



Extending the integrated phenotype: covariance and correlation in plasticity of behavioural traits

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In the field of behavioural ecology there has been a longstanding interest in the evolution of phenotypic plasticity, as plasticity in behavioural traits such as foraging, mating, and reproduction governs the capacity of organisms to cope with environmental variability. In this paper we highlight the need for an integrated perspective to phenotypic plasticity of traits, taking into account covariation among plastic responses of traits. We discuss new perspectives on the importance of integrated plasticity of traits for adaptive behavioural strategies. We review empirical evidence for correlated plasticity across behavioural traits in insects, for example, through genetic correlation, a shared pool of resources or dependency on a common developmental path. Taking on an integrated plasticity perspective, we suggest an alternative explanation for the apparent lack of costs of plasticity, and offer a better understanding of the relative benefits of plasticity or canalization of traits.

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“To assume that selection acts only on single characters is a tremendous oversimplification of life, since natural selection acts on the integrated phenotype of an individual and correlations between traits are abundant”. [1]

A common and powerful way of adaptation in nature is phenotypic plasticity, the capacity of an individual genotype to produce different phenotypes under different environmental conditions [2–4]. Phenotypic plasticity has been reported in a multitude of traits over the last decades, including morphological traits, life-history, behaviour, but also in patterns of gene expression and protein production [5,6]. It is now generally accepted that plastic

responses to environmental conditions during development or adult life can have important fitness consequences. Moreover, it has become apparent that the effect of exposure to biotic or abiotic conditions can be pervasive; as it can last for several generations, or give rise to transgenerational plasticity where parental environment induces phenotypic changes in the offspring or grand-offspring, see, for example [7]. Our understanding of adaptive processes has increased greatly since plasticity is fully recognized as an important parameter in evolutionary biology [8].

However, much of our understanding of phenotypic plasticity is based on studies that focus on single traits [9–11], implicitly assuming that plastic responses evolve independently and uncoupled for different traits and conditions. Many authors have pointed out the risks in neglecting possible correlations between plasticity of traits [8,12,13**]. Covariation between the plasticity of traits may constrain the development of an optimal phenotype if the fitness benefits of high plasticity in one trait are offset by a correlated response in the plasticity of other traits [14]. Vice versa, if two correlated traits have similar and additive effects on fitness, correlated plasticity between those traits may actually facilitate the evolution of adaptive phenotypes. A still increasing number of studies apply an integrated perspective to phenotypic plasticity of traits [15–17]. In this paper we want to highlight the importance of such an integrated plasticity perspective for important traits in insect behavioural ecology studies, such as foraging, mating, and reproduction.

Phenotypic plasticity has many examples in insects, and is particularly important for behavioural strategies since it allows insects to fine tune their reproduction, foraging behaviour or mating strategy to varying environmental conditions. Examples include dispersal polymorphisms in various insect species [18], flexibility in foraging behaviour in prey species [19], adjustment in sex ratio in parasitoids [20], polymorphy in sexual signalling in crickets [21], and alternative male morphologies in beetles [22]. However, in this review we do not aim to provide an exhaustive overview of phenotypic plasticity or the conditions under which it is expected to evolve. Instead, our goal is to review how recent advances in the understanding of phenotypic plasticity can aid studies in behavioural ecology of insects by informing researchers about appropriate experimental designs and variables to be included in measurements.

We will first review empirical evidence for plasticity integration among life-history and behavioural traits, focusing

on plasticity of insect traits that are coupled through genetic correlation or a shared developmental pathway. We then discuss the idea that correlated plasticity of traits that also acts at different organizational levels of the same mechanistic or developmental cascade. Finally, we expand on the implications of the integrated plasticity perspective by providing a better understanding of the costs and benefits of plasticity.

