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The next meeting for animal personality: population genetics

For over a decade, the study of animal personality (i.e. the consistency of individual behavioural differences) and behavioural syndromes (suites of correlated behavioural traits) has been of considerable interest to behavioural ecologists, particularly in the understanding of how individual differences can be maintained and evolve in natural populations (CARERE & MAESTRIPIERI 2013). For a given species, this can be studied within and among populations (DINGEMANSE & RÉALE 2005; RÉALE et al. 2007). A multitude of studies have found consistent behavioural differences in several taxa both in the lab and in the wild, and evidence for selection acting on these traits is provided (see DINGEMANSE & RÉALE 2013 for a review). These studies provide a direct assessment of the action of selection on personality traits but are mainly designed in a within-population framework. The way individuals behave and how they respond to environmental variations affect populations and communities both spatially and temporally (DUCKWORTH 2009; GORDON 2011). However, the ecological and evolutionary implications of individual differences at the population level have received less interest and remain quite speculative to date (WOLF & WEISSING 2012; CARERE & GHERARDI 2013). For example, it has been suggested (and some empirical studies tend to support this verbal argument) that invasion processes should select for behavioural traits linked to dispersal, establishment and proliferation in alien species (COTE et al. 2010; CHAPPLE et al. 2012; CARERE & GHERARDI 2013; MONCEAU et al. in press). Nevertheless, comparing the differences of personality traits and their fitness gain between native and invasive populations is only informative in the result of the invasion process but not on the core evolutionary processes driving the invasion. Characterising the evolutionary forces (directional, stabilising selection or neutral processes such as drift and migration) should thus be useful to distinguish adaptive from nonadaptive behavioural differences in wild populations and their role in population differentiation. However, this requires linking personality traits and/or behavioural syndromes measured at the individual level to selective forces acting at the population level. An approach linking individual behaviour to population genetics is thus required.

Interestingly, although behavioural ecologists working on personality have not yet utilised population genetics, they are headed in this direction. Indeed, very recently, quantitative genetics has been proposed to determine whether the correlations observed at the phenotypic level originate from genetic and/or environmental correlations (DINGEMANSE & WOLF 2010; DINGEMANSE & DOCHTERMANN 2014). Measuring heritability (in its narrow sense) allows quantifying the additive genetic variance, which is the result of natural selection (Fisher's fundamental theorem of natural selection, FISHER 1930). Several studies have already documented the heritability of behavioural traits (see DINGEMANSE et al. 2002; DRENT et al. 2003; SINN et al. 2006;

NIEMELÄ et al. 2013 for several examples and VAN OERS & SINN 2013 for a review). Here, I propose to move slightly forward and pass through the next step of comparing the inherited genetic variance of behavioural traits (and their correlations) to the neutral selective processes acting on populations.

The F_{ST}–Q_{ST} comparison

The F_{ST}–Q_{ST} comparison has had an impressive expansion in recent years (SPITZE 1993; MERILÄ & CRNOKRAK 2001; O'HARA & MERILÄ 2005; WHITLOCK 2008; EDELAAR & BJÖRKLUND 2011; EDELAAR et al. 2011; LAMY et al. 2012; see LEINONEN et al. 2013 for a recent review). In general, these studies have mainly focused on morphometric characters, and only two studies included behavioural traits but not personality and/or behavioural syndromes (COUSYN et al. 2001; ROGERS et al. 2002; LEINONEN et al. 2013).

Briefly, this approach is based on comparisons among populations using two genetic measures of differentiation: (i) F_{ST}, the proportion of genetic variance due to among-population differences using neutral genetic markers, and (ii) Q_{ST}, the proportion of additive genetic variance attributed to among-population differences using quantitative traits (here, personality traits). F_{ST} is used here as a reference for population differentiation only due to gene flow (migration) and stochasticity (drift). The F_{ST}–Q_{ST} comparison thus allows the detection of deviation from these neutral processes of differentiation. Three cases can be defined (Fig. 1): (i) $F_{ST} = Q_{ST}$: population differentiation for quantitative traits is only due to neutral processes (migration/drift); (ii) $F_{ST} > Q_{ST}$: population differentiation for quantitative traits is less than the null expectation as a result of uniform (similar personality traits are selected in different populations), stabilising selection (extreme personality traits are eliminated from the populations and intermediate ones are favoured) or, in some cases, canalisation (robustness to disturbance, see LAMY et al. 2012); (iii) $F_{ST} < Q_{ST}$: population differentiation for quantitative traits is greater than the null expectation as a result of directional selection (extreme personality traits are favoured from one side of the distribution while their opposites are eliminated).

