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Commentary

Contaminants as a neglected source of behavioural variation

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Animal behaviour has broad ecological and evolutionary implications. Among other things, it drives social group and population dynamics, affects interspecific interactions and influences how animals cope with environmental changes (Sih, Cote, Evans, Fogarty, & Pruitt, 2012). In addition to the average behaviour of a given species or population, behavioural variation among individuals within populations (i.e. so-called 'animal personality': Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004) has important implications for ecological and evolutionary processes relevant for multiple fields of research, such as community ecology and conservation (McDougall, Réale, Sol, & Reader, 2006; Réale et al., 2007; Sih et al., 2004).

A large amount of effort is currently devoted to identifying the mechanisms responsible for the maintenance of consistent behavioural variation (Dall, Houston, & McNamara, 2004; Réale et al., 2010; Wolf, Van Doorn, Leimar, & Weissing, 2007; Wolf, Van Doorn, & Weissing, 2008). A main hypothesis is that consistent behavioural variation can be maintained when the fitness benefits of expressing a certain behaviour differ consistently among individuals as a function of their state, such as their energy balance or energy allocation strategy (Houston & McNamara, 1999). For example, individuals with a negative energy balance may be consistently bolder than those with a positive energy balance (Rands, Cowlishaw, Pettifor, Rowcliffe, & Johnstone, 2008). Individuals that invest more energy into immediate reproduction than into long-term survival may also be bolder while foraging (Wolf et al., 2007). The behaviour expressed by individuals may further affect their state, leading to a feedback between behaviour and state (Dingemanse & Wolf, 2010). For example, individuals with positive energy balance may be better at dealing with predation risk and thus forage more, thereby maintaining a consistently positive energy balance (Luttbeg & Sih, 2010). Depending on the type of relationship between behaviour and state, feedback loops may either amplify or erode behavioural variation over time (Bergmüller & Taborsky, 2010; Luttbeg & Sih, 2010; Fig. 1). Determining the state variables associated with consistent individual differences in behaviour and investigating their potential feedback with behaviour is now a major area of research. There is an urgent need for more empirical work, particularly on how different state variables (e.g. age, size, energy level, residual reproductive value) interact with each other to affect individual behaviour (reviewed in Dingemanse & Wolf, 2010).

Anthropogenic contaminants (ACs), defined as products typically not found in nature and generated by human activity (e.g. heavy metals, fertilizers, pesticides, residual birth pill compounds: the British Geological Society, 2013) could be a particularly potent factor contributing to consistent behavioural variation within

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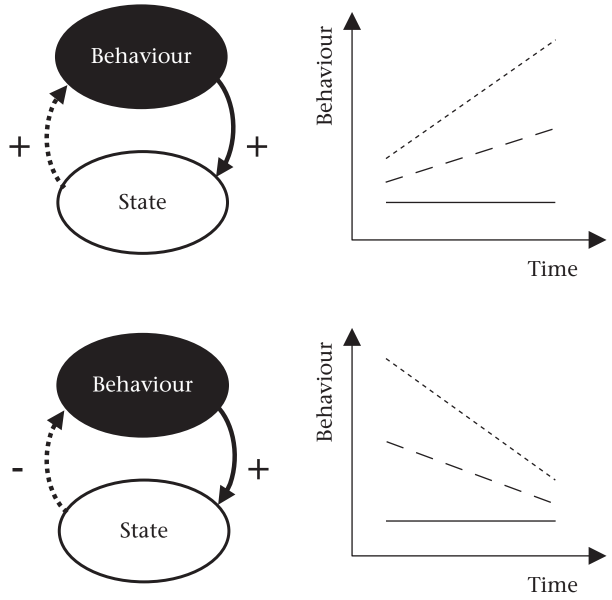

Figure 1. Examples of feedback loops between personality and anthropogenic contaminant (AC) state (left-hand diagrams) and their implication for consistent individual behavioural variation (right-hand graphs). The right-hand graphs present the behaviour of three individuals (solid, dashed and dotted lines) as a function of the time exposed to AC. Note that this axis may be continuous, or discrete (i.e. the behaviour of individuals before and after AC exposure). Upper panel: the behavioural trait value expressed by individuals may increase AC state, which may in turn increase the behavioural trait value of the individual. Such a positive feedback loop may act to exacerbate individual differences in behaviour, thereby increasing repeatability. Lower panel: the behaviour may increase the AC state of individuals, but an increased AC state may decrease the behavioural trait value expressed (e.g. through its toxicity). In such a case, the negative feedback loop will erode or eliminate individual differences in behaviour. Thus, we would expect the repeatability of this behaviour to decrease.

