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Does selection or genetic drift explain geographic differentiation of morphological characters in house sparrows *Passer domesticus*?

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Summary

Understanding the relative influence of genetic drift and selection is fundamental in evolutionary biology. The theory of neutrality predicts that the genetic differentiation of a quantitative trait (Q_{ST}) equals the genetic differentiation at neutral molecular markers (F_{ST}) if the quantitative trait has not been under selection. Thus, the relative magnitude of observed Q_{ST} and expected Q_{ST} under neutral expectations suggests the importance of selection and genetic drift for any observed phenotypic divergence. Because Q_{ST} is based on additive genetic variance, estimating Q_{ST} based on phenotypic measurements is problematic due to unknown environmental effects. To account for this, we used a model where the environmental component was allowed to vary when estimating Q_{ST}. The model was used on data from 14 house sparrow (*Passer domesticus*) populations in Norway. In accordance with the significant phenotypic inter-population differences our analyses suggested that directional selection may have favoured different optimal phenotypes for some morphological traits across populations. In particular, different body mass and male ornamental phenotypes seemed to have been favoured. The conclusions are, however, dependent on assumptions regarding the proportion of the observed inter-population variation that is due to additive genetic differences, showing the importance of collecting such information in natural populations. By estimating Q_{ST}, allowing the additive genetic proportion of phenotypic inter-population variation to vary, and by making use of recent statistical methods to compare observed Q_{ST} with neutral expectations, we can use data that are relatively easy to collect to identify adaptive variation in natural populations.

1. Introduction

Evolutionary biologists have long acknowledged the importance of identifying the relative contribution of the four different evolutionary processes mutation, selection, random genetic drift and gene flow for understanding the distribution of fitness-related phenotypic variation within and across populations (Hartl & Clark, 1989; Falconer & Mackay, 1996; Lynch *et al*., 1999; Freeman & Herron, 2004; Goodnight, 2004; Whitlock, 2004). First, such knowledge will help us understand the mechanisms that have generated the variation present within and among populations today. Equally important, it will enable us to better understand the future direction of evolutionary changes within and across populations (Palo *et al*., 2003; Leinonen *et al*., 2006).

Both empirical and theoretical studies suggest that a major force that drives phenotypic population differentiation in natural populations is natural selection (Merilä & Crnokrak, 2001; Riesenberg *et al*., 2002; Saint-Laurent *et al*., 2003; Leinonen *et al*., 2006, 2008). When populations are subdivided over a geographical range, local environmental conditions may create spatially and temporally varying selection pressures, thus creating population differentiation (Merilä & Crnokrak, 2001; Zhan *et al*., 2005). Although natural selection, creating local adaption, plays a major role in the phenotypic, and hence the underlying quantitative genetic differentiation of populations, genetic differentiation may also be affected by random genetic drift (Zhan *et al*., 2005).

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Small effective population size (N_e) increases the importance of genetic drift (Freeman & Herron, 2004). In addition to natural selection and genetic drift, divergence in quantitative traits is also influenced by migration (i.e. gene flow) (Porcher *et al*., 2006), which will restrain populations from diverging (Freeman & Herron, 2004). Along with the generation of new genetic variation through mutations, these evolutionary processes act to either generate quantitative genetic and phenotypic divergence between populations through genetic drift, mutation and/or divergent selection, or reduce such divergence by gene flow between populations and/or uniform selection (Whitlock, 1999).

Neutral genetic variation is on the other hand, by definition, only affected by mutation, genetic drift (increased by small N_e) and gene flow (Wright, 1951; Kimura, 1983; Hartl & Clark, 1989; Lande, 1992). Hence, it is possible to estimate the relative role of selection and other evolutionary processes, such as genetic drift for differentiation among populations in quantitative genetic variation by comparing the level of inter-population quantitative genetic variation and neutral genetic variation (Morgan *et al*., 2005; Zhan *et al*., 2005).

This theory of neutrality predicts that the genetic divergence in a quantitative polygenic trait should be identical to that in a marker locus if both are neutral to selection and the quantitative genetic trait has an additive genetic basis (Wright, 1951). An analogue to Wright's F_{ST}, the divergence among populations in neutral marker loci (Wright, 1922), is Q_{ST}, the genetic differentiation in a quantitative trait, described by Spitze (1993). The expression of Q_{ST} is analogous to F_{ST}

$$Q_{ST} = \frac{\sigma^2_{GB}}{2\sigma^2_{GW} + \sigma^2_{GB}} \quad (1)$$

where σ^2_{GB} and σ^2_{GW} is the (additive) genetic variance between and within populations, respectively (Spitze, 1993). Using theory for Q_{ST} and F_{ST} one can create a set of hypotheses to test the influence of natural selection on phenotypic differentiation within and among populations (Lynch *et al*., 1999; Merilä & Crnokrak, 2001; McKay & Latta, 2002): (1) We expect to observe a level of population differentiation for quantitative traits that exceeds that for differentiation in neutral marker loci when directional selection is favouring different phenotypes in different populations ($Q_{ST} > F_{ST}$). (2) A lower level of differentiation in quantitative traits than would have been obtained by genetic drift alone (i.e. lower than the level of differentiation in molecular markers) indicates that selection favours the same phenotypes in different populations ($Q_{ST} < F_{ST}$). (3) If Q_{ST} and F_{ST} estimates are not significantly different, the observed differentiation cannot be rejected as being caused by genetic drift ($Q_{ST} = F_{ST}$). These interpretations are subject to a number of assumptions underlying the inference based on Q_{ST} and F_{ST} estimates (see e.g. Kimura, 1983; Merilä & Crnokrak, 2001; Miller *et al*., 2008; Whitlock, 2008).

There are, however, three potential problems with such an approach, especially in studies of natural populations. Firstly, because Q_{ST} is based on purely additive genetic variance (Merilä & Crnokrak, 2001), its calculation is strictly speaking dependent on inter- and intra-population estimates of the additive genetic variance of a trait (Lande, 1992; Spitze, 1993; Merilä & Crnokrak, 2001). Secondly, to assess the additive genetic variance in a population, it is necessary to separate the genetic from the environmental components of the phenotypic variation (Lynch & Walsh, 1998). Thirdly, the Q_{ST} estimate can vary both because of sampling error, e.g. due to data from few populations or small samples within populations (Whitlock & Guillaume, 2009), and inter-population stochastic variation in the evolutionary process (Whitlock, 2008).

