Gene flow does not prevent personality and morphological differentiation between two blue tit populations

GABRIELLE DUBUC-MESSIER*† (iD), SAMUEL P. CARO*‡, CHARLES PERRIER*,
KEES VAN OERS‡, DENIS RÉALE†[1] & ANNE CHARMANTIER*†[1]

*Centre d'Écologie Fonctionnelle et Évolutive, Unité Mixte de Recherche CNRS 5175, Montpellier, France
†Département des sciences biologiques, Université du Québec à Montréal, Montréal, QC, Canada
‡Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

Abstract

Understanding the causes and consequences of population phenotypic divergence is a central goal in ecology and evolution. Phenotypic divergence among populations can result from genetic divergence, phenotypic plasticity or a combination of the two. However, few studies have deciphered these mechanisms for populations geographically close and connected by gene flow, especially in the case of personality traits. In this study, we used a common garden experiment to explore the genetic basis of the phenotypic divergence observed between two blue tit (Cyanistes caeruleus) populations inhabiting contrasting habitats separated by 25 km, for two personality traits (exploration speed and handling aggression), one physiological trait (heart rate during restraint) and two morphological traits (tarsus length and body mass). Blue tit nestlings were removed from their population and raised in a common garden for up to 5 years. We then compared adult phenotypes between the two populations, as well as trait-specific Q_{st} and F_{st}. Our results revealed differences between populations similar to those found in the wild, suggesting a genetic divergence for all traits. Q_{st}–F_{st} comparisons revealed that the trait divergences likely result from dissimilar selection patterns rather than from genetic drift. Our study is one of the first to report a Q_{st}–F_{st} comparison for personality traits and adds to the growing body of evidence that population genetic divergence is possible at a small scale for a variety of traits including behavioural traits.

Introduction

Understanding the evolutionary causes of phenotypic divergence among populations is an important aspect of the study of diversity. Environmental heterogeneity can have a major role in generating phenotypic divergence among populations (Wang & Bradburd, 2014). Spatial variation in selection pressures resulting from such environmental heterogeneity can lead to genotype by environment interactions for fitness and produce phenotypic and genetic divergence between populations

that can lead to local adaptations (Kawecki & Ebert, 2004; Wang & Bradburd, 2014). Spatial heterogeneity in ecological conditions can also favour the evolution of phenotypic plasticity, that is the adjustment of individual phenotypes in response to environmental factors (Pigliucci, 2005), and cause phenotypic divergence of populations in the absence of genetic divergence or local adaptation (Sultan & Spencer, 2002; Réale et al., 2003; Pigliucci, 2005). Phenotypic divergence of populations can also be produced by nonrandom dispersal of individuals between-habitat types (Wang & Bradburd, 2014). Importantly, phenotypic divergence of populations does not necessarily involve an adaptive process as phenotypic plasticity and nonrandom dispersal can be nonadaptive (Edelaar & Bolnick, 2012; Fitzpatrick, 2012; Wang & Bradburd, 2014) and can occur in same or in opposite direction to genetic divergence

Correspondence: Gabrielle Dubuc-Messier, Département des sciences biologiques, Université du Québec à Montréal, Case postale 8888, succursale Centre-ville, Montréal, QC H3C 3P8, Canada.
Tél.: 514 987 3000 (ext.2265); fax: 514 987 4647;
e-mail: dubuc-messier.gabrielle@courrier.uqam.ca
[1] Co-last authors.

(Fitzpatrick, 2012). In addition, strong founder effects or genetic drift can also lead to phenotypic and genetic divergence of populations (Slatkin, 1987). Establishing the relative importance of environmental vs. genetic effects involved in the phenotypic divergence of populations provides fundamental information about the origin of intraspecific diversity in the wild. In addition, determining if this divergence is adaptive or the result of neutral processes is essential because it gives important indications about the eco-evolutionary dynamics of traits and their evolutionary trajectories.

Traditionally, it has been considered that the homogenizing effect of gene flow prevents genetic divergence of populations (Lenormand, 2002; Sultan & Spencer, 2002). Thus, most research on genetic divergence focused on populations separated by large spatial scales or by important landscape barriers to dispersal (Slatkin, 1987; Lenormand, 2002). Nevertheless, recent theoretical and empirical studies revealed that even in the presence of gene flow, phenotypic divergence can have a genetic origin when there is strong divergent selection and/or nonrandom dispersal (Richardson et al., 2014; Wang & Bradburd, 2014). Despite growing interest for such isolation by environment, there is little empirical data on the mechanisms underlying the phenotypic divergence of populations separated by small geographic distances and connected by gene flow.

Behavioural traits have often been considered as highly plastic and thus less prone to genetic divergence. However, several studies are now showing that among-individual differences in behaviour can be repeatable (personality; Réale et al., 2007), heritable (van Oers & Sinn, 2011) and related to fitness (Smith & Blumstein, 2008) and could thus evolve in response to local conditions. In this context, an increasing number of studies have compared the personality phenotypes of individuals inhabiting contrasted ecological conditions (Bell, 2005; Quinn et al., 2009; Atwell et al., 2012; Herczeg et al., 2013; Miranda et al., 2013; Jacquin et al., 2016; Karlsson et al., 2016). However, fewer studies have disentangled the role of plasticity from that of genetic effects in shaping phenotypic divergence in personality traits between populations separated by distances that are within the dispersal ability of a species (Atwell et al., 2012; Miranda et al., 2013). Note that the plastic response to environmental factors can itself have a genetic basis, and hence, plasticity levels can differ across populations because plasticity can be heritable and evolve differently across populations (e.g. Laurila et al., 2002).