populations (see Bell, 2001, 2004). ACs are ubiquitous in most environments (e.g. Kolpin et al., 2002) and may directly alter the behaviour expressed by individuals (i.e. the level of exposure or contamination would act as a state, hereafter referred to as ‘AC state’; Zala & Penn, 2004). Examples of the effects of ACs on behaviour include residual psychiatric drugs present in the water increasing the boldness of fishes (Brodin, Fick, Jonsson, & Klaminder, 2013), brominated flame retardants altering male parental nest guarding (Verboven, Verreault, Letcher, Gabrielsen, & Evans, 2009), sublethal doses of pesticides altering navigation and orientation behaviours (Bortolotti et al., 2003; Colin et al., 2004), heavy metal accumulation decreasing antipredator behaviour or foraging activity (Cheung, Tai, Leung, & Siu, 2002) and exposure to pyrene affecting the probability of winning staged contests in males (Dissanayake, Galloway, & Jones, 2009).

AC state could also interact with other state variables. Hence, the behavioural shifts resulting from AC state could differ among individuals as a function of their life history strategy or energy balance (just as natural hormones do; Lancaster, Hazard, Clobert, & Sinervo, 2008). More importantly, an individual’s AC state and behaviour may feedback into each other if behaviour both determines and is affected by AC exposure and accumulation. This is likely to apply in cases where AC exposure and accumulation occur through feeding and affect the behaviours driving food acquisition. For example, individuals with a higher activity level may also incur higher encounter rates with ACs in their environment, which may further affect their activity level. Likewise, individuals with a higher voracity would be likely to consume more (potentially contaminated) prey items, which could affect further their voracity. A vast array of behaviours shown to be affected by AC exposure are associated with resource acquisition by animals (Clotfelter, Bell, & Levering, 2004), and so this first scenario is likely to be ubiquitous among animal study systems. ACs could also feedback with behaviour by affecting how much energy individuals allocate to various fitness functions such as growth, reproduction and body maintenance (i.e. ACs affect the resource allocation pattern of animals). For example, AC state could decrease the survival of animals or increase their reproductive effort (Massarin et al., 2011), which could lead them to express a more risk-prone behaviour (i.e. individuals would become bolder; Réale et al., 2010), leading to a further increase in AC state (e.g. Brodin et al., 2013). Interestingly, most behaviours currently investigated for their consistent variation among individuals within populations (i.e. so-called ‘personality traits’: Réale et al., 2007) are tightly associated with the life history strategy of individuals, regulating how resources are allocated to growth, reproduction and maintenance (Réale et al., 2010). Determining the interactions between behaviour and AC state is thus paramount to understanding how consistent variation in behaviour within animal populations is maintained and why the extent of such variation differs among study systems (Sih et al., 2004; Dingemanse & Wolf, 2010).

Since behaviour and ACs may interact through multiple pathways, we believe that investigating the relationship between behaviour and AC state requires a mechanistic approach, analysing the interactions between behaviour, AC state, resource acquisition and resource allocation patterns. Note that to be considered mechanistic, such a model need not directly analyse the proximate aspects of AC–behaviour interactions. Our objective is to provide such a conceptual framework that accounts for the interactions between ACs and consistent behavioural variation. We first discuss how ACs can act as a state variable and affect behaviour. Second, we outline how individual behaviour may mediate differences in exposure to and accumulation of ACs. Third, we suggest an experimental and mechanistic approach to study the feedbacks between ACs and behavioural variation. Finally, we present two case studies and show how the interaction between ACs and behavioural variation may be studied in these systems.

Anthropogenic Contaminants Contribute to State-dependent Behavioural Variation

Behavioural expression is sensitive to contaminants, and exposure to contaminants is increasingly regarded as a source of behavioural variation that must be taken into account (reviewed in Clotfelter et al., 2004; see also Dissanayake et al., 2009; Egea-Serrano, Tejedo, & Torralva, 2011; Henry et al., 2012). AC exposure or accumulation rates often act as state variables, affecting the expression of behaviour. For example, ethinyl oestradiol (derived from birth control pills and postmenopausal hormone replacement therapies) occurs in most freshwater streams and decreases aggressiveness of individuals (Bell, 2001). Other endocrine-disrupting chemicals also affect boldness under various risky situations (Eroschenko, Amstislavsky, Schwabel, & Ingermann, 2002; Schantz & Widholm, 2001). Nitrogenous compounds originating from farming and fossil fuel combustion decrease activity in many amphibians both during larval and adult stages (Egea-Serrano et al., 2011; Miaud, Oromí, Guerrero, Navarro, & Sanuy, 2011). By modifying particular behaviours, ACs may thus alter existing correlations between behavioural traits, or generate new ones (Brodin et al., 2013). Hence, exposure to contaminants may explain the occurrence of particular behavioural associations in the same way that exposure to predation (Bell, 2005) or parasitism does (Barber & Dingemanse, 2010).