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Pesticide-induced changes in personality depend on the urbanization level

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Globally increasing urbanization causes major anthropogenic changes in ecosystems, drastically altering phenotypes of organisms. Increased contamination is a well-known result of urbanization, and its effect on behaviour has been extensively studied. Yet, animal personality, consistent behavioural variation between individuals, has rarely been investigated in the context of anthropogenic contaminants. Changes in personalities may affect the viability of populations, and even alter community dynamics. We investigated the effects of exposure to a sublethal dose of the commonly used pesticide esfenvalerate on two personality traits, activity and boldness, and compared these effects between replicated rural and urban populations using larvae of the damselfly *Coenagrion puella*. We tested for effects on behaviour at three distinct levels: the average levels of behaviours, the consistency of behaviours (repeatability), and the structure of the behavioural correlations (behavioural syndrome). We found that the pesticide treatment changed the average activity and the behavioural covariation (activity and boldness), but not the behavioural repeatability. Importantly, these pesticide-induced patterns depended strongly on urbanization level. The average activity reduction due to pesticide exposure was only present in urban individuals. Moreover, while a behavioural correlation between activity and boldness in rural larvae appeared only after the pesticide treatment, this activity–boldness syndrome was consistently present in the urban larvae. These differential responses of urban and rural populations may be explained by the apparently more efficient coping mechanism with contaminants of urban populations, as well as the generally more stressful urban habitats. These results highlight the importance of measuring behavioural expressions at various levels when assessing contaminant effects, and not just the means. Further, we suggest that pollution may play an important role in understanding the evolution and maintenance of animal personalities in natural populations.

Urbanization is a major anthropogenic process (Seto, Guneralp, & Hutyra, 2012), causing rapid phenotypic change among a wide range of taxa (Alberti et al., 2017). One result of urbanization is an increase in contamination of aquatic habitats (e.g. Gilliom, 2007; Hayzoun et al., 2014; Wang et al., 2016), mainly driven by the increased runoff due to the impervious surface cover typically found in urban areas (Jiang et al., 2010; Paul & Meyer, 2001). Contaminants are well known to alter behaviour (Dell'Omo, 2002; Tuomainen & Candolin, 2011; Zala & Penn, 2004). Studying behavioural responses to contaminants is important, as changes in behaviours may have crucial ecological consequences (Pyle & Ford, 2017). Only recently have effects of contaminants been shown to go beyond changing mean levels of behaviours to include changing individual variation in behaviours (Montiglio & Royauté, 2014).

Personality is defined as consistent behavioural variation between individuals (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), and has been documented in diverse taxa (Wolf, van Doorn, & Weissing, 2008), including invertebrates (Kralj-Fišer & Schuett, 2014). Central to the study of personality is the concept of repeatability, the consistency of a single behaviour over time and context (Réale et al., 2007). Behavioural correlations (including those between nonpersonality traits) are referred to as behavioural syndromes (Sih, Bell, Johnson, & Ziemba, 2004), and are frequently integrated into personality literature (Réale et al., 2007). Populations of the same species have been shown to differ in terms of both repeatability and behavioural syndromes (Bell, 2007; Sih, Bell, & Johnson, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Evidence accumulates that this differentiation is linked to environmental

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conditions to which the populations are exposed (e.g. predation pressure; Dingemanse et al., 2007), including anthropogenic impacts (e.g. pesticide application; Royauté, Buddle, & Vincent, 2014). A change in personality structure is important for the viability of populations, as differentiation in personalities can affect biotic interactions (e.g. predator–prey interactions; Belgrad & Griffen, 2016; social interactions; Santostefano, Wilson, Araya-Ajoy, & Dingemanse, 2016), thereby potentially altering community dynamics (Moran, Wong, & Thompson, 2017; Start & Gilbert, 2017). Studies typically investigate contaminant effects only on repeatability (e.g. Kolok, Plaisance, & Abdelghani, 1998; White & Briffa, 2017) or only on behavioural syndromes (e.g. Brodin, Fick, Jonsson, & Klaminder, 2013; Royauté et al., 2014), but rarely consider both (but see Dzieweczynski, Campbell, & Kane, 2016; Royauté, Buddle, & Vincent, 2015).

Exposure to contaminants may alter behavioural repeatabilities in opposite ways, driven by two contrasting feedback loops (Fig. 1 in Montiglio & Royauté, 2014). On the one hand, the personality type of individuals (e.g. more active or bold personalities) may lead to an increased exposure to the contaminant, which in turn may increase the expression level of the behaviour. This positive feedback loop will cause an increase in repeatability by amplifying individual differences in behaviour. On the other hand, an increased exposure to the contaminant driven by the behavioural type may feed back negatively via the toxicity of the contaminant, decreasing the expression level of the behaviour. This would weaken individual differences in behaviour, leading to a lower repeatability. The majority of studies exploring effects of contaminants on behavioural repeatability have supported the latter prediction, i.e. a decrease in repeatability (e.g. Dzieweczynski, 2011; Dzieweczynski et al., 2016; Kolok et al., 1998; Royauté et al., 2015; but see Tosetto, Williamson, & Brown, 2017; White & Briffa, 2017). Behavioural syndromes may also be affected by contaminant exposure. Experimental manipulations have demonstrated that behavioural correlations may (dis) appear when animals are exposed to an environmental stressor (Barber & Dingemanse, 2010; Bell & Sih, 2007; Royauté et al., 2015; Snekser, Leese, Ganim, & Itzkowitz, 2009). It is suggested that certain combinations of behaviours are selected for as a result of different selection pressures (Bell, 2005; Sih, Bell A. et al., 2004; Sih et al., 2012). A frequent finding is the appearance of correlations of previously uncorrelated behaviours in stressful situations (e.g. predation pressure: Bell & Sih, 2007; contaminant exposure: Brodin et al., 2013; low-quality habitat: Snekser et al., 2009), yet the exact causes of and mechanisms influencing behavioural syndromes still remain poorly understood.