These problems mean that it often is problematic to estimate Q_{ST} in natural populations. Many recent studies have disregarded these problems and used population-specific phenotypic variances as a surrogate for additive genetic variance when estimating Q_{ST} (e.g. Morgan *et al*., 2001). This will either overestimate or underestimate the genetic population divergence, depending on the effect of the environment on the phenotypic variance (Leinonen *et al*., 2008; Whitlock, 2008).

The aim of this study was to explore the relative importance of random genetic drift and selection as causes of population differentiation in different quantitative morphological traits in house sparrow (*Passer domesticus*) populations along the coast of mid- and northern Norway. The inter-population variability in topography and habitat on islands and mainland along the coast of Norway may result in different environmental conditions, and thus suggest the existence of different selection pressures across the house sparrow populations. Because of the relatively low migration rate of house sparrows (see Blair & Hagemeijer, 1997; Altwegg *et al*., 2000; Tufto *et al*., 2005; Skjelseth *et al*., 2007; Pärn *et al*., 2009) genetic differentiation exists on a relatively small geographic scale among house sparrow populations along the coast of northern Norway (Jensen *et al*., in review). Furthermore, Jensen *et al*. (2003, 2004, 2008) and Ringsby *et al*. (2009) have in a sub-set of these populations identified heritable morphological traits that are associated with individual fitness. Accordingly, some of these traits are therefore acted upon by natural and sexual selection (Jensen *et al*., 2008). Consequently, this

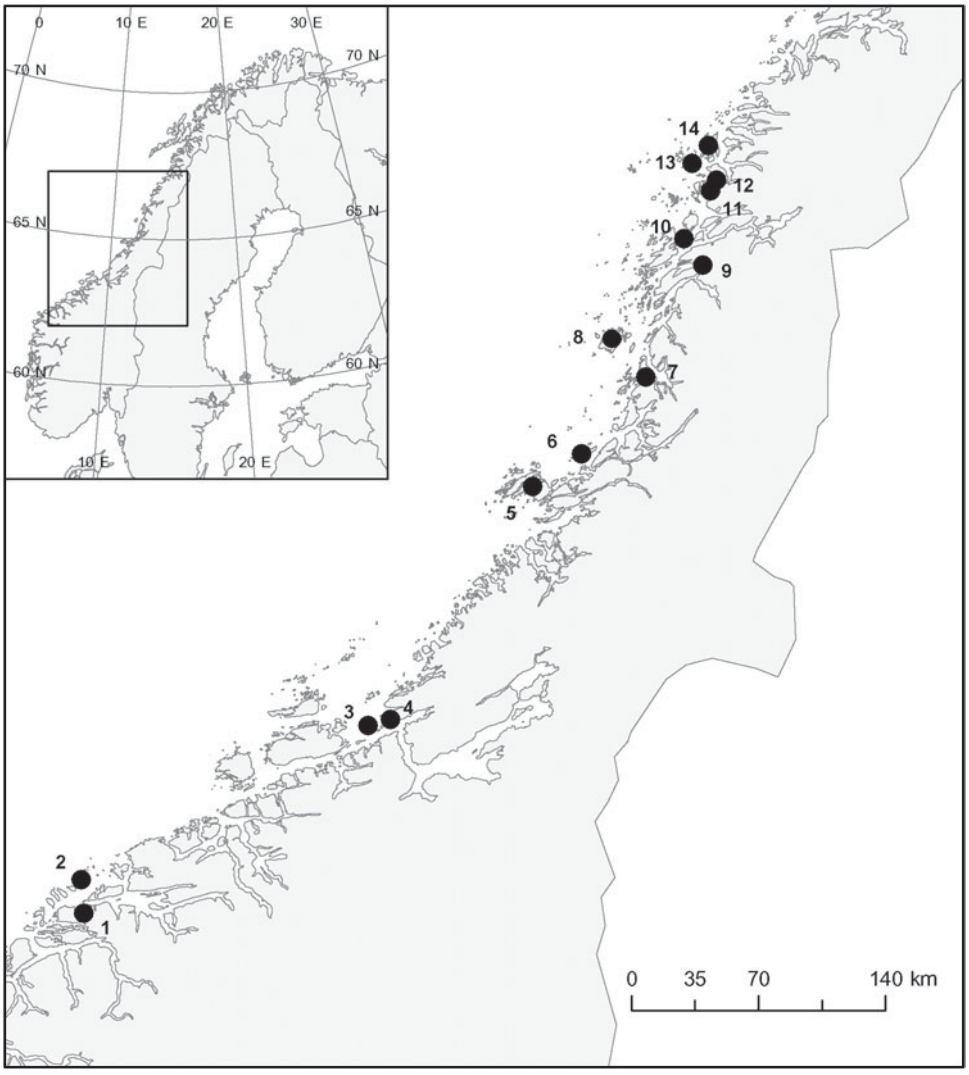

Fig. 1. Map showing sampled house sparrow populations (indicated with numbered dots) along the coast of mid- and northern Norway. Populations are numbered from south to north (see also Supplementary Table S1).

study system seems suitable to examine the effects of genetic drift and selection on population differentiation in quantitative traits. We do this by comparing the genetic differences at neutral microsatellite loci with phenotypic variation in fitness-related morphological characters with additive genetic basis in the same populations. We use existing theory on Q_{ST} and a model where the environmental component of population differentiation in natural populations is allowed to vary to estimate Q_{ST} without having estimates of additive genetic variance within each of the sub-populations (under certain assumptions). Furthermore, by combining this with a recent approach that compare the observed Q_{ST} of a trait versus F_{ST} to the distribution of Q_{ST} versus F_{ST} expected under neutrality, we obtain more reliable inference about the relative importance of selection and other evolutionary processes for any observed phenotypic population differentiation (Whitlock, 2008; Whitlock & Guillaume, 2009). These methods give us the opportunity to explore the possibilities for population divergence in natural populations.

