Opinion

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Interacting personalities: behavioural ecology meets quantitative genetics

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Behavioural ecologists increasingly study behavioural variation within and among individuals in conjunction, thereby integrating research on phenotypic plasticity and animal personality within a single adaptive framework. Interactions between individuals (cf. social environments) constitute a major causative factor of behavioural variation at both of these hierarchical levels. Social interactions give rise to complex 'interactive phenotypes' and group-level emergent properties. This type of phenotype has intriguing evolutionary implications, warranting a cohesive framework for its study. We detail here how a reaction-norm framework might be applied to usefully integrate social environment theory developed in behavioural ecology and quantitative genetics. The proposed emergent framework facilitates firm integration of social environments in adaptive research on phenotypic characters that vary within and among individuals.

Personality, plasticity, and social interactions

Behavioural ecology research increasingly acknowledges the characteristic multilevel nature of animal behaviour [1], investigating within-individual (cf. phenotypic plasticity) and among-individual variation (cf. animal personality) in conjunction [2] (see Glossary). Adaptive explanations for behavioural variation centre upon the proposition that 'state' (features of organisms affecting the balance of costs and benefits of behavioural actions [3]) varies both within and among individuals, explaining behavioural variation at both levels [3–6]. Adaptive personality theory, for example, explains among-individual variation in behaviour as an adaptation to endogenous features of individuals [4,5], such as metabolism [7] and cognitive ability [8]. Exogenous features, particularly social environments, have more recently come to the foreground as key state variables shaping variation among individuals [9–11]. Social environments are of major importance because interactions between conspecifics impose a diverse array of selective pressures on various behaviours.

Models of adaptive behaviour imply a key role for social interactions [11]. Classic examples such as hawk–dove, producer–scrounger, and leader–follower games demonstrate how interactions often induce selection favouring behavioural variation [12]. Interactions can give rise to either adaptive within-individual variation (cf. plastic, conditional strategies) or adaptive among-individual variation (cf. alternative, fixed strategies) [6,11]. Adaptive theory, for example, implies that predictability in aggressiveness can be favoured when it allows interacting individuals to avoid costly fights [13]. The resulting among-individual variation has been suggested to favour the emergence of 'socially responsive' [13] individuals who adjust their behaviour as a function of the previous

Glossary

Among-individual variation: individual differences in average phenotype across multiple observations.

Animal personality: among-individual variation in behaviour attributable to the combined influences of genetic effects and environmental effects that permanently affect the phenotype of an individual [2,6]. Pseudo-personality occurs when estimates of personality are inflated because of individual repeatability in environmental conditions that cause nonpermanent effects on behaviour [31,36].

Direct genetic effect (DGE): allelic variation in genes affecting the phenotype, where the phenotype of an individual is directly affected by its own genes [21].

Emergent character: a phenotypic character representing a characteristic or an outcome of an interaction rather than of an individual, such as the duration or intensity of a fight [43].

Indirect genetic effect (IGE): environmental influences on the phenotype of an individual resulting from the expression of genes in another conspecific [17,21].

Interactive phenotype: a phenotypic characteristic of an individual whose expression is affected by the phenotype of (a) conspecific(s).

Phenotypic gambit: an approach to the study of behavioural adaptation [33] viewing natural selection as an optimising process that is ultimately unconstrained by genetic architecture [59].

Reaction norm (RN): set of phenotypes that a genotype or individual produces as a function of an environmental gradient. Throughout this paper, we focus on individual-level reaction norms [2,34].

Social environment: environmental component of the phenotype caused by interactions with conspecifics.

Social responsiveness: phenotypic plasticity in response to the phenotype expressed by a conspecific, estimated as the slope of an individual-level reaction norm. Socially responsive individuals are characterised by a nonzero interaction coefficient (Ψ).

Trait-based approach: a statistical approach where phenotypes of focals are represented as a function of the phenotypic characteristics of conspecifics [53]. This dependency is captured by an interaction coefficient (Ψ).

Variance-partitioning approach: a statistical approach where phenotypic variance is partitioned in variance attributable to different effects [53]. Variance in phenotype of focals might, for example, be decomposed into variance explained by the identity of the focal versus social partner, or into variance explained by direct genetic effects versus indirect genetic effects [53].

Within-individual variation: phenotypes vary within individuals across instances, caused by nonpermanent environmental effects on the phenotype of an individual [2,6,31,34]. Throughout, we assume that variance attributable to measurement error represents a negligible component of within-individual variance.

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interactions of their social partner (cf. within-individual variance resulting from adaptive phenotypic plasticity) [14], which in turn causes intensified selection favouring further individual differentiation in various types of behaviour (e.g., aggressiveness [15], cooperation [14], or coordination [16]). Similarly, repeated interactions between individuals cooperating in stable social groups have been proposed to increase among-individual (but decrease within-individual) variation in behaviour [10] because negative frequency-dependent selection favours division of labour among individuals (cf. social niche specialisation [9]). Thus, social interactions might give rise to personality, plasticity, and individual differences in social responsiveness [9,11,13].

