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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.

Key-words: behavioural synchrony, *Carcinus maenas*, crustaceans, personality, plasticity, social environment

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 (Krause and Ruxton, 2002; Ward and Webster, 2016; King and Fürtbauer, in press). In recent years, personality variation (i.e. individual differences or heterogeneity in behaviour that are consistent over time and/or contexts; see e.g. Sih, Bell & Johnson, 2004; Réale et al., 2010; Dall et al., 2012) 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 and Krause, 2014). While heterogeneity in social groups can be adaptive (e.g. leader–follower dynamics in gregarious animals; Johnstone and Manica, 2011; Nakayama et al., 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 and 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 and 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, c). This type of social conformity means that some individuals will 'alter' their behaviour more than others (reviewed by Webster and Ward, 2011). In other words, behavioural plasticity might be dependent on (or constrained by) individual personalities (e.g. Guayasamin, Couzin, & Miller, 2017; Magnhagen and 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. Webster, Ward, & Hart, 2007; Dussutour et al., 2008; Magnhagen and Bunnefeld, 2009; Schuett and Dall, 2009; Herbert-Read et al., 2013; King, Williams, & Mettke-Hofmann 2015; Koski and Burkart 2015; McDonald et al. 2016; reviewed by Webster & Ward, 2011), and may be beneficial for predator avoidance, resource acquisition or facilitation of mating (reviewed by Krause and 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 and 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, Ward, & Hart, 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; Schuett and Dall, 2009; King, Williams, & Mettke-Hofmann, 2015; reviewed by Webster and 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, Williams, & Mettke-Hofmann, 2015). Similarly, in zebra finches, *Taeniopygia guttata*, individuals are more exploratory when paired with a more exploratory conspecific (Schuett and 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 and Neuhaus, 2006; Wearmouth and 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.

Similar to group-living species, environmental stimuli, such as resources and/or predators, may drive aggregation in solitary species (see e.g. Camazine et al., 2001). The proximate mechanisms underlying such aggregations are understudied but are believed to arise 'simply' through behavioural synchronization (e.g. Camazine et al., 2001; Sumpter, 2006); yet, how exactly this occurs is unclear. We hypothesized that individual differences in behavioural plasticity (see above and Fig. 1) might also be important in driving synchronized behaviour in nonsocial species.

We investigated potential social conformity effects in marine shore crabs. While social structure can be experimentally induced in shore crabs via manipulation of food resources (whereby individuals modify their competitive behaviours) they are considered a solitary species (Tanner and Jackson, 2012). However, it is plausible that individual differences in behaviour in a solitary context, which have recently been described for this species (Fürtbauer, 2015), could moderate social interactions and emergent group dynamics. We therefore investigated crab behaviour in a resource-free, homogeneous environment. Since personality differences have been described in this species (and study population; Fürtbauer, 2015), we expected that shore crabs would exhibit consistent individual variation in activity when tested alone. We then tested the hypothesis that the presence of conspecifics might affect individual behavioural responses (the 'conformity hypothesis'; Fig. 1b, c, d). Alternatively, while individuals may interact, their behavioural responses may remain unchanged (Fig. 1a). We also considered potential effects of sexual segregation whereby same-sex individuals are more likely to be similar in their behaviour

(e.g. Rockstuhl and Neuhaus, 2006; Wearmouth and Sims, 2008), by pairing individuals with same- and opposite-sex partners, respectively.

Methods

Subjects and housing

Shore crabs (N=60) were collected from Swansea docks and transferred to the laboratory in July 2015. The crabs were sexed (N=30 males, N=30 females) according to the shape of their abdomen (Crothers, 1976). Carapace width (47.5±4.7 mm) and length (36.5±2.9 mm) were measured using digital callipers to allow size matching of individuals (see below). Individuals were tagged for individual identification using coloured cable wires on different legs and body sides (left versus right). All crabs were housed together in a plastic tank (122 x 61 x 26 cm), supplied with aerated flowing sea water (10 cm depth) and concrete tunnels and bricks for enrichment and shelter. The temperature was kept constant at 13 °C throughout the data collection period. The crabs were fed mackerel every 3 days. All procedures described were conducted in accordance with the ASAB/ABS Guidelines for the use of animals and were approved by Swansea University's Ethics Committee (IP-1314-4).