2. Materials and methods

(i) *Study populations and estimates of* F_{ST}

The study was carried out on 14 island and mainland populations on the coast of mid- and northern Norway, from Gjerøy (67°N, 13°E) to Brattvåg (63°N, 6°E) (see Fig. 1 and Supplementary Table S1 available at http://journals.cambridge.org/grh).

Morphological measurements and blood samples from individual house sparrows were collected from the study populations during summer 2006, and for some island populations during summer 2001 or 2002 (see Jensen *et al*., in review).

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Table 1. *Tests of inter-population variation in mean size and heritability ($\hat{h^2}$) with SE of morphological traits of male and female house sparrows in 14 populations on the coast of mid- and northern Norway*

Phenotypic trait	Sex	*df*	*F*	*P*	$\hat{h^2}$ (SE)
Tarsus length	Females	13/399	2·5188	0·0025	0·524 (0·061)
	Males	13/416	2·7820	0·0008	0·343 (0·023)
Wing length	Females	13/399	3·8041	<0·0001	0·587 (0·052)
	Males	13/416	4·2267	<0·0001	0·423 (0·025)
Bill depth	Females	13/399	2·3337	0·0053	0·299 (0·039
	Males	13/416	3·6113	<0·0001	0·333 (0·034)
Bill length	Females	13/399	2·4109	0·0039	0·500 (0·070)
	Males	13/416	3·3515	<0·0001	0·470 (0·026)
Body mass	Females	13/399	4·2222	<0·0001	0·331 (0·088)
	Males	13/416	8·4077	≪0·0001	0·353 (0·026)
Total badge size	Females	–	–	–	–
	Males	13/416	9·0764	≪0·0001	0·090 (0·018)
Visible badge size	Females	–	–	–	–
	Males	13/416	4·9428	<0·0001	0·078 (0·016)

Degrees of freedom is denoted by *df*. The *F* statistics and the levels of significance (*P*) are from separate ANOVAs for each trait within each sex.

Males and females were analysed separately because of the sexual differences previously documented in strength of selection and amount of additive genetic variation of different traits (Jensen *et al*., 2003, 2008).

The sex-specific estimated levels of genetic differentiation among the study populations (see Supplementary Table S1 for populations sizes and sample sizes) on neutral molecular markers, F_{ST}, were estimated with the R package HIERFSTAT (Goudet, 2005) based on 17 presumably neutral microsatellite loci. See Jensen *et al*. (in review) for description of genotyping methods.

(ii) *Phenotypic traits and heritability* (h^2)

Morphological characters measured were tarsus length, wing length, bill depth, bill length and body mass (of both sexes) and for males also total and visible badge size. To correct for any differences between field workers in measurement technique, the measurements of each field worker were adjusted to the corresponding measurement of T. H. Ringsby using regression techniques. See Jensen *et al*. (2008) for further description of measurements.

The sex-specific heritability (h^2) and its standard error (SE) (presented in Table 1) for each of the morphological traits within males and females used in this study had previously been estimated with high precision using animal models and restricted maximum likelihood (REML) methods (Lynch & Walsh, 1998; Kruuk, 2004) with phenotypic information on >3500 individuals in a large genetically determined pedigree from six islands off the coast of northern Norway (Jensen *et al*., 2003, 2008). Three of these populations (Aldra, Gjerøy and Hestmannøy) were also included in the present study (see Supplementary Table S1).

3. Statistical analyses

(i) *Estimation of* Q_{ST} ($\hat{Q}_{ST}$)

To estimate Q_{ST} in eqn (1) based on phenotypic measures in a set of populations (under certain assumptions) Sæther *et al*. (2007) (see also Merilä, 1997; Brommer, 2011) suggested including a constant that reflects the proportion of differences between population phenotypes due to genetic differences when estimating Q_{ST}.

The genetic between population variance, σ^2_{GB} in eqn (1) was estimated as

$$\hat{\sigma}^2_{GB} = c\,\hat{\sigma}^2_{PB}, \quad (2)$$

where c is the additive genetic proportion of differences between populations, $c \in [0, 1]$, allowing for environmental between-population variance in the phenotypic variance between populations, $\hat{\sigma}^2_{PB}$. If $c = 0$ this means that the environment is causing all the phenotypic variance seen between the populations. On the other hand, $c = 1$ means that all the phenotypic variation seen between populations is determined by genetic variation between them, and thereby that none of the phenotypic differences observed between populations are influenced by environmental differences. Note, however, that $c = 1$ does not exclude the possibility that variation among populations in strength and direction of selection in the past, e.g. because populations have adapted to different population-specific environments, may be the cause of the observed inter-population phenotypic, and hence

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genetic, variation. The value of c only reflects the relative proportion of any phenotypic between-population differences that is due to environmental conditions per se. In reality c will probably lie somewhere between 0 and 1, and the exact value may vary between traits (e.g. morphological, behavioural and fitness-traits; Crnokrak & Roff, 1995; Merilä & Sheldon, 1999).

Furthermore, assuming a constant heritability (but allowing for different amounts of additive genetic variance) within populations, the genetic within population variance, σ^2_{GW}, can be estimated as

$$\hat{\sigma}^2_{\mathrm{GW}} = \hat{h}^2 \hat{\sigma}^2_{\mathrm{PW}}, \tag{3}$$

where $\hat{\sigma}^2_{\mathrm{PW}}$ is the observed within-populations variance and $\hat{h}^2$ is the estimated narrow sense heritability. The genetic variance is assumed to have only an additive genetic basis (i.e. $\sigma^2_{\mathrm{AW}} = \sigma^2_{\mathrm{GW}}$).

We now have estimates for σ^2_{GB} and σ^2_{GW} (see Section 3 (ii) for practical estimation of parameters), and by inserting eqns (2) and (3) into eqn (1) and reorganizing we obtain an equation for estimating Q_{ST} using phenotypic data:

$$\hat{Q}_{\mathrm{ST}} = \frac{\hat{\sigma}^2_{\mathrm{PB}}}{2(\frac{\hat{h}^2}{c})\hat{\sigma}^2_{\mathrm{PW}} + \hat{\sigma}^2_{\mathrm{PB}}}. \tag{4}$$

where $\hat{\sigma}^2_{\mathrm{PB}}$ is the observed between-populations variance and $\hat{\sigma}^2_{\mathrm{PW}}$ is the observed within-populations variance, $\hat{h}^2$ is the estimated trait-specific heritability and c is the additive genetic proportion of phenotypic differences between populations. This expression has been rewritten slightly from the expression used by others (see e.g. Sæther *et al.*, 2007; Brommer, 2011).