Previously, we have revealed a phenotypic divergence for personality and morphological traits between two wild populations of blue tits (Cyanistes caeruleus) living in contrasting habitats in a Mediterranean landscape (Charmantier et al., 2016; Dubuc-Messier et al., 2017). These populations occupy habitats and valleys dominated by either evergreen (holm oak, Quercus ilex) or deciduous oaks (downy oak, Quercus pubescens) yet are separated only by 25 km, which is within the typical dispersal range of the species (Winkel & Frantzen, 1991; Tufto et al., 2005). The dominant tree species in each habitat and valley is suspected to have an important influence on blue tits' ecological context that translates into phenotypic divergence between populations for numerous types of traits despite a spatial proximity and gene flow among them (Charmantier et al., 2016). For example, blue tits from the evergreen habitat have on average higher adult survival probability, lower body mass, smaller tarsus length, higher docility (lower handling aggression) and slower exploration in a novel environment, compared to birds from the deciduous habitat (Table S1; Grosbois et al., 2006; Charmantier et al., 2016; Dubuc-Messier et al., 2017). In addition, past studies in this system revealed that small birds (mass and tarsus length) have a selective advantage in the evergreen habitat (Blondel et al., 2002; Teplitsky et al., 2014), suggesting that at least some of the observed phenotypic divergence between habitats could be adaptive.

In this study, we used a common garden experiment to assess whether the personality and morphological divergence between these two blue tit populations could have a genetic basis. We collected blue tit nestlings from the evergreen and deciduous habitats and raised them for up to 5 years in aviaries, subsequently comparing their personality, physiological and morphological phenotypes once adults. Previous experiments in aviaries on this system have found a genetic divergence between these habitats for life history traits (Lambrechts et al., 1997). Based on these results, we hypothesized that the phenotypic divergence found previously in the wild for personality and morphological traits would also reflect a genetic divergence. Therefore, we predicted that, following the common garden experiment, individuals originating from the evergreen habitat would show a slower exploration in the novel environment, higher docility (lower handling aggression), smaller tarsus and lower body mass then individuals originating from the deciduous habitat. We also compared heart rate during manual restraint of birds originating from the two habitats, a physiological measure of stress reaction often used in personality studies (Koolhaas et al., 1999).

Second, we investigated whether the potential genetic divergence between these habitats could be attributed to different selection pressures or to genetic drift using a Q_{st}–F_{st} comparison approach (Leinonen et al., 2013). A trait Q_{st} measures the amount of additive genetic variance among populations relative to the total genetic variance in the trait (Leinonen et al., 2013). F_{st} is the equivalent measure for neutral molecular variance (Weir & Cockerham, 1984) and can be used as a null expectation for the degree of population divergence due to genetic drift and gene flow. If

$Q_{st} > F_{st}$, the trait divergence is higher than the neutral expectation and is likely the result of directional selection favouring local adaptation rather than the result of drift (Leinonen *et al.*, 2013). The two blue tit populations have very large effective population sizes (roughly estimated around 10 000 in each valley, Perrier *et al.*, genomic work in progress) and have been found weakly genetically differentiated (Szulkin *et al.*, 2016). Consequently, it is unlikely that any genetic divergence for these traits would be produced by genetic drift. We considered that, because birds were raised in a common garden, a phenotypic difference among individuals was a realistic approximation of an additive genetic effect. We thus used the phenotype of the common garden birds to calculate the Q_{st} and predicted that the Q_{st} of each trait would significantly exceed the F_{st} estimated between both populations. In addition, to better understand the importance of environmental factors in shaping the observed phenotypic differentiation in the wild, we compared the traits genetic differentiation (Q_{st}) for birds from the common garden experiment with the phenotypic differentiation of wild birds for the same traits (P_{st}; the amount of phenotypic variance among wild populations relative to the total phenotypic variance in the trait).

Materials and methods

The population located in the evergreen habitat (Evergreen-Pirio) is in the Corsican Fango valley (42°34′N, 08°44′E; 200 m elevation) and contains 205 nest-boxes distributed across two study plots. The population located in the deciduous habitat (Deciduous-Muro) is in the Corsican Regino valley (42°32′N, 08°55′E, 350 m elevation) and contains 110 nest-boxes distributed across three study plots. A weekly to daily monitoring over the course of the breeding season (from early April to the end of June) allowed the recording of exact laying dates and hatching dates for all broods established in nest-boxes.

