



## Social conformity in solitary crabs, *Carcinus maenas*, is driven by individual differences in behavioural plasticity

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Group living is widespread in the animal kingdom and recent studies into the mechanisms underlying group cohesion and behavioural synchrony have highlighted the importance of between-individual behavioural differences ('animal personality'). In group-living animals, social conformity occurs when animals compromise their own behaviour to the level of a certain behaviour displayed by another individual or a group, and the degree to which individuals conform can depend upon interindividual differences in behavioural types. Social conformity can increase group cohesion and ultimately predator avoidance and/or resource acquisition for group-living individuals. However, it remains unclear whether similar conformity effects exist in solitary species, many of which form temporary aggregations and, if so, whether changes in behaviour in the presence of conspecifics are dependent on individuals' personalities in solitary contexts. We studied the effects of social context (i.e. the presence of a conspecific) on behaviour in solitary shore crabs, using automated video tracking. Individuals differed consistently in their activity levels within and across contexts and were significantly more active in solitary than dyadic contexts. No differences in activity between same- and opposite-sex dyads were found. Crabs' activity levels were more similar when tested together than when tested alone, indicating a social conformity effect. Furthermore, more active behavioural types decreased their activity to a greater extent when paired with a conspecific. The sex composition of the dyad had no effect on changes in activity. Overall, our findings suggest that social conformity is moderated by individual behavioural differences in a solitary organism. It is often presumed that, over evolutionary time, the social structure of animal populations has important consequences for the evolution of personalities and vice versa. We suggest that studying solitary or facultatively social organisms may allow researchers to tease out causality between personality differences and socioecological dynamics.

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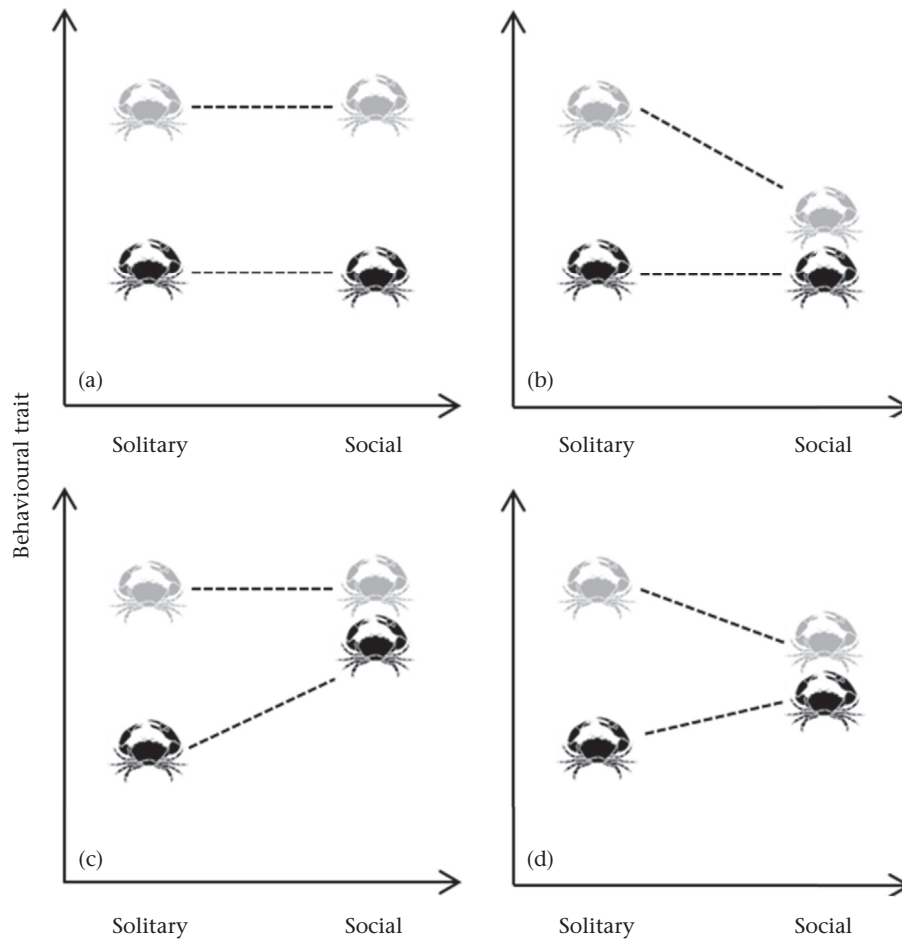
Group living is widespread in the animal kingdom and is associated with costs and benefits which, in turn, drive patterns of grouping and with whom individuals associate (King & Fürtbauer, *in press*; Krause & Ruxton, 2002; Ward & Webster, 2016). In recent years, personality variation (i.e. individual differences or heterogeneity in behaviour that are consistent over time and/or contexts; see e.g. Dall, Bell, Bolnick, Ratnieks, & Sih, 2012; Réale et al., 2010; Sih, Bell, & Johnson, 2004) has received increasing attention by those studying social behaviour because of its potential to shape the structure and function of animal groups (reviewed by e.g. Farine, Montiglio, & Spiegel, 2015; Wolf & Krause, 2014). While heterogeneity in social groups can be adaptive (e.g.