(ii) *Practical estimation of parameters*

Partitioning of the phenotypic variance of a character into σ^2_{PW} and σ^2_{PB}, respectively, was carried out using a single classification analysis of variance with unequal sample sizes, n_i (ANOVA Model II; Sokal & Rohlf, 1995). The F-test in the ANOVA permits us to detect any significant differences in average phenotype between populations (Sokal & Rohlf, 1995). σ^2_{PW} was estimated by MS_W, and σ^2_{PB} was estimated by (Storz, 2002),

$$\frac{\mathrm{MS}_B - \mathrm{MS}_W}{n_0}, \tag{5}$$

where MS_B is the observed mean squares (variance) between sub-populations and MS_W is the observed mean squares (variance) within subpopulations given from the ANOVA (Sokal & Rohlf, 1995; Storz, 2002).

Because the sample size, i.e. n_i, differs among subpopulations (i) (see Supplementary Table S1), we used a kind of average sample size n_0, calculated as

$$n_0 = \frac{1}{a-1}\left(\sum^a n_i - \frac{\sum^a n_i^2}{\sum^a n_i}\right) \tag{6}$$

where a is the number of sub-populations and n_i the number of individuals in the ith subpopulation sample (Storz, 2002).

(iii) *Comparing* $\hat{Q}_{\mathrm{ST}}$ and $\hat{F}_{\mathrm{ST}}$ across populations

To test whether $\hat{Q}_{ST}$ and $\hat{F}_{\mathrm{ST}}$, based on data from all populations, were significantly different from each other for different values of c, we used the approach proposed by Whitlock & Guillaume (2009). This approach tests whether the observed Q_{ST} of a trait falls within the distribution of Q_{ST} expected under neutrality, predicted using the mean F_{ST} ($\bar{F}_{\mathrm{ST}}$) and the χ^2 distribution of Lewontin & Krakauer (1973). Using this approach the problem that a relatively small number of loci often is used when estimating F_{ST} is taken into consideration, as well as the variation in neutral Q_{ST} due to variation in evolutionary history among populations and sampling error due to small sample size (Whitlock, 2008; Whitlock & Guillaume, 2009). In addition, this method requires the F_{ST} to be small, which is the case in this study.

Under the null hypothesis of neutrality, the statistic $\hat{Q}_{\mathrm{ST}}/\bar{F}_{\mathrm{ST}}$ will have a distribution that is almost independent of the true parameter value of F_{ST}, essentially because F_{ST} is a scale parameter in the distribution of both $\hat{Q}_{\mathrm{ST}}$ and $\bar{F}_{\mathrm{ST}}$, when the amount of genetic differentiation is small. This test statistic is thus close to being a so-called pivotal statistic (Shao, 2003). This makes it more suitable as test statistic, because the critical values and P values can be determined without the knowledge of the true value F_{ST} than a test based on the test statistic $Q_{\mathrm{ST}} - F_{\mathrm{ST}}$ (Whitlock & Guillaume, 2009).

We use the parametric simulation approach used in Whitlock & Guillaume (2009) to find the sampling distribution of $\hat{Q}_{\mathrm{ST}}/\bar{F}_{\mathrm{ST}}$ under the null hypothesis. To simulate the sampling error in estimates of $\bar{F}_{\mathrm{ST}}$, we draw randomly from the bootstrap distribution of $\bar{F}_{\mathrm{ST}}$ obtained from the R-package HIERFSTAT (Goudet, 2005), bootstrapping loci 10 000 times. To take into account the sampling error of σ^2_{GW} and σ^2_{GB} when estimating Q_{ST} (eqn 1), we simulated values of σ^2_{GW} by multiplying $\hat{h}^2 \mathrm{MS}_{\mathrm{W}}/\sum_i^a n_i - a$ with a number drawn randomly from the χ^2 distribution with $\sum_i^a n_i - a$ degrees of freedom, where a is the number of populations (see Sections 3 (*ii*) and 3 (*iii*)). To account for sampling error in h^2 estimated from field data (accounting for environmental variation), we draw samples of $\hat{h}^2$ from a beta distribution, defined on

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the interval (0,1), with shape parameters calculated from the h^2 estimate and squared SE of the h^2 estimate as the mean and variance, respectively, in the beta distribution. Whitlock & Guillaume (2009) showed that the expected value of σ^2_{GB} under neutrality is

$$\hat{\sigma}^2_{GB} \cong \frac{2\bar{F}_{ST}\,\sigma^2_{GW}}{1-\bar{F}_{ST}}. \quad (7)$$

Thus, we simulated values of σ^2_{GB}, as calculated in eqn (7), by multiplying $\hat{\sigma}^2_{GB}/(a-1)$ with a number drawn randomly from the χ^2 distribution with $a-1$ degrees of freedom.

We randomly draw values of $\bar{F}_{ST}$, $\hat{h}^2$, σ^2_{GW} and $\hat{\sigma}^2_{GB}$ (described above), and then calculated $\hat{Q}_{ST}/\bar{F}_{ST}$ from these simulated values. A sampling distribution of $\hat{Q}_{ST}/\bar{F}_{ST}$ was obtained by repeating this random sampling with 1000 iterations.

To compare the test statistics of observed $\hat{Q}_{ST}/\bar{F}_{ST}$ for different c values with the sampling distribution of $\hat{Q}_{ST}/\bar{F}_{ST}$ under neutrality, we found the 0·025 and 0·975 % quantiles of the neutral sampling distribution of $\hat{Q}_{ST}/\bar{F}_{ST}$. If the observed $\hat{Q}_{ST}/\bar{F}_{ST}$ for a given c-value was smaller or larger than the 95 % confidence limits for the neutral sampling distribution, $\hat{Q}_{ST}$ was defined as significantly smaller or larger than expected by neutrality, respectively ($P<0{\cdot}05$) (Manly, 2007; Whitlock & Guillaume, 2009). These c-values are the limits for where $\hat{Q}_{ST}=\bar{F}_{ST}$.