Nestlings were collected for the common garden experiment at 7–12 days of age and were brought to the Netherlands Institute of Ecology (NIOO-KNAW, Wageningen, The Netherlands) where they were hand raised under standardized conditions. We used 169 blue tits that were collected in 2010 and 2011 in the deciduous habitat (2010: 42 birds, 7 broods; 2011: 39 birds, 6 broods) and in the evergreen habitat (2010: 44 birds, 10 broods; 2011: 44 birds, 8 broods). In 2010, before collecting chicks, broods were cross-fostered between nests for another experiment. For this experiment, at 2–4 days old, half of the chicks from a given brood were exchanged with half of the chicks of another brood from the same population.

Once collected, all birds were transported by car and hand-fed from Corsica to the Netherlands, and were hand reared until independence as described in Reparaz *et al.* (2014). Briefly, all the chicks from a given habitat and year were kept in boxes divided into multiple compartments that were not isolated from one another, each compartment containing one nest of three to five nestlings, until fledgling. Chicks from adjacent nests could easily change compartment, meaning that chicks from different nests were quickly mixed. After fledgling, birds were housed in cages in groups of two to four birds, irrespective of their sex and nest of origin (assigned randomly). Up to that period, chicks were fed every half-hour, 14 h day^{-1} (7:00 am–9:00 pm), with a diet consisting of a mixture of curd cheese, ground beef heart, baby cereal, multivitamin solution and calcium carbonate, supplemented with wax moth larvae and bee larvae, until independence. Raising chicks from the different habitats at exactly the same time would have been ideal but was impossible because chicks in the Regino and the Fango valleys hatch 1 month apart. However, chicks from different nests and habitats could easily see and hear each other, as they were raised in the same rooms, and fledglings from the Regino valley were still present in the cages when the younger chicks from the Fango valley arrived in the laboratory. Caretakers were the same for birds of different origins.

At independence, about 35 days after hatching, birds were relocated to larger individual cages or aviaries. Food and water were provided *ad libitum*. In 2012 and 2015, birds were moved to the Centre d'Écologie Fonctionnelle et Évolutive (CEFE-CNRS, Montpellier, France), where they were kept in outdoor aviaries before being released back into their natal habitat in Corsica. Morphological measurements were taken during the period at the NIOO-KNAW. Tarsus length was measured once (at > 1 year of age), but body mass was measured several times, always by the same person. We were interested in testing for a difference in adult body mass and thus kept in the analysis only the measures made at 1 year of age and older.

Behavioural and physiological trials

In total, 169 birds were tested for their exploration behaviour and, among these birds, 137 were tested for handling aggression and 57 for heart rate. All behavioural and physiological traits were measured once for each bird, which prevented us from reporting their repeatability. However, these behavioural and physiological traits have been shown to be repeatable in these two populations in the wild, with repeatability estimates ranging from 0.26 to 0.75 depending on the trait (see Dubuc-Messier *et al.*, 2017 for details). In this study, exploration behaviour was measured using a different protocol (see below) than the one used in the wild (Dubuc-Messier *et al.*, 2017). Nevertheless, we are confident that the exploration behaviour measured here represents repeatable characteristics of the individuals because this type of measure has been shown to

be repeatable in blue tits in several studies using different protocols (Kluen & Brommer, 2013; Mutzel *et al.*, 2013; Dubuc-Messier *et al.*, 2017). For details regarding the phenotyping of wild birds used in the P_{st} calculations, please refer to Dubuc-Messier *et al.* (2017).

Exploration behaviour

Exploration behaviour trials were performed in fall 2011 in the Netherlands Institute of Ecology as described by Reparaz *et al.* (2014) and using a novel environment chamber slightly modified from Drent *et al.* (2003). The novel environment chamber consisted of a $4.0 \times 2.4 \times 2.5$ m room with five artificial trees. Individuals were placed in cages adjacent to the main chamber 30–120 min before the trials and introduced in the main chamber through a sliding door. For 2 min, the observer counted the number of movements between trees and the number of small jumps on a given tree/branch. Exploration scores were the sum of both and varied from 10 (a very slow exploration pattern) to 92 (a very fast exploration pattern; Reparaz *et al.*, 2014).

Handling aggression

Handling aggression was measured assessing the bird's behaviour towards a manipulator (Dubuc-Messier *et al.*, 2017). We used a score ranging from 0 to 3. A score of 0 was the lowest aggression score (no reaction; high docility) and 3 the highest (see Table S2 for detailed protocol). Handling aggression was recorded in 2012 and 2015 at the CEFE-CNRS (France). Birds from the 2010 cohort were tested for handling aggression in 2012 or 2015 (at 2 or 5 years of age), whereas the entire cohort from 2011 was tested for handling aggression in 2015 (at 4 years of age). Handling aggression score was assessed blindly with respect to habitat of origin in 2015 and was assessed by two different observers, one in 2012 and one in 2015.

Heart rate during manual restraint

Heart rate was recorded in 2012 at the CEFE-CNRS (for the 2010 cohort only), as described by Dubuc-Messier *et al.* (2017). Within a few minutes after capture, we recorded heart rate for 30 s using a digital recorder. We used the software Avisoft SASLab Pro version 5.1 (Avisoft Bioacoustics Schönfließer, Germany) to extract the mean time interval (s) between two heartbeats using approximately 100 consecutive heartbeats per individual.