Behavioural trials

The crabs were tested repeatedly alone (solitary context) and with a partner (dyadic context). Behavioural trials were conducted in a circular test tank (80 cm in diameter) filled with white gravel and 3 cm of sea water (Fig. 2). Behaviour in a solitary context was

assessed by placing individual crabs into the test tank containing a shelter (a black plastic half pipe under which they were placed at the start of the trial) in the centre, and filming each individual for 10 min. A second trial was conducted a week after the first to assess repeatability in behaviour. The order in which crabs were tested was random in both trials. To assess behaviour in a dyadic context, individuals that had not lost any limbs following experiments in a solitary context were assigned to size-matched same-sex (total $N=27$; $N=14$ female–female, $N=13$ male–male) and opposite-sex dyads ($N=20$). As for the solitary context, all dyads were tested twice, 5 days apart, to assess repeatability in behaviour (the order in which dyads were tested was randomized in the two trials). We first tested same-sex dyads, starting 3 days after the second solitary context trial, followed by opposite-sex dyads. Each dyad was placed into the same test tank as used in the solitary context, without the shelter in the centre to provide a resource-free environment (Fig. 2). Individual crabs were initially placed under a plastic basket at opposite ends of the test tank for 2 min to acclimatize. After the baskets were removed the crabs were filmed for 10 min. To rule out potential order effects (e.g. habituation) on crab activity, a subset of crabs ($N=25$) was again tested in a solitary context following the experiments with dyads (see Appendix 1).

Video analysis and behavioural measures

The behavioural trials were filmed with a Panasonic HDC-SD60 video camera. Using ID tracker software, which allows individual identification of several individuals throughout tracking (Perez-Escudero et al., 2014), x,y coordinates of crab movements were extracted. From these coordinates crab activity levels, measured as the total distance travelled (m)

during 10 min, were calculated. Body contact duration (s) was also calculated from observation of videos.

Data analysis

Repeatability in activity levels within solitary and dyadic contexts was assessed using Spearman rank correlations. To investigate activity patterns across solitary and dyadic contexts, we used three linear mixed models (LMMs) in R (R Development Core Team, 2010) and the functions lmer in the lmertest package (Bates et al., 2015). Where necessary, data were transformed (log, square root) to meet model assumptions, prior to analysis (Sokal and Rohlf, 2012). First, to compare crab activity across solitary and dyadic contexts, we fitted a model with total distance travelled as our response variable, and context as a categorical fixed effect (LMM1). Crab ID was included as a random effect. Second, to test whether dyad partners behaved more similarly when tested together than when tested alone, we first calculated the dyad difference in total distance travelled (distance crab$_i$ – distance crab$_j$) within solitary and dyadic contexts, and then fitted an LMM with the dyad difference as the response variable and context as a categorical fixed effect (LMM2). 'Dyad' was included as a random intercept and 'context' as a random slope. Third, we tested whether average activity in a solitary context predicted the change in behaviour between solitary and dyadic contexts (LMM3). For this we calculated the difference between the average distance travelled in a solitary context and the distance travelled in a dyadic context ('change in activity'= distance solitary – distance dyadic; see e.g. Sih, Bell, & Johnson, 2004) which we fitted as the response variable. The average distance travelled in a solitary context ('personality') was included as a continuous fixed effect while controlling for time spent in

body contact (to account for changes in activity due to social interactions, e.g. aggression), sex and sex of the dyad partner. 'ID' and 'Dyad' were included as random effects. Model assumptions were checked using graphical procedures (Q–Q plot and standardized residuals versus fitted values). For all analyses, the level of significance was set at $P < 0.05$.

Results

Crab activity within and across contexts

Individual crab activity was consistent across the two trials when solitary (r_S=0.419, N=59, P=0.001) and when in a dyad (r_S=0.341, N=40, P=0.031).

Crabs were significantly less active (travelled less far) in dyadic than solitary contexts (LMM1: estimate±SE=-1.83±0.17, t=-10.76, P<0.001; N=283 observations, N=60 individuals; Fig. 3) and data on a subset of crabs tested again in a solitary context following the experiments with dyads revealed comparable results, ruling out a habituation effect (see Appendix 1). No significant difference in activity levels was found between same- and opposite-sex social contexts (see Appendix 2). A significant effect of individual was found, indicating that individuals differed significantly in their activity across solitary and dyadic contexts (LMM1: random effect 'ID': P<0.001).

Social conformity in activity levels

The difference in activity (i.e. total distance travelled) within dyads was, on average, smaller in a dyadic context than when tested alone (in other words, crabs were more similar when tested together; Fig. 4a, b), indicating a social conformity effect (LMM2: estimate±SE= -

0.65±0.23, *t*=-2.82, *P*=0.007, *N*=174 observations, *N*=47 dyads; Fig. 4c). Furthermore, we found that more active individuals reduced their activity to a greater extent than less active individuals (LMM3: estimate±SE= -0.01±0.002, *t*=-6.86, *P*<0.001, *N*=164 observations, *N*=53 ID, *N*=47 dyads; Fig. 5), controlling for time spent in body contact (LMM3: estimate±SE=-0.01±0.003, *t*=-2.35, *P*=0.02), sex (LMM3: estimate±SE=0.03±0.04, *t*=0.76, *P*=0.452) and sex of the dyad partner (LMM3: estimate±SE=0.03±0.03, *t*=1.16, *P*=0.249).