4. Results

(i) *Inter-population phenotypic variation*

All phenotypic traits showed considerable and significant variation between populations (Table 1). The variation between populations in mean trait sizes was largest in males and for the traits body mass, total and visible badge size.

(ii) *Relationship between $\hat{Q}_{ST}$ and $\hat{F}_{ST}$ allowing for environmental causes of inter-population variance*

We found that the mean male $\hat{F}_{ST}$ was 0·0246 and mean female $\hat{F}_{ST}$ was 0·0240. The 95 % confidence intervals for $\hat{F}_{ST}$ were for both males and females quite narrow (males: [0·0216, 0·0279]; females: [0·0218, 0·0278]).

Assuming that all the phenotypic differences between populations (Table 1) were due to genetic differences ($c=1$) our results suggest that spatially divergent selection have caused the observed inter-population variance in phenotypic traits in females and males (Table 2 and Figs 2 and 3).

However, allowing for environmental causes of phenotypic inter-population variance, the quantitative genetic divergence, $\hat{Q}_{ST}$, for female tarsus length and bill length was not significantly different from neutral expectations for most values of c (Table 2 and Fig. 2). Furthermore, only for large values of c was $\hat{Q}_{ST}$ for wing length and bill depth significantly larger than the neutral expectation (Table 2 and Fig. 2). $\hat{Q}_{ST}$ for female body mass was on the other hand significantly higher than neutral expectations for most values of c (Table 2 and Fig. 2). If we use $\hat{h}^2 >$ critical c value as a reasonable limit for selection, for female traits the critical c is either larger or approximately similar to the $\hat{h}^2$ (Tables 1 and 2). This indicates (without knowing anything about the effect of environment and hence the true value of c) that we cannot distinguish the effects of genetic drift and selection for the observed spatial phenotypic differentiation in most female traits, but that differences across populations in female body mass may have been caused by spatially divergent selection.

Table 2. *Critical values for c where observed $\hat{Q}_{ST}/\bar{F}_{ST}$ are smaller or larger, respectively, than expected under neutrality* (*i.e. outside the null sampling distribution $\hat{Q}_{ST}/\bar{F}_{ST}$ under neutrality*) *in morphological traits of males and females in 14 house sparrow populations on the coast of mid- and northern Norway*

Trait	$c \leqslant 0{\cdot}025$ quantile	$c \geqslant 0{\cdot}975$ quantile
Males		
Tarsus length	0·108	0·536
Wing length	0·075	0·380
Bill depth	0·074	0·380
Bill length	0·119	0·583
Body mass	0·024	0·141
Total badge size	0·006	0·033
Visible badge size	0·010	0·056
Females		
Tarsus length	0·196	0·901
Wing length	0·113	0·587
Bill depth	0·124	0·611
Bill length	0·199	0·999
Body mass	0·056	0·269

For males $\hat{Q}_{ST}$ was significantly higher than the neutral exception for a larger range of values for c for all traits (Table 2 and Fig. 3). Accordingly, $\hat{Q}_{ST}$ for all traits except tarsus length and bill length was significantly higher than neutral expectations for most values of c (Table 2 and Fig. 3), and the critical c value was either larger or approximately similar to the $\hat{h}^2$ (Tables 1 and 2). For male body mass, total badge size and visible badge size genetic drift could have caused the observed phenotypic inter-population variation for only very small values of c (Table 2 and Fig. 3). Accordingly, for these traits the critical c value was much lower than $\hat{h}^2$ (Tables 1 and 2). Without knowing anything about the actual environmental influence on the spatial phenotypic variation, and hence the true value of c, it seems that selection has been directional

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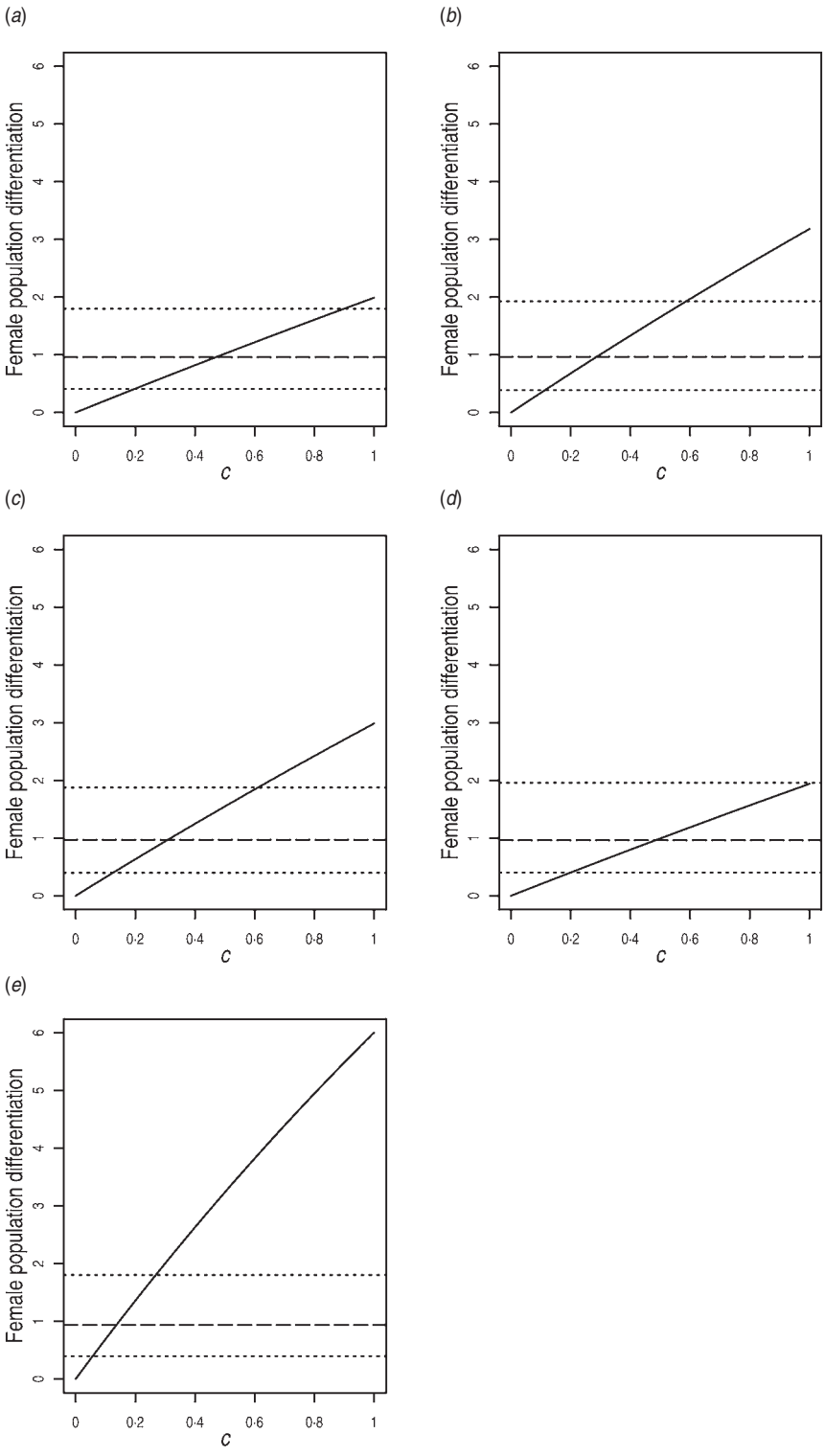