Molecular markers and F_{st} calculation

For logistical reasons, we were not able to perform a molecular analysis on the birds used in the common garden experiment. As an alternative, we used a data set, published by Szulkin *et al.* (2016) of wild birds from these two populations (i.e. deciduous, $n = 49$; evergreen, $n = 83$ individuals) and genotyped at several thousand SNP using RAD-sequencing. We retained loci genotyped over at least 75% of the individuals. To avoid bias during filtering and in the F_{st} estimates, we pruned highly related individuals from the data set to keep only individuals linked with values of kinship lower than 0.05 (coefficient of Loiselle; Loiselle *et al.*, 1995; Cheverud, 1996) computed in Genodive 2.27 (Meirmans & Van Tienderen, 2004). In order to retain loci more likely to be informative, we applied a 5% MAF threshold (*Minor Allele Frequency*, using vcftools 0.1.11; Danecek *et al.*, 2011). We pruned the data set for SNPs that deviated from Hardy–Weinberg equilibrium in at least one of the two populations (P-value < 0.05) using vcftools 0.1.11. We retained only the first SNP of each 100 bp locus. To obtain a set of SNPs more likely to be neutral, we filtered out SNPs potentially under divergent selection between the two habitats (P-value < 0.015; 0.7% of total SNPs removed). This was performed with a Bayescan 2.0 test (Foll & Gaggiotti, 2008; 5000 pilot iterations, 50 000 burn-in, prior odds of 100). Average F_{st} and 95% confidence intervals were estimated using the R package hierfstat 0.04-22 (Goudet, 2005). The final data set contained 69 individuals (32 and 37 individuals in the deciduous and evergreen habitats, respectively) genotyped at 5407 SNPs.

Statistical analysis

Genetic divergence between habitats of origin

We tested for a genetic difference between the two habitats for each trait with univariate linear mixed models using the phenotype of each bird as a response variable and habitat of origin, sex and their interaction as fixed effects. When we found a significant interaction between habitat of origin and sex, we ran a separate model for each sex. Specific confounding variables were added as fixed effects for each particular trait. For exploration score, we added a cohort term as a fixed effect to test for any environmental effect early in life or during the hand-rearing period in captivity. Novel environment tests were carried out on the two cohorts at the same time (in autumn 2011). Thus, at the time of the test, individuals born in 2010 were almost 1½ years old, whereas individuals born in 2011 were 5 months old. Hence, in this model, the cohort term controlled for the combined effect of cohort and age. For handling aggression score, we added cohort, time of day (hour) and year of test (2012 or 2015) as fixed effects. For heart rate models, we added as fixed effect mean individual adult body mass because heart rate is related to the metabolic rate and both are positively related to body mass (Green, 2011). Heart rate recordings were carried out in 2012 on the 2010 cohort only.

We therefore did not add a fixed effect for bird age, cohort or year to avoid redundancy. We also added in heart rate models the time of day (hour) as a fixed effect. For body mass, we added age as a continuous variable, cohort and time of day (hour). For tarsus length, we added cohort only as a fixed effect (i.e. 2010 and 2011).

In all models, we used random intercepts for the brood of origin and rearing brood to account for the nonindependence of birds coming from the same brood and/or the effect of foster parents for nestlings that have been cross-fostered prior to the captivity period. Because body mass was measured several times for each bird, we also added a random intercept for bird identity for this trait.

All response variables were Z-transformed prior to analyses. We tested the significance of the fixed effects and selected a minimal model by LRT (log likelihood ratio test) in a stepwise elimination procedure starting with a model that included all variables (Bates *et al.*, 2014). We kept all the random effects in final minimal models. We present in Table S3 the L-ratios and P-values associated with all variables in initial models. Analyses were carried out with R (R Core Team 2017) using the function *lmer* of the package *lme4* (Bates *et al.*, 2015). Confidence intervals (95%) were generated with the function *confint.merMod* (*lme4*). We assumed a Gaussian distribution for all traits, which was confirmed after visual inspection of the residuals. We also evaluated the population of origin effect across all five traits using Fisher's combined probability test run with the *sumlog* function of the R package *metap* (Dewey, 2017).

Q_{st}, P_{st} and F_{st} comparison

Because birds were raised in a common garden, we considered that a phenotypic difference among individuals was a realistic approximation of an additive genetic effect. For each trait, we thus calculated the Q_{st} between the two habitats based on the phenotypes of birds from the common garden using a procedure similar to Bertrand *et al.* (2016) with univariate mixed models in a Bayesian framework. We calculated Q_{st} as:

$$Q_{st} = \sigma_B / (\sigma_B + 2 \times \sigma_W)$$

where σ_B is the between-habitat phenotypic variance and σ_W the within-habitat variance (or residual; Wright, 1949). The two variance components were extracted from a univariate linear mixed model including habitat of origin (and identity of the bird for body mass) as random intercepts. We also included the fixed effects structure selected previously (minimal model) excluding the term habitat of origin. We calculated σ_B as the variance attributable to the habitat of origin and σ_W as the residual variance (or for body mass as the sum of the variance attributable to the residual and to the individual identity; Bertrand *et al.*, 2016). We did not include any broods effects in these models because

the variance attributable to the brood is also attributable to the population of origin. We present the between-habitat variance for each study trait extracted from the models used to calculate Q_{st} in Table S5. We calculated P_{st} as Q_{st} but used as random intercepts habitat of origin, the identity of the bird and the observer identity (for handling aggression and heart rate) along with the significant fixed effects detailed in Dubuc-Messier *et al.* (2017). For P_{st} calculation, we calculated σ_B as the variance attributable to habitat of origin and σ_W as the sum of the variance attributable to the observer, to the residual variance and the individual identity.

