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Editorial

Ecological and evolutionary connections between morphology, physiology, and behavior

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1 Introduction

Phenotype variation within populations both provides the raw material for and is the product of evolutionary change. An individual's phenotype, defined as the amalgamation of morphology, physiology, and behavior, is highly complex. It has been common to try to isolate each of these aspects of phenotype rather than directly examine their integration. For example, despite the demonstrated importance of single aspects of phenotype for acquiring mates it is well known that signal traits are not evaluated in isolation, but rather in conjunction with associated behaviors, and sometimes with other signal traits (Møller and Pomiankowski, 1993; Candolin, 2003; Hebets and Papaj, 2005; Hebets, 2011). Indeed, the multidimensional components of phenotype are influenced by a dynamic interplay among morphology, physiology, and behavior, as well as the social and environmental context in which phenotypes are expressed. Such interactive feedbacks indicate that current models of the function and evolution of complex phenotypes, including those used as signal traits, must be updated to incorporate these dynamic interactions.

2 Current Research in Phenotypic Integration

Providing a model for moving forward with an integrative view of phenotypic complexity was an overall goal of this issue. This special column is comprised of six articles that range from comparative and empirical research to syntheses and new conceptual frameworks. The authors of these contributions draw on different study systems from insects to vertebrates, including lizards and various avian taxa.

2.1 Synthesis and new directions

We start this collection of papers with an overview of the many different ways in which aspects of phenotype interact to influence the development and display of social signals (Vitousek et al., 2014). In this contribution we indicate and outline the important but often-neglected role that social context can play in shaping these links. The integrative model of signaling phenotype that we propose here places social context as a central influence on both signal elaboration and other aspects of phenotype. This conceptual model, together with a discussion of the gaps in our current knowledge, provide a framework for addressing questions about the mechanisms, development, and function of signals, and about how signals evolve within and among closely related populations.

In a second conceptual piece, Husak and Lailvaux (2014) offer a nuanced view of how conflict can differentially influence the evolution of phenotypic variation. Here, they summarize and contrast different types of conflicts include inginter locus and intralocus sexual conflict, pre- and post-mating conflicts, and conflicts related to alternative reproductive tactics. An important insight is that conflict may be a fundamental yet overlooked integrator of physiological and functional trait evolution with various types of selection pressures acting on the same trait in different ways.

2.2 Empirical studies of ecological and evolutionary connections between morphology, physiology, and behavior

In the article 'The evolution of copulation frequency and the mechanisms of reproduction in male *Anolis* lizards' Johnson and her colleagues (Johnson et al., 2014) offer a comparative evolutionary view of the integration between reproductive behavior and morphology. Here, they examined whether and how reproductive behavior is predicted by copulatory organ size. Using field-collected morphological and behavioral data from nine members of the genus *Anolis*, their analyses revealed that, controlling for body size, the evolution of higher copulation rates is positively correlated with larger reproductive morphology, including hemipenis size and traits related to hemipenis movement. These results suggest an evolutionary response to integrated behavioral, morphological, and physiological aspects of phenotype.

Bubak and coauthors (2014) address the neural mechanisms of aggressive behavior and the relationships between aggression and morphological and physiological traits. Highlighting the role of several neuromodulators, including octopamine, serotonin and pheromones, the authors discuss recent advances in our understanding of the mechanisms of agonistic behavior in both vertebrates and invertebrates. Integrative research in highly tractable insect model systems is a particularly promising source of insight into the interactions and feedbacks among the neural mechanisms of aggression, other aspects of phenotype, and the dynamic social environments in which these traits are expressed.

Rosvall and Peterson (2014) address feedback between phenotype and another aspect of social context: social instability. During periods of social instability agonistic interactions are more common; thus, mechanisms that respond to cues of instability by priming phenotypes to prepare for future challenges may be adaptive. Yet while testosterone is often implicated as a mechanism of social priming, the degree to which testosterone levels respond to social cues and mediate organismal responses to unstable environments has not been clear. Data on genome-wide transcriptional patterns in dark eyed juncos suggests that testosterone is not the primary mediator of the phenotypic response to social challenges. As Rosvall and Peterson (2014) report, experimental elevation in testosterone and alterations in the social system induce divergent changes in gene expression across a number of tissues. Furthermore, by reviewing the hormonal and gene regulatory mechanisms of socially-induced phenotypic change the authors reveal that testosterone is often not the primary mediator of behavioral and physiological responses to the social environment. Instead, a diversity of mechanisms appear to be involved in linking the social environment with adaptive phenotypic changes, with different primary mechanisms operating not only between species but even among tissues of the same organism. Intriguingly, similar changes in behavior and physiology are often regulated by different mechanisms. Identifying the mechanisms that enable organisms to prepare for future challenges, and determining the potential for selection to shape these responses, has important implications for the ability to coordinate phenotype with social context.

In the final article in this column, Schwabl et al. (2014) address the interaction between behavior and physiology in the context of female mate choice. Here, they examine the associations between hormones, social environment, and reproductive investment in females of a highly promiscuous species, the red-backed fairy wren. This is a fascinating study system because females are confronted with variation in social context due to differing male reproductive strategies, frequent extra-pair mating decisions, and the potential for additional help at the nest through cooperative breeding. A strength of this study is a cross-seasonal analysis of how female hormones vary according to social and reproductive factors associated with different stages of reproductive investment. The results indicate that androgen, estrogen and glucocorticoid levels covary with reproductive stage in females, but are not clearly associated with male phenotype or the presence of helpers at the nest. Thus, in this system, aspects of a female's social environment appear to be less important than reproductive stage in predicting seasonal variation in steroid hormones.

3 Overall Summary

The contributions to this special theme issue suggest novel ways of studying complex phenotypes, and present new information on the extent to which various aspects of phenotype, including measures of behavior, physiology, and morphology are integrated. Taken together, these contributions suggest that an integrative view of phenotype can offer more nuanced and even surprising results about the mechanisms of integration (e.g., Rosvall and Peterson, 2014; Bubak et al., 2014), that longitudinal sampling schemes are important for revealing phenotypic complexity (Schwabl et al., 2014), and that addressing patterns of trait covariance on evolutionary time scales can provide insight into the evolution of integrated phenotypes (Johnson et al., 2014). We anticipate that the two synthesis articles will stimulate new, integrative approaches for studying the function and evolution of flexibility in complex aspects of phenotype.

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