Fig. 2. The relationship between observed and neutral $\hat{Q}_{ST}/\bar{F}_{ST}$, indicated with the solid and dashed lines, respectively, when the environmental component of the between-population variance varies between 0 % ($c = 1$) and 100 % ($c = 0$) ($c \in [0,1]$) for five morphological traits in female house sparrows in 14 populations in mid- and northern Norway. The critical values for the null sampling distribution of the neutral $\hat{Q}_{ST}/\bar{F}_{ST}$ are indicated with the dotted lines. The different panels correspond to the relationship between $\hat{Q}_{ST}/\bar{F}_{ST}$ and c for different phenotypic traits (*a*) tarsus length, (*b*) wing length, (*c*) bill depth, (*d*) bill length and (*e*) body mass.

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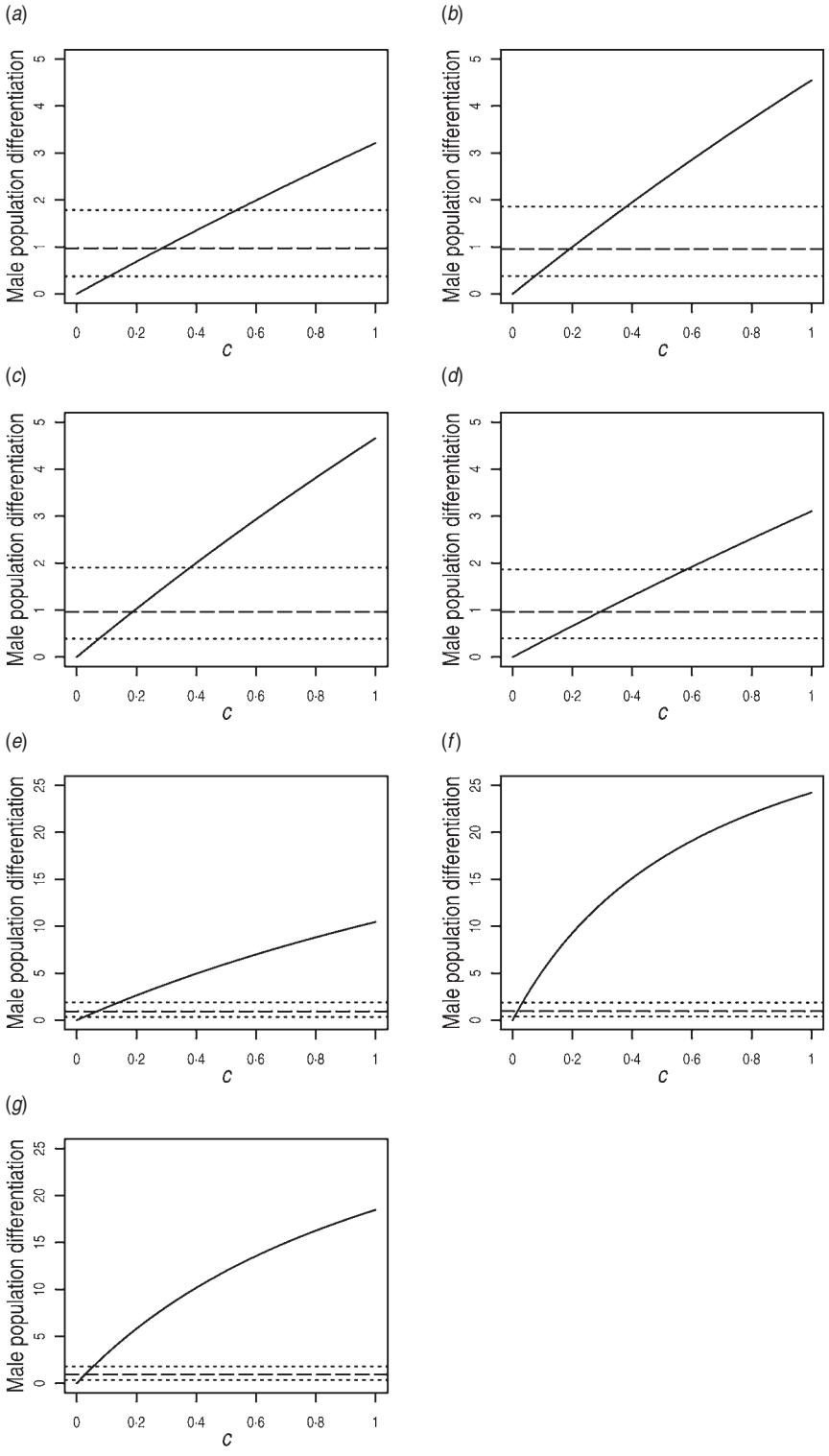

Fig. 3. The relationship between observed and neutral $\hat{Q}_{ST}/\bar{F}_{ST}$, indicated with the solid and dashed lines, respectively, when the environmental component of the between-population variance varies between 0 % ($c=1$) and 100 % ($c=0$) ($c \in [0,1]$) for seven morphological traits in male house sparrows in 14 populations in mid- and northern Norway. The critical values for the null sampling distribution of the neutral $\hat{Q}_{ST}/\bar{F}_{ST}$ are indicated with the dotted lines. The different panels correspond to the relationship between $\hat{Q}_{ST}/\bar{F}_{ST}$ and c for different phenotypic traits (*a*) tarsus length, (*b*) wing length, (*c*) bill depth, (*d*) bill length, (*e*) body mass, (*f*) total badge size and (*g*) visible badge size.