These models were performed with *MCMCglmm* package (Hadfield, 2010) in R using slightly informative priors (i.e. $V = V_P/n$, $nu = 1$ or 0.5; V_P is the total phenotypic variance of the trait and n the number of random effects), 10 million iterations, a thinning of 200 and a burn-in phase of 500. Because the results of the models with different nu were similar, we used the posterior distribution of models with $nu = 1$ in Q_{st} and P_{st} calculations. We assessed the presence of autocorrelation with the function *autocorr* (*MCMCglmm* package). All models showed an autocorrelation less than 10^{-4}. We checked for model convergence with the function *gewe.diag* of the *coda* package (Plummer *et al.*, 2006). For all traits, we calculated the ratio Q_{st}/mean F_{st} for each sample of the posterior distribution and report the posterior mode of the ratio and its 95% credibility intervals (calculated using the *HPDinterval* function of the package *lme4*). We assumed that Q_{st} differed significantly from F_{st} when the credibility interval around the ratio did not include one.

Results

Divergence between habitats of origin

The Fisher combined probability test method on all studied traits indicated an overall significant effect of the habitat of origin (χ^2: 54.647, d.f. = 10 and P-value < 0.001). Below, we present the results for each trait separately.

Behavioural and physiological traits

For birds in the common garden experiment, habitat of origin had a significant effect on the two behavioural traits: blue tits from the deciduous habitat were faster explorers and were more aggressive to the handler (Table 1; Fig. 1). Birds from the deciduous habitat had a lower heart rate than birds from the evergreen habitat (Table 1; Fig. 1). We found a trend for an interaction between habitat of origin and sex for heart rate (L-ratio = 3.360, d.f. = 1, P-value = 0.067): evergreen males had a higher heart rate than deciduous males [estimate = 1.24 (95% CI: 0.31; 2.17), L-ratio = 6.260, d.f. = 1, P-value = 0.010], but there was no habitat of

Traits	Terms	Estimates	95% CI	*L*-ratio	d.f.	*P*-value
Exploration score	Intercept	−0.32	−0.62; −0.03			
	Habitat of origin	−0.48	−0.78; −0.19	9.70	1	0.002
	Sex	0.26	0.004; 0.52	3.97	1	0.046
	Cohort	0.88	0.59; 1.17	23.91	1	< 0.001
Handling aggression	Intercept	0.45	0.18; 0.72			
	Habitat of origin	−0.82	−1.18; −0.46	14.96	1	< 0.001
Heart rate during	Intercept	−0.57	−1.06; −0.09			
restraint (HR)	Habitat of origin	0.98	0.35; 1.62	8.17	1	0.004
Body mass	Intercept	−1.07	−1.40; −0.74			
	Habitat of origin	−0.33	−0.63; −0.03	4.46	1	0.034
	Sex	−0.56	−0.77; −0.35	25.08	1	< 0.001
	Age	0.27	0.21; 0.33	74.23	1	< 0.001
	Time of day	0.09	0.07; 0.11	75.50	1	< 0.001
Tarsus length	Intercept	−0.25	−0.58; 0.08			
	Habitat of origin	−0.60	−1.00; −0.19	7.74	1	0.005
	Sex	1.04	0.81; 1.28	61.46	1	< 0.001

Table 1 Final models describing the phenotype of blue tits originating from two distinct populations and habitats (deciduous and evergreen) in Corsica (France) and reared in a common garden.