Discussion

Individual variation in behavioural traits and activity patterns can generate variation in the abundance and spatiotemporal distribution of individuals in the environment. This in turn can impact upon group and community dynamics (e.g. Krause, James, & Croft, 2010). To this end, much research has focused on group-living species and the importance of individual behavioural differences for group function and cohesion (Farine, Montiglio, & Spiegel, 2015; Wolf and Krause, 2014; Biro, Sasaki, & Portugal 2016). The aim of the present study was to adopt this framework and to investigate the potential for social conformity (for a review see Webster and Ward, 2011) in a solitary species, as a hypothesized mechanism of behavioural synchrony (and potentially aggregation).

We found repeatability in individual activity levels (i.e. total distance travelled) for individuals tested alone and in dyads, supporting recent work on shore crabs showing they are repeatable in their levels of exploration, immobility and hiding ('shyness') (Fürtbauer, 2015). Despite the presence of repeatable individual differences, individuals' activity did become more similar (or 'conformed') when paired with a conspecific (see Fig. 4). In fact, individuals were roughly half as active when paired with a conspecific as when tested alone

(see Fig. 3). Analysis of data on a subset of crabs that were tested again in a solitary context following the trials with dyads suggests that this finding represents a true social partner effect, and cannot be attributed to any habituation effects. Note that the absence of a shelter in the dyadic context (to provide a resource-free environment) is also unlikely to be the cause of, or contribute to, the difference in activity levels since one would expect individuals to be less (not more) active when a shelter is present (see Fig. 3; activity and shelter use are negatively correlated in our study population, Fürtbauer, 2015). Therefore, our experiment provides strong evidence that those changes in activity levels we observed are due to the presence of a social partner and not a consequence of environmental heterogeneity (see Tanner and Jackson, 2012). Similarity in activity could, in theory, also occur if the crabs actively avoided each other, i.e. if they maintained the largest possible distance between them. This alternative hypothesis, however, can be ruled out given that the average distance between dyad partners was much lower than the diameter of the test tank (trial 1: mean±SD: 27.7±11.5 cm; trial 2: mean±SD: 34.3±11.2 cm; tank diameter= 80 cm), indicating a certain level of attraction rather than avoidance.

For individuals to accrue the benefits associated with sociality they need to remain cohesive and exhibit some level of collective (synchronized) behaviour (e.g. Sumpter, 2006; Sumpter, 2010; King and Fürtbauer, in press). Recently, researchers have focused upon the importance of individual differences for maintaining the structure and enhancing the functioning of such groups (e.g. Farine, Montiglio, & Spiegel, 2015; Krause and Ruxton, 2002; Modlmeier et al., 2014). As hypothesized, our study suggests a role of personality in behavioural synchronization also in solitary species. Interestingly, in contrast to previous studies where less exploratory individuals often showed more plastic responses to their social environment (e.g. Guayasamin, Couzin, & Miller, 2017; Magnhagen and Bunnefeld,

2009; King, Williams, & Mettke-Hofmann, 2015), we found that more active (and, hence, presumably more exploratory, see e.g. Hoset et al., 2010; also see Réale et al., 2010) behavioural types showed greater behavioural flexibility in the presence of a conspecific (see Figs 1 and 5; also see Tanner and Jackson, 2012).

Given that previous work exploring the effect of social context on personality has almost exclusively focused on group-living species, we speculate that the differences we found in responsiveness of different behavioural types may be explained by differences in social motivation and responsiveness between solitary and group-living species. Group-living species actively seek out conspecifics and often increase activity and exploration in groups, for example perch are shyer and sticklebacks less active when tested alone than when tested in a group (Webster, Ward, & Hart, 2007; Magnhagen and Bunnefeld, 2009), and such effects are often interpreted as a consequence of reduced perception of risk (see e.g. Ferrari, Sih, & Chivers, 2009; Ward, 2012). In contrast, the reduction in activity observed in the dyadic context for our crabs may represent a different mechanism, one that potentially promotes aggregation but does not appear to be driven by social contact per se, given that we controlled for this in our analyses.