The basic procedure of the F_{ST}–Q_{ST} comparison does not take into account genetic correlation between quantitative traits, which is relevant in the study of personality (genetic covariation with fitness traits) and/or behavioural syndromes (genetic covariation between personality traits); this leads to the use of mean values for F_{ST} and Q_{ST}, which in turn alters the statistical power of the comparison, especially in small sample sizes (less than 20 populations, according to O'HARA & MERILÄ 2005). However, several procedures have been developed to include the matrix of genetic covariances (G matrix, CHENOWETH & BLOWS 2008; MARTIN et al. 2008; OVASKAINEN et al. 2011) as well as the R packages 'Driftsel' (KARHUNEN et al. 2013) and 'QstFstComp' (GILBERT & WHITLOCK in press) to facilitate the analysis and statistical detection of differences between F_{ST} and Q_{ST} values even in small sample sizes.

The choice of the genetic markers is also fundamental and should be driven by their degree of variability, their low mutation rate and their neutrality. Indeed, the degree of variability (i.e. polymorphism) and high mutation rates in regard to migration rates are known to affect F_{ST} estimates (KRONHOLM et al. 2010; EDELAAR & BJÖRKLUND 2011; EDELAAR et al. 2011; MEIRMANS & HEDRICK 2011). In addition, the neutrality of genetic markers is a fundamental assumption of the F_{ST}–Q_{ST}
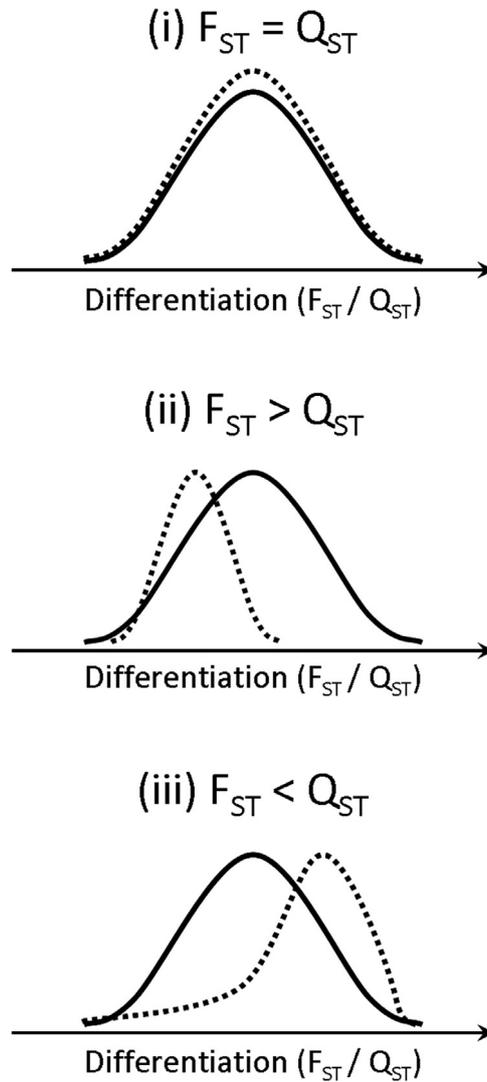
(i) $F_{ST} = Q_{ST}$

Differentiation (F_{ST} / Q_{ST})

(ii) $F_{ST} > Q_{ST}$

Differentiation (F_{ST} / Q_{ST})

(iii) $F_{ST} < Q_{ST}$

Differentiation (F_{ST} / Q_{ST})

Fig. 1. — The three cases defined by the F_{ST}–Q_{ST} comparison. F_{ST} and Q_{ST} distributions are shown by solid and dashed lines, respectively. The pairwise differences between populations increase with the increasing value of F_{ST} and/or Q_{ST}.

comparison, because F_{ST} values represent the reference for neutral process-based differentiation. Microsatellite markers are the most popular marker for population genetics; however, single-nucleotide polymorphisms (SNPs) have gained ground particularly due to the constant progress of sequencing techniques (LUIKART et al. 2003; GUICHOUX et al. 2011). Both markers have advantages and disadvantages that have been discussed in the literature (JARNE & LAGODA 1996; LUIKART et al. 2003; GUICHOUX et al. 2011; DEFAVERI et al. 2013). Regardless of the marker, their neutrality must be assessed

before performing genetic differentiation analyses (LUIKART et al. 2003), and several tests have been developed to identify and discard loci under selection (BEAUMONT & NICHOLS 1996; LUIKART et al. 2003; ANTAO et al. 2008).