The deciduous habitat, females and cohort 2010 were set as references in models. Estimates are from a model with the brood of rearing and brood of origin in random effect (and individuals identity for body mass), and variance estimates are shown in Table S4. *L*-ratio and *P*-values are from the comparison of a full model and a model without the variable of interest. The *P*-values and *L*-ratio associated with each parameter in initial models before selection are presented in Table S3.
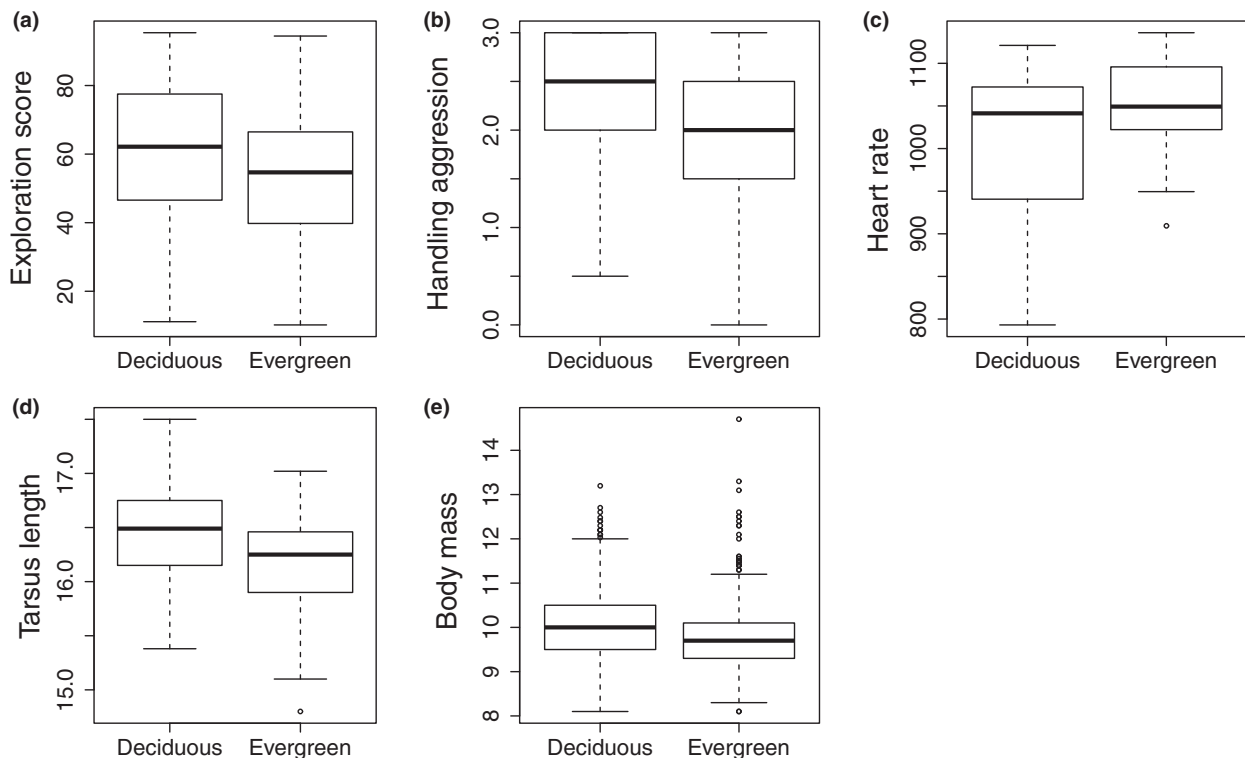
Fig. 1 Mean phenotypes of blue tits originating from two distinct populations and habitats (deciduous and evergreen) in Corsica (France) and reared in a common garden. (a) Exploration score, (b) handling aggression score, (c) heart rate during manual restraint (heart beats/ min.), (d) tarsus length (mm) and (e) adult body mass (g). Boxplots on raw data, the boxes represent the first and the third quartile, the lines represent the median, the ends of the whiskers represent the minimum data included in the 1.5 * the interquartile range, dots represent extreme data. All differences are significant (see Table 1 for details).

origin effect for females (L-ratio = 2.150, d.f. = 1, P-value = 0.142). There was no interaction between sex and habitat of origin for the two behavioural traits, but there was a difference in exploration score between sexes (Table 1).

Morphological traits

Habitat of origin also had a significant effect on the two morphological traits: deciduous birds were heavier and had a longer tarsus than evergreen birds (Table 1; Fig. 1). We did not find any interaction between habitat of origin and sex for these two traits (tarsus length: L-ratio = 0.226, d.f. = 1, P-value = 0.634; body mass: L-ratio = 0.155, d.f. = 1, P-value = 0.694). Among-individual differences in body mass were significant and represented 45% of the total variance of the trait [variance = 0.34 (95% CI: 0.26; 0.46), L-ratio = 421.95, P-value < 0.001].

Brood effects

Differences among broods of origin explained a significant portion (78%) of the total phenotypic variance in body mass, but not for the other traits (Table S4). Differences among rearing broods explained a significant portion of the total variance in tarsus length (22%) and a marginally significant portion of total variance in heart rate (30%, P-value = 0.07) but not for the other traits.

Q_{st}, P_{st} and F_{st} comparison

We found a significant but small genetic differentiation between the two populations [mean F_{st} over all loci = 0.004 (95% CrI: 0.003; 0.005), P-value < 0.001]. Q_{st} was higher than F_{st} with nonoverlapping intervals for all traits. The ratio between the Q_{st} and F_{st} was significantly greater than one for all traits (Table 2). Credibility intervals for Q_{st} and P_{st} overlapped for all traits (Table 2).

Discussion

Our common garden experiment suggests a genetic divergence in personality, physiological and morphological traits between two blue tit populations inhabiting contrasted habitats separated by a small spatial distance in regard to the species dispersal capacity. Adult blue tits originating from the evergreen habitat displayed slower exploration behaviour, lower handling aggression (higher docility), faster heart rate, lower body mass and shorter tarsus compared to birds from the deciduous habitat (Table 1; Fig. 1). These differences are similar to the ones measured in the wild suggesting that plasticity alone is not responsible for the observed phenotypic divergence in the wild (Charmantier et al., 2016; Dubuc-Messier et al., 2017). In addition, we found a significant F_{st} between the two populations, but its low value (0.004) indicates current or past gene flow, in concordance with previous findings (Szulkin et al., 2016). The Q_{st}–F_{st} comparisons revealed that blue tits from these populations are more differentiated for personality, physiological and morphological traits then they are at the genomewide level (Table 2). These results suggest that genetic drift alone does not explain the observed divergence between the two populations and that differences in selection regimes are responsible for this divergence.