Because of its link with anthropogenic stressors, the level of urbanization has also been associated with differences in personality and behavioural syndromes. Anthropogenic disturbances such as increased temperature anomalies (e.g. Benz, Bayer, & Blum, 2017; Jones, Lister, & Li, 2008), increased pulses of pollution (e.g. Gilliom, 2007; Hayzoun et al., 2014) and altered food sources (e.g. Ditchkoff, Saalfeld, & Gibson, 2006; Murray, Edwards, Abercrombie, Cassady, & Clair, 2015) are frequently associated with urbanization. This suggests urban habitats are more unpredictable than natural rural habitats (Parris, 2016). Anthropogenic disturbances in general are expected to influence behavioural repeatabilities and syndromes (Killen, Adriaenssens, Marras, Claireaux, & Cooke, 2016; Killen, Marras, Metcalfe, McKenzie, & Domenici, 2013; Sih et al., 2012). Although lower repeatabilities (Kralj-Fišer & Schneider, 2012) and increased behavioural flexibility (Lowry, Lill, & Wong, 2013) have been suggested to be beneficial for coping with the unpredictable nature of urban habitats, the only explicit study on this found no difference between repeatabilities of rural and urban populations of the European blackbird, *Turdus merula* (Miranda, Schielzeth, Sonntag, & Partecke, 2013; but see preliminary results by Charmantier, Demeyrier, Lambrechts, Perret, & Grégoire, 2017 indicating lower repeatability in urban great tits, *Parus major*). Behavioural syndromes, on the other hand, frequently differ between rural and urban populations (Miranda et al., 2013). Most empirical evidence comes from studies with birds, and indicates weaker behavioural correlations in urban populations (Evans, Boudreau, & Hyman, 2010; Riyahi, Björklund, Mateos-Gonzalez, & Senar, 2017; Scales, Hyman, & Hughes, 2011) due to assumed weaker selection pressures in urban habitats (e.g. abundant food resources, fewer predators; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). Finally, there is ample evidence from studies on vertebrates for urbanization-related differences in mean levels of personality traits. The emerging pattern points towards higher boldness in urban individuals (Lapiedra, Chejanovski, & Kolbe, 2016; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015), assumed to be caused by the adaptation to human presence or relaxed predation pressure in urban populations (Miranda et al., 2013; Samia et al., 2015; Sih, Ferrari, & Harris, 2011; Sol, Lapiedra, & González-Lagos, 2013). Yet, it is not clear how invertebrates respond behaviourally to urbanization.

We investigated the effects of exposure to a sublethal dose of a pesticide on personality traits and their covariation, and compared these effects between rural and urban populations using damselfly larvae as study organisms. We studied activity and boldness, two commonly used fitness-related personality traits (Réale et al., 2007; Smith & Blumstein, 2008) that typically form a syndrome with more active animals being bolder (Réale et al., 2007). We tested for effects of the pesticide not only on the average levels of behaviours, but also on the consistency of the behaviours (i.e. repeatability) and the behavioural correlations (i.e. behavioural syndrome). We used replicated rural and urban populations of the damselfly *Coenagrion puella* (abundant in ponds in both rural and urban areas; Goertzen & Suhling, 2013), which shows local adaptation to urban ponds in its behavioural response to pesticides (Tüzün, Debecker, Op de Beeck, & Stoks, 2015). We further tested whether a pesticide-induced change in the different levels of the behaviour (i.e. average, repeatability and behavioural syndrome) predictably depends on the level of urbanization of the populations. As aquatic insects are not expected to habituate to humans, and predation pressure does not differ between the rural and urban ponds studied in this experiment (Tüzün, Op de Beeck, Brans, Janssens, & Stoks, 2017), we did not predict any distinct differentiation in mean levels of behavioural traits between rural and urban damselfly larvae. Instead, we predicted that individuals inhabiting urban areas would show a lower behavioural consistency, i.e. lower repeatabilities, as this is expected to help populations cope with the unpredictable nature of urbanized habitats (Kralj-Fišer & Schneider, 2012). As weaker selection pressures have been shown to relax behavioural correlations (e.g. Bell & Sih, 2007; Scales et al., 2011), we predicted more stable correlations across contexts (i.e. from pre-exposure to postpesticide exposure periods) in population inhabiting the more stressful urban areas. As for the effects of the pesticide, we predicted a decrease in repeatability after pesticide exposure due to the suggested negative feedback between behaviour and contaminant exposure (Montiglio & Royauté, 2014), stronger behavioural correlations due to the imposed stressful conditions (as in Brodin et al., 2013), and a decrease in mean levels of behaviours (Dinh Van et al., 2016).

METHODS

Study Species and Populations

Coenagrion puella is one of the commonest damselflies in Europe (Dijkstra & Lewington, 2006). Adult *C. puella* reproduce in early