlieland breeds in the other area (also, see below), which allows for a separation of genetic and environmental effects. Additionally, the properties of this long-term study population allow for an accurate estimation of both immigration and selection (see Methods).

Whereas the difference in clutch size between the western and eastern part of the island ('East' and 'West', respectively) can partly be attributed to the area of breeding, and thus to phenotypic plasticity, approximately half of the difference is accounted for by where a female is born, which suggests a genetic component to the difference in clutch size between the West and the East (Fig. 2a). Although females that have dispersed to the other side of the island may either represent a non-random subset of birds or breed, for

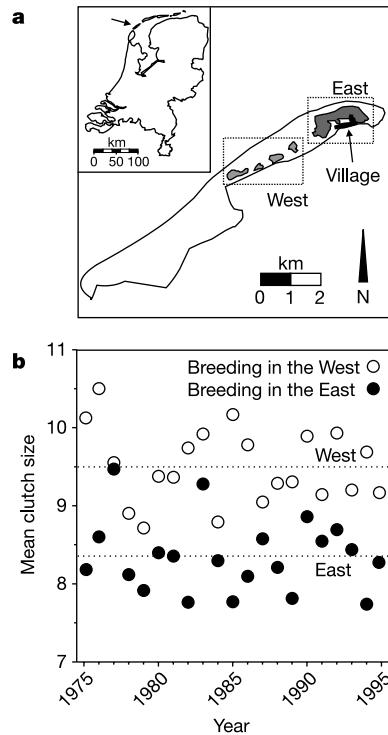


Figure 1 Clutch sizes on the island of Vlieland. **a**, Map of Vlieland, with the location of the woodlands that provide suitable nesting habitat in grey, and their grouping into West and East. **b**, Yearly mean clutch size in the West and the East from 1975 to 1995. Dotted lines give the overall mean.