The divergence we describe in personality, physiological and morphological traits is likely to be mainly of genetic origin, as birds from both habitats were raised in identical conditions from their first week of life to up to 5 years. In addition, the divergence found in this study for adult body size is consistent with previous studies that have found divergent selection between the two populations for morphological traits (Blondel et al., 2002; Teplitsky et al., 2014) and moderate to high heritability for these traits (0.29–0.51; Teplitsky et al., 2014). However, we cannot completely exclude that early environmental effects such as nongenetic inheritance, occurring before the chicks were sampled from their nest were at least partly responsible for the observed patterns (Kruuk & Hadfield, 2007; Räsänen & Kruuk, 2007; Bonduriansky & Day, 2009; Bouwhuis et al., 2010; van Oers et al., 2015). Such early environmental effects might be particularly important for tarsus length, which is usually fixed at 15 days of age for this species. However, for behavioural traits, such strong environmental effects lasting for up to 5 years are

Table 2 Q_{st} and P_{st} values (posterior mode) for each trait [and 95% credible interval (CrI)], mean F_{st} and Q_{st}/F_{st} ratio [posterior mode and associated 95% CrI)] between two blue tits populations originating from distinct populations and habitats (deciduous or evergreen) in Corsica (France) and reared in a common garden.

Traits	Q_{st} (95% CrI)	P_{st} (95% CrI)	Q_{st}/F_{st} ratio (95% CrI)
Exploration score	0.084 (0.029; 0.804)	0.063 (0.018; 0.727)	20.982 (7.266; 201.065)
Handling aggression	0.129 (0.034; 0.832)	0.045 (0.011; 0.692)	32.309 (8.525; 208.025)
Heart rate during manual restraint (HR)	0.101 (0.033; 0.846)	0.032 (0.007; 0.562)	25.320 (8.244; 211.475)
Body mass	0.069 (0.018; 0.736)	0.095 (0.030; 0.773)	17.144 (4.541; 183.998)
Tarsus length	0.197 (0.050; 0.872)	0.212 (0.048; 0.864)	49.368 (12.455; 217.881)
Mean F_{st}	0.004 (0.003; 0.005)		

Q_{st} have been calculated from the phenotype of birds raised in a common garden and P_{st} from the phenotype of wild birds.

unlikely, as very few studies have reported long-term consequences of early environmental conditions for the studied traits (Taylor *et al.*, 2012; Petelle *et al.*, 2015) and since maternal effects are known to decrease during ontogeny (Cheverud *et al.*, 1983; Wilson *et al.*, 2007). One way to control for very early environmental effects would be to allow the birds to breed in captivity and compare the phenotypes in the offspring generation. However, this type of experiment presents significant challenges that have so far prevented their feasibility in our study system. In particular, whereas it is possible to maintain blue tits in aviaries for short time experiments (Reparaz *et al.*, 2014), it is difficult to make them breed in captivity (Lambrechts *et al.*, 1999).

Some studies have raised concerns regarding Q_{st} and F_{st} estimation and their comparison (Leinonen *et al.*, 2013). In particular, between-population variance and thus Q_{st} estimation may be imprecise when a small number of populations are compared like it is the case in our study (O'Hara & Merilä, 2005; Leinonen *et al.*, 2013). However, simulations have shown that a small number of populations results in a downward bias in Q_{st} estimation when Q_{st} is high (O'Hara & Merilä, 2005). Another important concern is whether genetic markers involved in F_{st} estimation are truly neutral (Leinonen *et al.*, 2013). In this study, we used an F_{st} calculated from markers that included the whole genome. Although we filtered SNPs under potential divergent selection, it is possible that we included potentially non-neutral regions (or that we removed some neutral ones). However, using microsatellites, Porlier *et al.* (2012) have found a lower F_{st} (0.001) between the same populations during a similar time period (year 2009). Hence, although Q_{st} and F_{st} comparison have some limitations, these limitations should most probably have limited our capacity to detect significant Q_{st}–F_{st} differences rather than reveal false differences.

Environmental heterogeneity, divergent selection and local adaptations

The importance of environmental heterogeneity and gene flow for phenotypic divergence has mainly been studied for life history and morphological traits and much less for behavioural traits. Indeed, few studies have disentangled so far the role of plasticity from that of genetic differences in shaping the phenotypic divergence of populations for behavioural traits (Bell, 2005; Dingemanse *et al.*, 2007; Herczeg *et al.*, 2013; Jacquin *et al.*, 2016; Karlsson *et al.*, 2016) and even fewer for highly mobile avian species (Atwell *et al.*, 2012; Miranda *et al.*, 2013). In addition, to our knowledge, no studies have until now reported Q_{st}–F_{st} comparisons involving personality traits. This shortage of study is probably due to the fact that personality traits are often considered plastic and thus less prone to genetic divergence and local adaptations than morphological traits.