leader–follower dynamics in gregarious animals; Johnstone & Manica, 2011; Nakayama, Harcourt, Johnstone, & Manica, 2012) more broadly, the need for social animals to maintain group cohesion can result in the suppression of individual differences in personality, resulting in 'social conformity' (reviewed by Webster & Ward, 2011). That is, individuals may converge on a common rate of behavioural expression (they become more synchronous), and personality differences observed in isolation may become less pronounced or disappear in a social setting (e.g. Herbert-Read et al., 2013; reviewed by Webster & Ward, 2011; Fig. 1).

Individuals with different behavioural phenotypes can achieve conformity by 'meeting in the middle' (Fig. 1d) or by shifting their behaviour towards the most or least responsive individuals within a group or population (Fig. 1b and c). This type of social conformity means that some individuals will 'alter' their behaviour more than others (reviewed by Webster & Ward, 2011). In other words, behavioural plasticity might be dependent on (or constrained by)

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**Figure 1.** The effect of conspecific presence on individuals' behaviour, for behavioural traits that are consistently expressed (i.e. 'personality'). (a) No effect of social context on individual responses (absence of 'plasticity'). (b) More responsive individuals change their behaviour to a greater extent when in a social context. (c) Less responsive individuals change their behaviour to a greater extent when in a social context. (d) Individuals converge at the average response (they 'meet in the middle'). Note that the list of scenarios presented here is not exhaustive and that personality differences may be either maintained or suppressed in scenarios b–d.

individual personalities (e.g. Guayasamin, Couzin, & Miller, 2017; Magnhagen & Bunnefeld, 2009; Fig. 1).

Social conformity effects and associated influences of personality expressed in isolation have been reported in many social species, including vertebrates and invertebrates (e.g. Dussutour, Nicolis, Despland, & Simpson, 2008; Herbert-Read et al., 2013; King, Williams, & Mettke-Hofmann, 2015; Koski & Burkart, 2015; Magnhagen & Bunnefeld, 2009; McDonald, Rands, Hill, Elder, & Ioannou, 2016; Schuett & Dall, 2009; Webster, Ward, & Hart, 2007; reviewed by Webster & Ward, 2011), and may be beneficial for predator avoidance, resource acquisition or facilitation of mating (reviewed by Krause & Ruxton, 2002). In perch, *Perca fluviatilis*, for instance, individuals are bolder when in a group than when tested in isolation, with bolder fish exhibiting the smallest change in behaviour and 'conforming' to a lesser extent (Magnhagen & Bunnefeld, 2009; see Fig. 1c). Sticklebacks, *Gasterosteus aculeatus*, are more active and resume foraging more rapidly following a simulated predator attack when tested in groups than when tested alone (Webster et al., 2007), and their individual personality is 'suppressed' when making consensus decisions about foraging (McDonald et al., 2016). Nutmeg mannikins, *Lonchura punctulata*, in contrast, exhibit consistent between-individual differences in behaviour irrespective of group size (Rieucau, Morand-Ferron, & Giraldeau, 2010).

In addition to sociality, group composition and the behavioural type of social partners can also affect conformity (e.g. Dussutour et al., 2008; King et al., 2015; Schuett & Dall, 2009; reviewed by

Webster & Ward, 2011). For example, colonies of social caterpillars, *Malacosoma disstria*, are less cohesive when comprising a majority of active (as opposed to inactive) behavioural types (Dussutour et al., 2008). In Gouldian finches, *Erythrura gouldiae*, shy birds take more risks when paired with a bolder conspecific, and bold birds take fewer risks when paired with a shyer conspecific (King et al., 2015). Similarly, in zebra finches, *Taeniopygia guttata*, individuals are more exploratory when paired with a more exploratory conspecific (Schuett & Dall, 2009). Furthermore, in numerous species, conformity is more pronounced between members of the same sex, due to different activity budgets and motivation in males and females ('sexual segregation'; for reviews see e.g. Rockstuhl & Neuhaus, 2006; Wearmouth & Sims, 2008).

Generally, when researchers investigate the effects of social conformity, they tend to use a group-living species, and observe behaviour for individuals (1) in isolation and (2) in pairs/groups (see above). The inference is that the behaviour when solitary (personality) is 'altered' by the presence of others. This approach offers much insight but, in our opinion, may be problematic since the 'normal' state for group-living individuals is to be with others; the unusual situation is to be alone. We would thus argue that social conformity effects (in group-living species) may be better understood as responses to the removal of others, that is, a reaction to being a singleton. In contrast, one could study the effect of conspecific presence (not absence) in solitary species which only form temporary aggregations at resources or during mating.

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