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on at least some male traits, favouring different phenotypes in different populations.

5. Discussion

The estimated level of additive genetic differentiation in morphological traits among 14 house sparrow populations along the coast of Norway suggest that the differentiation may be higher than expected if caused by random genetic drift for some traits (see Figs 2 and 3).

Importantly, this was demonstrated using a model where we can explore and estimate the over-estimation (if no selection on the phenotypic trait) of the degree of genetic differentiation in quantitative traits when using phenotypic data. This method allowed us to vary the effect of the environmental component of the phenotypic between population variance on the observed Q_{ST} estimates. Furthermore, the test of significance for each trait was carried out by comparing the observed additive genetic differentiation to the probability distribution for the trait if it was neutral, improving the type I error rate in this test (Whitlock & Guillaume, 2009). However, this method, using phenotypic data to approximate Q_{ST}, shows the importance of common garden studies in these types of studies of genetic differentiation. It is not possible to safely conclude anything about the actual inter-population level of additive genetic variation in different types of traits without such studies. Currently, it is unfortunately a problem to infer the likely amount of additive genetic variance between populations in different traits, because few common garden studies actually give these estimates in the results. We ask that common garden studies give these estimates because this will help us infer likely values of c, so that results from methods based on phenotypic data such as the one used here might be interpreted and discussed more reliably.

The phenotypic differentiation observed between the populations for all traits in both sexes (Table 1, see also Supplementary Table S1), might lead one to believe that a spatially varying environment has resulted in local adaption to different optima in different populations (Bürger & Krall, 2004; Dieckmann & Ferrière, 2004). The observed $\hat{Q}_{ST}$ was, however, not significantly different from the distribution of $\hat{Q}_{ST}$ under neutrality for most traits for a wide range of c values (Table 2; Figs 2 and 3). Consequently, we cannot rule out random genetic drift as the cause for the phenotypic differentiation in many morphological traits across house sparrow populations along the coast of Norway (Whitlock, 1999, 2008; Whitlock & Guillaume, 2009).

Recent reviews on divergence in quantitative traits and neutral markers found that studies in most cases showed that Q_{ST} values were higher than F_{ST} values, suggesting that directional selection is the prevailing evolutionary force in quantitative trait divergence (reviews in Merilä & Crnokrak, 2001; McKay & Latta, 2002; Leinonen *et al*., 2008).

One reason why our results seem to contrast with general findings from other species could be due to the fragmented landscape along the Norwegian coast, where the sea separates house sparrow populations on islands from populations nearby, and populations on the mainland are separated from other populations by fjords or mountains. Combined with relatively short dispersal distances (Blair & Hagemeijer, 1997; Altwegg *et al*., 2000; Tufto *et al*., 2005; Skjelseth *et al*., 2007; Pärn *et al*., 2009) and relatively small population sizes (see Supplementary Table S1) this may lead to increased importance of random genetic drift relative to selection in these house sparrow populations (Hartl & Clark, 1989; Freeman & Herron, 2004). In turn, this could increase both (neutral) genetic differentiation of marker loci used to estimate F_{ST} (see e.g. discussion in Kekkonen *et al*., 2011) as well as the expected differentiation of additive genetic variation of phenotypic traits (Q_{ST}) under neutrality (Whitlock, 1999; Whitlock & Guillaume, 2009).

Despite the possible importance of random genetic drift in the sampled house sparrow populations, the results for body mass of both sexes and in particular the badge size of males suggest (although not knowing the true value of c) that directional selection was likely to have influenced the observed phenotypic divergence between populations in these traits (Table 2, Figs 2 and 3). The badge of male house sparrows is assumed to act as a sexual ornament (Møller, 1987; Veiga, 1993), signal dominance (Liker & Barta, 2001; McGraw *et al*., 2003) and is thus correlated with the social status of males (Nakagawa *et al*., 2007). Accordingly, Jensen *et al*. (2004) found that badge size was positively associated with lifetime reproductive success (LRS), showing it is related to male fitness. Furthermore, the results of Jensen *et al*. (2008) suggest that the total badge of male house sparrows is subject to sexual selection through a positive effect on mating success. In the same study populations the badge size has also been found to increase with the population density in which the males grow up (Jensen *et al*., 2006). Jointly, these results indicate that social mechanisms, such as sexual selection and dominance, can give different optimal phenotypes in different populations. Furthermore, the results in Jensen *et al*. (2006), showing that badge size is partly environmentally dependent, suggest potential for population-specific plastic variation in badge size. This is further supported by the low heritability ($\hat{h}^2 = 0{\cdot}090$) found for this trait. Body mass is another fitness-related trait (Jensen *et al*., 2008) with moderate

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heritability in house sparrows (Table 1). In other species, this is also a trait shown to have potential for plastic changes (Larsson, 1993; Madsen & Shine, 1993; Pelletier *et al.*, 2007). Accordingly, fitness-related traits have been found to be influenced by the environment and thus have low heritability in general (Merilä & Sheldon, 2000). Irrespective of the proximate mechanism causing population differentiation in badge size, the results presented here suggest that despite relatively low heritability and potential for plastic variation of total badge size and body mass, the strength and perhaps direction of directional selection vary sufficiently between populations for the evolutionary consequences of selection to exceed that of random genetic drift. Although we do not know the actual importance of any variation in environmental conditions for phenotypic inter-population variance and hence the value of c for male badge size or body mass in both sexes, our results show that this conclusion, for example, holds even when less than approximately 3·3 % of the phenotypic inter-population variation in total badge size is due to genetic differences between populations (Table 2 and Fig. 3).

