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Variation in behavioural plasticity regulates consistent individual differences in *Enallagma* damselfly larvae

Allison L. Brown, Beren W. Robinson*

Department of Integrative Biology, University of Guelph, Ontario, Canada

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Plastic behavioural responses by individuals to different conditions and consistent individual differences in mean behaviour across situations both contribute to variation in a population. The relationship between behavioural plasticity and consistent individual differences is not clearly understood but may help predict personality variation in animals. High variation in mean behaviour and low variation in individual plastic responses will tend to maintain the rank order of individuals across situations and so permit consistent individual differences. Conversely, low variation in mean behaviour and high variation in plastic responses, by changing the rank orders of individuals, will erode consistent individual differences. Thus, selection that reduces variation in individual plastic responses should increase the opportunity for consistent individual differences in a population. We tested for relationships between heterogeneous predation regimes, the mean and variance of behavioural plasticity and consistent individual differences among three species groups of larval damselflies. Larvae of *Enallagma signatum* probably face consistent predation from fish over successive generations, whereas *Enallagma ebrium/hageni* and *Enallagma annexum/boreale* face a changing predation regime over generations either from fish or larval dragonflies. The behavioural reaction norms of larvae in repeated exposure trials to cues from a predatory fish, dragonfly larvae or no predator differed between species groups. *Enallagma ebrium/hageni* expressed the most consistent plastic response to predator cues, less variability in plasticity and greater consistent individual differences across cues compared to more variable plastic responses and low consistent individual differences in *E. signatum*. Selection on behavioural plasticity may enhance consistent individual differences in *E. ebrium/hageni* whereas relaxing selection on plasticity may reduce consistent individual differences in *E. signatum*. More generally, selection on plastic behaviour may enhance behavioural types while selection on mean behaviour may reduce behavioural types in animal populations.

Behavioural variation present in an animal population integrates variation among individuals in their mean behaviours (when averaged over different ecological or social situations) and variation among individuals in their plastic responses to different situations. Both are important components of behaviour, but how either may be influenced by the other is poorly understood. When the component of mean behaviour is large, then individuals repeat their rank-ordered behaviour from one situation to another (Bell, Hankison, & Laskowski, 2009). Such consistent individual differences may arise from underlying differences in development or physiology (Biro & Stamps, 2008, 2010). They can have important ecological consequences for feeding, avoiding predators and mating, etc. (Biro & Post, 2008; Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Mittelbach, Ballew, Kjelvik, & Fraser, 2014; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). When these differences are heritable (Van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005) and influence relative fitness, they may also drive adaptive evolution (Dall, Houston, & McNamara, 2004; Dingemanse et al., 2009; Réale, Dingemanse, Kazem, & Wright, 2010; Smith & Blumstein, 2008; Wolf & Weissing, 2010). Consistent individual differences occurring along particular behavioural axes can indicate 'personality' differences among individuals (Gosling & John, 1999; Réale, Reader, Sol, McDougall, & Dingemanse, 2007), and when correlated across multiple axes, can reveal behavioural 'syndromes' (Garamszegi, Markó, & Herczeg, 2012; Sih & Bell, 2008; Sih et al., 2012). Consequently, predicting consistent individual differences in animal populations is of interest for a better functional understanding of the causes and the ecological and evolutionary consequences of behavioural variation.

* Correspondence: B. W. Robinson, Department of Integrative Biology, University of Guelph, Guelph, ON, N1G 2W1, Canada.
E-mail address: berenrob@uoguelph.ca (B. W. Robinson).

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Behaviour is also a highly plastic trait category because most animals can express rapid, reversible and repeatable behavioural responses to changes in local conditions. An individual's behavioural reaction norm represents plasticity by defining the set of behavioural outputs to a set of particular ecological or social conditions (Dingemanse, Kazem, Réale, & Wright, 2010). Adaptive, or at least functionally plastic, behaviour in response to changes in predation risk, resources, social environment, et cetera, is almost ubiquitous in many animals (Snell-Rood, 2013). Consequently, understanding how plasticity evolves and how plastic behaviour mediates interactions among individuals within and among species is also of great interest (Cousyn et al., 2001; Nussey, Wilson, & Brommer, 2007; Whitman & Agrawal, 2009). However, despite some progress, the interplay between behavioural plasticity and consistent individual differences is not yet well understood (Dingemanse et al., 2010).

There is some tendency to expect that behavioural plasticity may be incompatible with consistent individual differences because plasticity potentially allows behaviours to vary in different situations (Figure 1 in Van Oers et al., 2005). But the relationship between behavioural plasticity and consistent individual differences is complex because it depends on differences among individuals in their plastic responses rather than on the average amount of plasticity expressed by individuals. Variation in individual behavioural reaction norms influences how the order of individuals ranked by their behaviour in one situation remains consistent or changes in another situation (Fig. 1). Consistent individual differences arise when the same rank order of individual differences persists over situations (Bell et al., 2009), regardless of whether behaviour is nonplastic or plastic (Fig. 1a, b). However, when individuals differ in their plastic behavioural responses, then their rank-order differences change between one situation and another (Fig. 1c, d). In other words, greater variation in the slopes of individual behavioural reaction norms and less variation in behavioural reaction norm intercepts will have a negative influence on consistent individual differences in a population.