Yet, the results of our study suggest a genetic divergence for personality traits and that this divergence could be as strong as for morphological traits (Tables 1 and 2).

Past studies in this system and on personality variation suggest that the genetic divergence found here could be the result of the coevolution of multiple types of traits in response to the ecological context of each habitat. Indeed, an increasing number of studies are suggesting that life history and personality traits could have co-evolved to form a pace-of-life syndrome (Réale *et al.*, 2010). For example, empirical and theoretical studies are suggesting that high investment in early reproduction at a cost of reduced residual reproductive value (either via survival or future reproduction) should be associated with boldness, fast exploration and high aggressiveness (Wolf *et al.*, 2007; Réale *et al.*, 2010). Our results on this system are consistent with the pace-of-life syndrome hypothesis. Blue tits from the deciduous habitat, which are more aggressive and faster explorers, have a shorter lifespan and a lower residual reproductive value, but larger clutch sizes than birds from the evergreen habitat (Grosbois *et al.*, 2006; Charmantier *et al.*, 2016; Dubuc-Messier *et al.*, 2017; Table S1). Our results suggest that these divergences for personality traits are genetic and the Q_{st}–F_{st} comparisons revealed that they are likely the result of divergent selection pressures rather than drift. In addition, studies on other blue tit or great tit (*Parus major*) populations have found that the personality phenotypes are heritable and related to fitness (van Oers & Sinn, 2011; Class *et al.*, 2014). Therefore, taken together, our results suggest that the personality phenotypes of birds living in these habitats could have evolved and be implicated in blue tit adaptation to local ecological conditions prevailing in each habitat.

Brood effects

We did not find any significant brood-of-origin effect for handling aggression, exploration score, heart rate and tarsus length. As all these traits except heart rate have been shown to be heritable in previous studies on blue tits (van Oers & Sinn, 2011; Class *et al.*, 2014; Teplitsky *et al.*, 2014), the absence of heritable variance in our analysis is most probably explained by the relatively small number of broods. Estimating heritability was not the goal of this study, we only wanted to control for dependence issues associated with the use of sibs.

The partial cross-fostering manipulation before the common garden experiment revealed a significant rearing brood effect for tarsus length. This result suggests that the rearing environment between 2 and 12 days old can have a significant impact on this morphological trait. Contrarily to the other traits that are more labile, tarsus length generally stabilizes at 15 days of age in

blue tits. We were therefore able to capture the early environmental effect for this trait by measuring the adult phenotype. We found a marginally significant brood of rearing effect for heart rate but not for other traits. There may be several reasons for such results. First, these traits may not be sensitive to the rearing environment. Second, it is possible that – as for brood of origin – these traits are slightly sensitive to early environmental effect (2–12 days) but that we lack power to detect it.

Genetic and environmental effects are not mutually exclusive

Genetic divergence does not preclude a plastic response to ecological conditions specific to each habitat. For example, in the wild, the phenotypic difference in male heart rate between habitats was not significant (Dubuc-Messier *et al.*, 2017), but using the common garden experiment we found here a significant difference in male heart rate. It is thus possible that plastic responses of heart rate to habitat-specific ecological conditions in the wild may have hidden the genetic divergence (Conover & Schultz, 1995). In addition, the important temporal variation in mean handling aggression in the wild shown by Dubuc-Messier *et al.* (2017) in each population suggests that individuals can partly adjust their personality phenotype for this trait depending on the current local conditions. However, for all traits, the P_{st} between wild birds was not statistically different from their Q_{st}, suggesting that environmental effects in the wild might not result in stronger or weaker differentiation compared to the genetic differentiation.

Conclusion

Our study suggests a genetic divergence for personality, physiological and morphological traits between two blue tit populations that occupy different habitats but that are separated by small spatial distances compared to the dispersal ability of the species and connected by gene flow. This study and past results for this system suggest that these differences are likely due to different selection pressures and may represent local adaptations. These results thus emphasize the role of environmental heterogeneity for intraspecific phenotypic diversity and suggest that genetic population divergence is possible at small spatial scales (relative to their dispersal ability) for behavioural traits.

Acknowledgments

Conflict of interests

We declare no conflict of interests.

Data accessibility

The data set will be shared on dryad upon publication.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article:

Table S1. Caterpillar abundance, life-history, morphological and personality phenotypes [mean (*n*)] of the two Corsican blue tit populations (France) in the wild.

Table S2. Blue tit handling aggression scale.

Table S3. *L*-ratio, degree of freedom and *P*-values associated with each parameter in initial models describing the phenotype of blue tits originating from two distinct habitats (deciduous and evergreen) in Corsica (France) and reared in a common garden.

Table S4. Variance components, *L*-ratio and *P*-values for studied traits in two blue tits populations in Corsica (France) reared in a common garden.

Table S5. Between-habitat variance (posterior mean and 95% CrI) for each study trait extracted from the models used to calculate Q_{st}.