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Proximate mechanisms of among-individual behavioural variation in animals

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One could easily argue that among individual variation in behaviour is hardly something new in biology. On one level, behaviour is simply an aspect of phenotypic variation, which is the raw material of evolution (provided that some variants are favoured by selective forces) (Darwin, 1859). Yet consistent among individual variation in behaviour – animal personality (Dall et al., 2004; Gosling and John, 1999; Sih et al., 2004) – has been the focus of increasing efforts in animal behaviour research. So why has this seemingly obvious aspect of biology been the focus of so much recent attention? First, a branch of evolutionary theory, game theory, shows that negative frequency dependent selection can result in a stable mix of phenotypes (Maynard Smith, 1982). This rationale has been used to explain the stability of mixed fighting strategies, alternative mating tactics and more recently to animal personalities (Wolf and Weissing, 2010). Indeed, this latest application seems like a logical conclusion of evolutionary game theory; as well as promoting the evolution of hawks and doves, could frequency dependence also lead to a wider continuum of behavioural phenotypes? The fact that phenotypic variation could be a consequence as well as a basis for evolution makes animal personalities inherently interesting to study. However, there is a second reason for interest in the topic; the presence of animal personalities seems to imply that behavioural plasticity – the ability of animals to calibrate their behaviour to match current circumstances – must be subject to constraints. Out of all the phenotypic traits we could study behaviour is expected to be the most labile. That is, in comparison with morphological and physiological traits behaviour is more reversible and responds more rapidly to abiotic and biotic stimuli. Nevertheless, in the vast range of animal species where personalities have now been studied we find that most individuals express only a limited range of the behavioural responses seen across their populations as a whole. These limits on behavioural plasticity could contribute to the following patterns in longitudinal data on behaviour: significant repeatability, significant among

individual variation in behavioural plasticity (also called behavioural reaction norms, Dingemanse et al., 2010) and significant among individual variation in within-individual variation in behaviour (also called intra-individual variation, Stamps et al., 2012, or in terms of statistics, residual phenotypic variance, Westneat et al., 2014).

As with consistent among-individual variation in behaviour itself, the apparent constraints on behavioural plasticity were recognised (e.g. Hazlett, 1995) prior to the current upwelling of interest in animal personalities. What has emerged over recent years, though, is a body of conceptual work that has the potential to explain why there should be limits on behavioural plasticity, and to predict specific proximate mechanisms that might underpin such constraints. For example, the Pace of Life Syndrome (POLS) hypothesis is based on the idea that there should be a trade-off between longevity and metabolic rate (Careau et al., 2008; Wolf et al., 2007), as captured in the phrase '*live fast die young*'. POLS posits the presence of a syndrome of positive covariation among risk-prone behaviours (e.g. high boldness, exploration, aggressiveness), growth-rates, and metabolic rate (Careau et al., 2008). Similarly, the idea of coping styles, in particular stress coping styles, emphasises the neuroendocrine traits that might predict variation in how animals behave in challenging situations (Coppens et al., 2010). These potential mechanisms may be studied directly using techniques such as respirometry and hormone assays. There is also the potential to understand personality variation by investigating the upstream regulation of genes that determine the expression of metabolic rates, hormones and receptors using molecular biology and genomics. And, of course any underlying mechanism that might cause personality variation is subject to influences during ontogeny (e.g. through initial differences in state that are reinforced by positive feedback between state and behaviour; see Wolf et al., 2008), so a developmental perspective should also give valuable insights into the proximate causes of animal personalities (Groothuis and Trillmich, 2011).

Examples of all of these approaches, applied to a diverse range of animal taxa (crustaceans, echinoderms, vertebrates; Figure 1) are included in the collection of studies in this special issue. The idea for a special issue followed a symposium entitled *Understanding intraspecific variation in animal phenotypes from genes to behaviour*, held at the 2015 Society for Experimental Biology conference in Prague. This symposium was actually the third in a series, beginning in 2011, organised by L. Sneddon and M. Briffa. Many of the papers included here are authored by contributors to the 2015 session (Figure 2), but we also opened the special issue to other authors working on similar topics. The result is a range of studies demonstrating (a) the potentially ubiquitous nature of consistent variation among behavioural phenotypes, and (b) approaches for studying the physiology that might contribute to this intraspecific variation in behaviour.