Our aim in the present study was to evaluate the influence of variation in plastic behaviour on the expression of consistent individual differences in natural populations. Standing variation in any heritable trait is a function of the strength and duration of selection (Conner & Hartl, 2004). Plastic behaviour comes under selection when individuals face unavoidable heterogeneity in conditions that influence their fitness, specific responses match different situations better than a fixed general behaviour, matching is reliable and timely, and the benefits of plasticity outweigh its costs (Snell-Rood, 2013; Whitman & Agrawal, 2009). Selection on plastic behaviour can reduce variation in behavioural reaction norm slopes (Fig. 1b) in comparison to a population where plastic responses are not under selection (Fig. 1c, d) (Biro & Post, 2008; Dingemanse et al., 2010). Relaxed selection on behavioural reaction norm slopes occurs in at least two ways: (1) when individuals experience increasingly homogeneous conditions (Alpert & Simms, 2002; Rodríguez, 2013), or (2) when selection acts on behaviour in one but not in other situations (Fig. 1e, f). Thus, we expect that consistent individual differences in behaviour are less likely as selection on behavioural plasticity is relaxed.

Variability in predation risk can drive the evolution of adaptive plastic antipredator behaviour (Bernard, 2004; Dodson, 1989; Relyea, 2001a, 2001b; Tollrian & Harvell, 1999). Here, we evaluate the relationships between temporal variation in predation regime, behavioural plasticity, standing variation in plastic behaviour and consistent individual differences by comparing larval behaviour among closely related species of damselflies. First, we indirectly tested the hypothesis that the strength of selection on plastic behaviour probably varies among species. We interpret positive

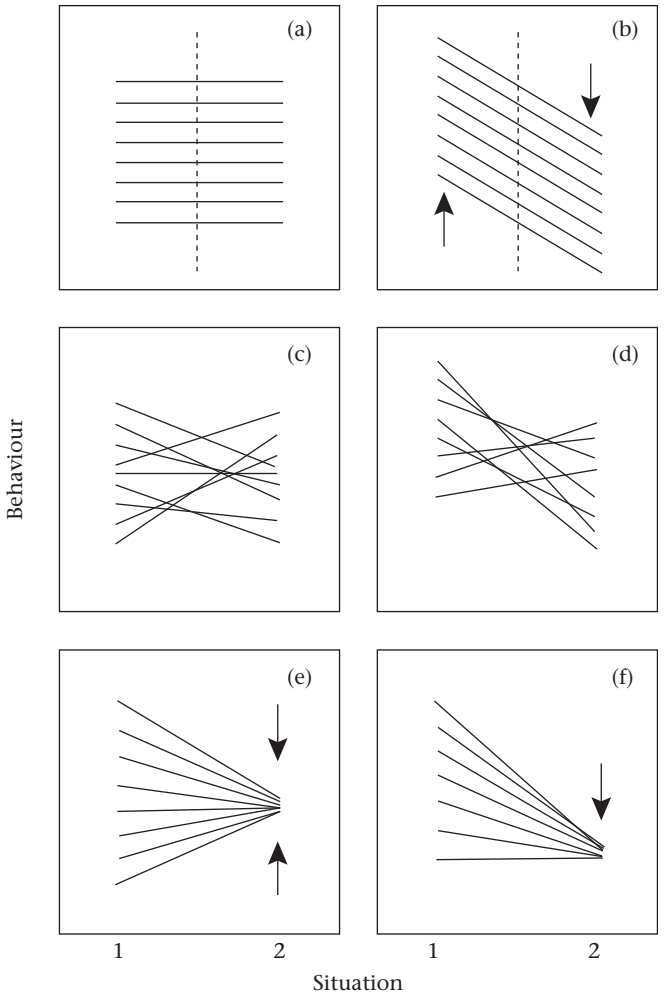

Figure 1. Behavioural variation among individuals in each of two situations (1 and 2). Each line represents an individual's behavioural reaction norm, a behavioural response to a change of situation, such as a predator cue. Lines with a slope of zero indicate no change in individual behaviour between situations (a). An individual's mean behaviour, averaged over situations, is represented by the intercept of the individual behavioural reaction norms (dashed vertical line). An individual's plasticity is represented by the slope of its behavioural response across the situations. Variation in behavioural reaction norms influences whether or not consistent individual differences in behaviour occur from one situation to another. Consistent individual differences are expressed across situations in nonplastic individuals (a), or in individuals with plastic behaviour (b). Selection (arrows) that reduces variation in behavioural reaction norms allows the rank order of individuals in one situation to carry over to another situation. Selection that reduces variation in mean behaviour tends to reduce consistent individual differences. Increasing variation in behavioural reaction norm slopes limits consistent individual differences in behaviour (c, d) as the rank order of individuals changes across situations. Relaxing selection on behavioural reaction norm slopes increases variation in slopes, such as when a population experiences only one situation, or when behaviour is under stabilizing selection (e) or directional selection (f) in one situation and is selectively neutral in the other situation.

associations between variation in larval predation risk and greater behavioural plasticity and also with less variation in individual behavioural reaction norms as consistent with different strengths of selection on behavioural plasticity. We then evaluate whether species with greater variation in individual behavioural reaction norms also express weaker consistent individual differences in behaviour.

DAMSELFLY STUDY SYSTEM

Coenagrionid damselfly (Odonata: Zygoptera) larvae can experience temporal variability in predation risk among generations.