Social environment effects in quantitative genetics

Quantitative geneticists have studied social environments from a different perspective. Their emphasis has been on predicting evolutionary responses to selection [17,18]. Quantitative genetic theory developed by animal breeders and evolutionary biologists implies that social environments can have major evolutionary repercussions when heritable phenotypes affect the phenotypes of other conspecific individuals [19,20]. In such cases, the social environment is itself heritable because of 'indirect genetic effects' (IGEs) and, thus, is evolvable [17,21]. IGEs represent a special form of phenotypic plasticity where environmental effects on the phenotype of an individual are caused by the expression of genes in another conspecific [21]; the familiar 'direct genetic effects' (DGEs) instead occur when the phenotype of an individual is directly affected by its own genes. Genetic variation in maternal investment influencing offspring development (cf. maternal genetic effects [22]) and genetic characteristics of social partners affecting life-history decisions of mates [23] represent examples of IGEs. Importantly, IGEs influence evolutionary responses to selection, such as when there are functional interactions between traits of interacting individuals [24] or when DGEs and IGEs are genetically correlated [21]. In gulls, for instance, genes expressed in females contributing to early laying (DGEs) are negatively correlated with genes expressed in males facilitating early laying in female partners (IGEs) [23]. Such sexually antagonistic effects can impose constraints on evolution [25]. Positive genetic correlations might instead speed up evolutionary responses (depending on the selective landscape [17,20]); genes for aggressiveness in mice (a DGE), for example, correlate positively with genes eliciting aggressiveness in opponents (an IGE) [26]. Thus, phenotypic plasticity as a function of phenotypes expressed by conspecifics (i.e., social responsiveness) represents a key factor in the evolutionary process. However, little is known about the ecological conditions (dis)favouring indirect genetic effects [27] and whether social responsiveness is heritable and evolvable [28,29].

Behavioural ecology meets quantitative genetics

In this opinion article, we propose a reaction-norm framework to combine social environment theory developed in behavioural ecology and quantitative genetics, and to facilitate cross-fertilisation between these research fields. We detail how quantitative genetics approaches might be usefully incorporated in behavioural ecology research (cf. [10,30,31]) to empirically study the adaptive nature of 'social responsiveness'. Conversely, we argue that behavioural ecology theory on this topic usefully provides quantitative genetics with predictions concerning ecological conditions (dis)favouring the evolution of variance components such as indirect effects (cf. [32]). Behavioural ecologists apply a 'phenotypic gambit' [33] in their adaptive studies; in this opinion article, we adopt this approach by focusing on among-individual (rather than additive genetic) variation; both approaches intricately contribute to our understanding of evolutionary processes (Box 1). The proposed framework enables integration of social environments between distinct fields of evolutionary biology.

Phenotypes as environmental gradients

Incorporating social environments into studies of personality and plasticity requires a particular way of thinking about both behaviour and social environments. Instead of characterising individuals by their behaviour, we view the

Box 1. Behavioural ecology, variance components, and evolutionary adaptation

Quantitative genetics focuses on predicting evolutionary responses to selection, and this explicitly requires the partitioning of phenotypic variation in traits (and fitness) in genetic versus environmental components [22]. Behavioural ecology, by contrast, commonly applies a 'phenotypic gambit' [33], viewing natural selection as an optimising process that is ultimately unconstrained by genetic architecture [59], which might therefore be studied at the phenotypic level. Behavioural ecology approaches nevertheless contribute importantly to our understanding of evolutionary processes. Specifically, interest in (repeatable) among-individual differences has stimulated the development of theory predicting the ecological conditions under which natural (and sexual) selection (dis)favour specific (co)variance components [31,32] such as among-individual (co)variance [4,5,13], within-individual variance [60], and among-individual variation in behavioural plasticity [6,11,14]. Here, behavioural ecology theory implies a key role for ecology (cf. resource availability, predation risk [61]) in causing selection (dis)favouring among-individual variance [4,5]. Models typically involve adaptive state-dependence of behaviour [3–5,13,61], leading to testable predictions concerning the magnitude of permanent-environmental (e.g., [62]) and within-individual variances (e.g., [63]). The expression of such non-genetic variance components directly affects the heritability of phenotypic characters, hence their evolutionary potential [22]. Despite its application of a phenotypic gambit, behavioural ecological theory therefore contributes substantially to our understanding of evolutionary processes. At the same time, their focus on 'unpartitioned' among-individual variance hampers the application of quantitative genetics theory in predicting evolutionary responses to selection.

Adaptive theory concerning the emergence of direct (cf. among-individual) and indirect (cf. social partner) effects developed by behavioural ecologists, importantly, does not hinge upon the nature of state-dependence: various types of predictive theory apply generally to both heritable (cf. additive genetic) and nonheritable (cf. permanent environmental) parts of among-individual variance components [4]. In other words, behavioural ecology theory concerning the emergence of social responsiveness (cf. indirect effects), or among-individual variation in social responsiveness, can readily be utilised to study the ecological conditions (dis)favouring both indirect environmental effects and indirect genetic effects, and thereby meaningfully enables the integration of ecology into the study of heritable variation.

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