In this special issue, variation in metabolic rate is the focus of two studies on aquatic species, the European hermit crab *Pagurus bernhardus*, and the Trinidadian guppy *Poecilia reticulata*. In line with conflicting results from a range of previous studies (see citations in these papers) neither show evidence of a correlation between metabolism and the average behaviour of individuals. However, in the case of hermit crabs metabolic rate does vary with the amount of intra-individual variation, but resting and activity metabolic rate might differentially influence behaviour. Behavioural consistency is also assessed in the context of increasing experience in a study on the Caribbean sea star, *Oreaster reticulatus*, where potential links between the roles of experience and physiology are discussed. The role of cortisol in mediating stress responses in vertebrates is well studied, especially in the rainbow trout *Oncorhynchus mykiss* (Øverli et al., 2007). Therefore, it seems that there is substantial potential for differences in cortisol expression, or sensitivity to stress, to underpin variation in animal personality in this species. In a study where the personality type of group members that focal rainbow trout individuals are exposed to is manipulated, we see how personality types can

change as a result of social experience, while cortisol levels are not affected. A second study on the same species shows how stress coping styles might be related to differences in cognition and to immediate early gene responses in the forebrain linked to emotionality. In a related species, the brook trout *Salvelinus fontinalis*, a developmental approach is taken to investigate the links between pre-fertilisation and embryonic exposure to cortisol and subsequent personality variation in the resulting juveniles. Corticosteroids play a similar role in birds and a study on the blue tit *Cyanistes caeruleus* explores the differing roles of base-line and stress induced corticosterone in mediating exploration. Additionally, exploration of the links between cortisol and personality variation in a mammal, the kangaroo rat *Dipodomys stephensi*, provides a special focus on how our understanding of the links between physiology and behaviour can enhance conservation efforts. Thus, many of the studies herein attempt to delineate the links between physiological and behavioural phenotypes. One such study, on the three spined stickleback *Gasterosteus aculeatus*, focusses on the molecular underpinnings of behavioural phenotypes by looking at gene expression profiles across four regions of the brain. Fish models are also used here to investigate the roles of brain lateralisation (in the Port Jackson shark, *Heterodontus portusjacksoni*) and among individual differences in circadian rhythms (in embryonic zebrafish, *Danio rerio*) in driving wider personality variation.

One should perhaps be cautious in attempting to draw overly general conclusions about the role of specific proximate mechanisms, which can vary across species, life stages, context and situation. Indeed, two studies in this special issue show that the same aspect of physiology (e.g. metabolic rate and hormone levels) can have different effects within the same experiment depending on the situation or behavioural context. The studies in this special issue offer a snapshot of the approaches currently being used to advance our understanding of consistent among individual variation in behaviour by focussing on potential proximate mechanisms that may underpin behavioural variation. Future studies should continue to investigate the elusive

molecular and physiological mechanisms of animal personality and this special issue highlights the need for translation between laboratory studies and field tests in understanding the proximate causes of potentially adaptive behavioural variation.

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Figure 1: A selection of the species studied in papers in this special issue. Clockwise from top left: European hermit crab emerging from its shell, rainbow trout, adult zebrafish, California sea star, Stephens' kangaroo rat, Port Jackson shark. Photo credits: M. Briffa, L. Sneddon, L. Sneddon, L. Gutowski, L. Baker, J. Piroška Kadar.



Figure 2: A selection of participants in the symposium on intraspecific variation in behavioural phenotypes at SEB 2015. Among these the following have contributed papers to this special issue: Jack Thompson (first left), Nadia Aubin-Horth (2nd left), Øyvind Øverli (4th left), Erik Hoglund (back centre), Lynne Sneddon (front centre), Mark Briffa (4th right) and Christian Tudorache (first right).