However, an important restriction to consider in the F_{ST}–Q_{ST} comparison is the complexity of such an approach. Indeed, reliable Q_{ST} estimates require well-designed quantitative genetic studies to eliminate maternal, environmental and nonadditive genetic effects, as they are known sources of bias (MERILÄ & CRNOKRAK 2001). Measuring the heritability of behavioural traits on several individuals from wild populations is not always feasible depending on the species, and thus alternative approaches should be adopted. One of the most convenient is to use the phenotypic alternative of Q_{ST}, i.e. P_{ST}, the phenotypic index of population differentiation (RAEYMAEKERS et al. 2007; SÆTHER et al. 2007; LEHTONEN et al. 2009; KEKKONEN et al. 2012; WOJCIESZEK & SIMMONS 2012; MONCEAU et al. 2013a). Although it is considered analogous to Q_{ST}, the results from F_{ST}–P_{ST} comparisons should be cautiously interpreted, because P_{ST} includes both the genetic and environmental components of phenotypic variation. Thus, the approximation $P_{ST} \approx Q_{ST}$ mainly depends on the proportion of additive genetic variance responsible for population differentiation (PUJOL et al. 2008; BROMMER 2011). Such an approach may represent an insightful step for behavioural ecologists who want to encompass behavioural differentiation among populations without the cost of a quantitative genetic procedure.

Conclusions and perspectives

In behavioural ecology, animal personality and behavioural syndromes have been extensively studied over the past decade. Surprisingly, in working at the individual level, the consequences on population structure appear to have been experimentally neglected; however, this has not occurred conceptually, as several studies have discussed the importance of personality on population processes (WOLF & WEISSING 2012). The applications of the F_{ST}–Q_{ST} comparison are multiple (see LEINONEN et al. 2013) and can be adapted to several questions (see Table 1). This approach could allow us to understand the role of natural selection in shaping the behavioural differences between urban and nonurban populations questioned by SOL et al. (2013). Personality

Table 1.

Examples of the applications of the F_{ST}–Q_{ST} comparison in the study of personality traits and behavioural syndromes. Adapted from LEINONEN et al. (2013).

Context	Inference	Example study
Biological invasions	Behavioural traits favouring invasion process should be selected (directional selection)	MONCEAU et al. (in press)
Adaptation to human-induced perturbation	Role of natural selection in behavioural differences observed between urban and nonurban individuals	SOL et al. (2013)
Sexual selection	Differential selective processes between sexes responsible for differences in personality traits	HEDRICK & KORTET (2012)
Timing of adaptive genetic evolution	Comparisons across generations to understand the temporal change in behavioural differences	COUSYN et al. (2001)

traits may also differ between sexes due to sexual selection (HEDRICK & KORTET 2012). The spatial parameter of population distribution can be replaced by a temporal parameter to analyse the temporal variation of behavioural differences among generations (see COUSYN et al. 2001). One promising feature is to understand the role of behavioural traits in biological invasions (CHAPPLE et al. 2012; WOLF & WEISSING 2012; CARERE & GHERARDI 2013). For example, social hymenopterans are known to be successful invaders because the flexibility of sociality promotes invasiveness (MOLLER 1996). *Vespa velutina*, the yellow-legged hornet, originated from Asia and is invasive in Europe and Korea (MONCEAU et al. 2014). The success of the invasion in hornet species depends primarily on nest establishment assumed by foundresses because it is considered the most critical step in the hornet life cycle (SPRADBERY 1973). Testing the behaviour of *V. velutina* compared to the native European hornet *V. crabro* showed that the invasive hornet foundresses always outperform the natives in activity, boldness and exploration, although these traits are similarly correlated in both species (MONCEAU et al. in press). These results suggest that this behavioural syndrome is common in hornet species and that these traits favoured the invasion of *V. velutina*. The F_{ST}–Q_{ST} comparison (using P_{ST} because hornets can be maintained but not easily bred in the lab; see MONCEAU et al. 2013b) between native and invasive populations of *V. velutina* may help us to understand if directional selection for highly active, explorative and bolder individuals has occurred. *Vespa crabro* is also invasive in North America (AKRE et al. 1980; BUCK et al. 2008; KIMSEY & CARPENTER 2012), and a similar study could be conducted with equivalent predictions. The conclusions of these two studies may help to understand if these traits, which are involved in nesting behaviour and thus common in vespid species, may promote invasiveness.

The several examples mentioned here only represent a sample of the questions that could be approached in the context of animal personality. Obviously, the F_{ST}–Q_{ST} approach (and surrogate P_{ST}) is not a perfect plug-and-play method and may be adapted based on the situation/species; it is also important to be aware of its limitations. Although controversial due to its limitations, it is a valuable candidate to distinguish between natural selection and neutral processes to enhance our comprehension of the evolution of personality traits and their role in population processes. The popularity of the F_{ST}–Q_{ST} comparison and the constant progress that have been achieved to perfect and simplify its use are symbols of its value to provide insightful research perspectives.

Disclosure statement

The author has no conflicts of interest, including specific financial interests and relationships and affiliations, relevant to the subject of this manuscript.

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