Similar results have been found for the sexually selected trait tail white (length of white on the outermost tail feather) (Höglund *et al.*, 1990), in the great snipe (*Gallinago media*) (Sæther *et al.*, 2007). Furthermore, Chenoweth & Blows (2008) looked at a set of sexually selected traits in *Drosophila serrata*, using a multivariate analogue of Q_{ST}, accounting for correlations between traits. Their study suggested that divergent selection acting in a sex-specific direction caused population divergence. Similar results have also been found for other traits that are directly connected to fitness (reviews in Merilä & Crnokrak, 2001; McKay & Latta, 2002; Leinonen *et al.*, 2008). That studies of sexually selected traits generally demonstrate higher levels of Q_{ST} than F_{ST} suggests that variation in the strength of sexual selection across populations may be a general pattern. The strength of sexual selection will depend on the social mating system, which in turn may be determined by factors such as the population sex ratio, population density and distribution of males and females due to variation in important ecological resources (Bennett & Owens, 2002; Kokko & Johnstone, 2002). Furthermore, in birds, it has, for example, been found that the strength of sexual selection may be connected with the degree of sexual dimorphism and occurrence of extra-pair paternity (Petrie & Kempenaers, 1998; Bennett & Owens, 2002). Because all these factors may vary in space and time (e.g. Bennett & Owens, 2002; Engen *et al.*, 2007) this may also give rise to inter-population variation in strength of sexual selection (Kwiatkowski & Sullivan, 2002).

In many studies of natural populations, obtaining estimates of additive genetic variation within and among populations is problematic. To estimate the population-specific additive genetic variance σ^2_{AW} (see σ^2_{GW} eqn 3) from measures of phenotypic variances within populations, we assumed a constant trait-specific heritability (h^2) equal for each population, based on actual estimates from a sub-set of the populations included in the study. The possible sampling error in the h^2 estimates, due to environmental variation in field data, giving lower heritability estimates, were included in the sampling procedure.

Studies suggest that heritability can change over time under different environmental conditions, indicating a higher heritability under more favourable conditions (although h^2 depends on the phenotypic variance, additive genetic variance was also found to be higher under better conditions), indicating genotype-by-environment ($G \times E$) interactions (Kruuk *et al.*, 2008; Husby *et al.*, 2011). There are also a number of empirical examples where morphological traits in birds show higher additive genetic variance under favourable environmental conditions (Larsson, 1993; Merilä & Sheldon, 2001; Charmantier *et al.*, 2004). Studies indicate, however, that life-history traits (traits closely related to fitness) show less change in h^2 in different environmental conditions than morphological (morphometric) traits (Charmantier & Garant 2005; Kruuk *et al.*, 2008). This suggests that the environment may be very important for the response to selection (Kruuk *et al.*, 2008). If different environmental conditions can create different heritability in the study populations (i.e. that the additive genetic variance is not proportional to phenotypic variance), this means that the estimated Q_{ST} may be lower than the true one. If this is the case in the current study, it follows that $\hat{Q}_{ST}$ in reality may exceed neutral expectations for a wider range of c values. Hence, the conclusions for the importance of selection for population differences in badge size would hold regardless of this potential bias.

It is important to carefully think of the potential pitfalls when estimating Q_{ST} and to interpret the results with this in mind. Using the simulation method described in Whitlock & Guillaume (2009) for estimating the neutral distribution of Q_{ST}, we take into consideration many of the different problems while estimating the error in Q_{ST} and problems related to comparing Q_{ST} to F_{ST} (O'Hara & Merilä, 2005). This includes the sampling error caused by finite samples of individuals and populations, which is a problem in many studies of Q_{ST} where the number of populations is often too low (Miller *et al.*, 2008). Pairwise Q_{ST} were not estimated because of large uncertainties in Q_{ST} due to sampling error (finite sample of individuals and small sample of population).

Another potential bias when comparing $\hat{Q}_{ST}$ and $\hat{F}_{ST}$ may be introduced if gene flow is not random with respect to quantitative genetic variation in traits used

in the study. In the present study, this may be a possible factor explaining some of the patterns. For example, Skjelseth *et al*. (2007) found that female dispersers have longer wings. Because wing length is genetically correlated with most other morphological traits within and across sexes (Jensen *et al*., 2008) this means that gene flow might not be random with respect to the genes underlying quantitative morphological traits that are transferred among populations. These effects of gene flow may in addition to the possibly relatively high levels of random genetic drift (see above) be a contributing factor to the low levels of $\hat{Q}_{ST}$ found for most morphological traits in this study.

6. Conclusion

The results in this study show that for body mass in both sexes and for badge size in males directional selection may have been a more important evolutionary force than genetic drift in driving phenotypic differentiation among populations. However, we must conclude that for most of the morphological traits in both females and males, we cannot rule out random genetic drift or environmentally induced differences as the cause for the phenotypic differentiation, even with the low to moderate values found for $\hat{F}_{ST}$.

The popularity of comparing estimates of Q_{ST} and F_{ST} in order to understand the relative importance of random genetic drift and selection for adaptive population divergence among natural populations will probably increase as the cost decreases and efficiency increases for obtaining good estimates of F_{ST} (e.g. Freeland, 2005). Here, we have used a method that can help us explore the possibilities for population divergence based on phenotypic measurements of individuals in a set of populations and only one estimate of the heritability of the trait(s) of interest. This is the information that is likely to be available for many natural populations. At present, a critical assumption of a constant heritability across populations has to be made. Importantly, this method makes evolutionary biologists able to explore the potential influence of environmental causes of phenotypic differentiation when estimating Q_{ST} based on phenotypic measures. Because population-specific estimates of additive genetic variance are difficult to obtain in natural populations, avoiding the need for this by instead using phenotypic data and being able to quantify the effect of varying environmental contribution to phenotypic differentiation is advantageous. To draw general and reliable conclusions from such analyses, it is, however, necessary to know more about the proportion of any observed phenotypic inter-population variation which is due to additive genetic differences (i.e. the value of c) for different types of traits and species. Consequently, proper common garden experiments are needed for more populations and species. Furthermore, we urge that such studies also present the variance components, so that one can examine whether any general rules about likely values for c for different traits can be generated.

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