Covariation in the plastic responses of traits

Phenotypic integration refers to the relationships among multiple characters of a complex phenotype [9,23]. It describes how adaptation and constraints on evolution are determined by networks of closely correlated traits (modules) and their relationships with other functional units in an organism [23]. Such a modular organization of traits enhances proper functioning of complex phenotypes in different selective environments. A well-known illustration of an integrated phenotype are behavioural syndromes, which form a suite of correlated behaviours that are expressed consistently across behavioural contexts such as feeding, mating, parental care, etc., or across ecological conditions [24,25]. In other words, an individual that is aggressive in competition for food also shows high aggression levels in competition for mates. The crux of the matter is that the behavioural traits expressed in different situations do not evolve independently; therefore their evolution can only be understood when considering them in an integrated perspective.

A similar integrated perspective can be applied to phenotypic plasticity of traits. Just like an organism's phenotype shows coherence among characters, the level of plasticity displayed in individual traits is also part of the integrated phenotype. If two or more traits have similar and additive effects on the same fitness parameter, genetic coupling between these traits may facilitate the evolution of optimal phenotypes. In the next sections, we discuss several possible (but not exhaustive) processes that could lead to covariation of plastic responses of traits.

One possible and common cause of correlation between traits is pleiotropy or genetic linkage between traits, for instance in trade-offs between life-history traits [26]. Through the same mechanisms, plasticity of traits within an individual's phenotype (i.e. an organism's whole collection of expressed properties) can also be coupled. To illustrate this point, consider two traits that are correlated. If phenotypic plasticity would cause one of the traits to change in response to environmental variation, necessarily this would lead to a correlated plastic response in the other trait, either because both traits rely on the same resource pool, or because genetic variation for the phenotypes is linked [26].

The existence of such genetically correlated responses in behaviour has been documented for insects. For example,

the response in foraging behaviour in different species of sawfly larvae to low food quality can take two, almost mutually exclusive, forms. Larvae displayed either an increased consumption rate to compensate for the poor leaf quality, or increased dispersion of feeding sites, potentially allowing them to find higher quality leaves [27]. These behavioural traits responded as an integrated trait network with physiological efficiencies of larvae, leading to relatively stable growth rates. In a similar fashion, life history traits of the springtail *Orchesella cincta* showed genetically correlated plasticity when exposed to an increase in temperature [28]. Hence, evolution of the thermal plasticity of a trait cannot be understood in isolation of the response of other traits.

Also, for reproductive behaviours trade-offs are common, particularly for ornamented males that face a higher predation risk than non-ornamented males due to their higher conspicuousness [29,30]. The plasticity response to increased predation should therefore be dependent on secondary sexual characters, as was indeed found for polymorphic male wolf spiders [31]. Visually conspicuous brush-legged males increased their time to courtship initiation more strongly under predation risk than non-ornamented males. This greater degree of behavioural plasticity may offset increased predation costs associated with high display rates, and ultimately alter the trade-off between natural and sexual selection.

Another angle from which we can expect plastic responses of traits to be correlated is when these traits share a dependence on the same developmental pathway, and act as a 'module' in which responses are more tightly correlated than between modules [32*]. To explain complex behaviours in insects a modular organization of the brain is often assumed where horizontal integration of diverse modules takes place in central sites [33]. This organization would account for the ability of insects to perform new adaptive behaviours like displaying diverse types of generalization of learned stimuli and storing context-specific memories [34]. Learning is generally regarded a form of phenotypic plasticity [35,36] with cognitive modules of behavioural traits that depend on a shared neurologic pathway. Many of these pathways that are associated with learning and memory are conserved across taxa [37]. Evidence for the organization of learning into cognitive modules was found in two independent studies performing selection experiments for improved learning and memory skills. During selection females of *Drosophila melanogaster* and *Nasonia vitripennis* learned to associate a predetermined cue with oviposition opportunity, resulting in significantly improved learning ability for this task after several generations in both species. However, this improved learning behaviour extended to other, novel, tasks and different chemosensory stimuli (odour and taste) in *Drosophila* [38,39] and could even be extended to different stimulus domains (odour

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