From an ultimate perspective, mechanisms that promote aggregation (and therefore potential for dilution of predation risk) and allow the use of public information (Krause and Ruxton, 2002; King and Fürtbauer, in press) could be adaptive, even in solitary species. Our experimental design does not allow us to speculate further on the idea that conformity facilitates aggregation which, in turn, may provide social information benefits. We deliberately chose to test crabs in a resource- and predator-free environment since both could induce conformity, and tested dyads of crabs so that we could observe the directionality of any conformity effects. Therefore, future work should explore conformity

effects in larger group sizes and using simulated predator attacks (see e.g. Webster, Ward, & Hart, 2007; Fürtbauer et al., 2015), and test the idea that conformity increases information transfer and appropriate responses to external threats (see e.g. Day et al., 2001; Kendal, Coolen, & Laland, 2004).

Overall, behavioural synchronization in dyads of crabs appears to be driven by greater behavioural plasticity in crabs with more active personalities. This conformity effect is comparable to those found in gregarious species (e.g. Koski and Burkart, 2015; reviewed by Webster and Ward, 2011) and thus may have important implications for understanding the evolution of personality variation and sociality. It is often presumed that, over evolutionary time, the social structure of animal populations has consequences for the evolution of personalities, and vice versa (Wolf and Krause, 2014). Our study suggests that understudied solitary species, like the shore crab, that exhibit consistent individual differences in behaviour and behavioural plasticity may allow researchers to tease out causality between personality differences and socioecological dynamics.

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Appendix 1: Additional data for crab activity

Crab activity was recorded in solitary and dyadic contexts. Data are presented here for a subset of crabs that were tested again in a solitary context after the experiments with dyads.

To rule out any order effects (e.g. habituation) on crab activity levels, we tested a subset of crabs (N=25) again in a solitary context (trials 3 and 4) following completion of the main experiments. Trial 3 took place a week after testing crabs in a dyadic context and trial 4 was conducted 1 month later. The results are comparable to our results with crabs showing lower activity in a dyadic than a solitary context, indicating that the order of our experiments did not affect crab activity (estimate±SE=-8.23±1.83, t=-4.49, P<0.001; N=213 observations, N=54 individuals; Fig. A1).

Appendix 2: Activity levels in same- and opposite-sex contexts.

No significant difference in activity levels was found between same- and opposite-sex dyadic contexts (estimate±SE=0.14±0.23, t=0.62, P=0.538; N=164 observations, N=53 individuals; Fig. A2).
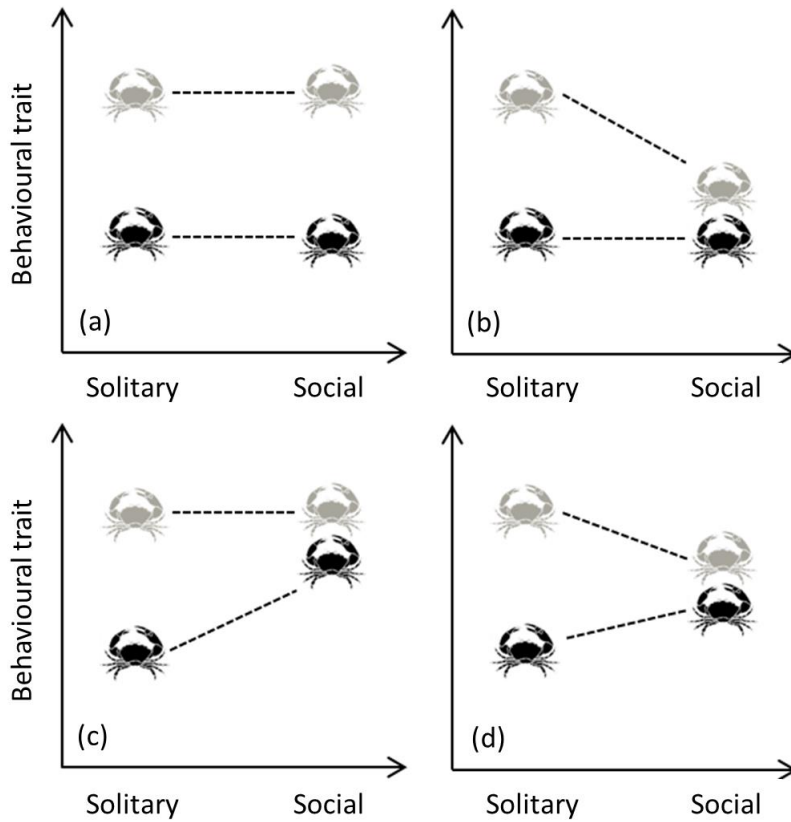
Figures:

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.

Solitary context

Dyadic context
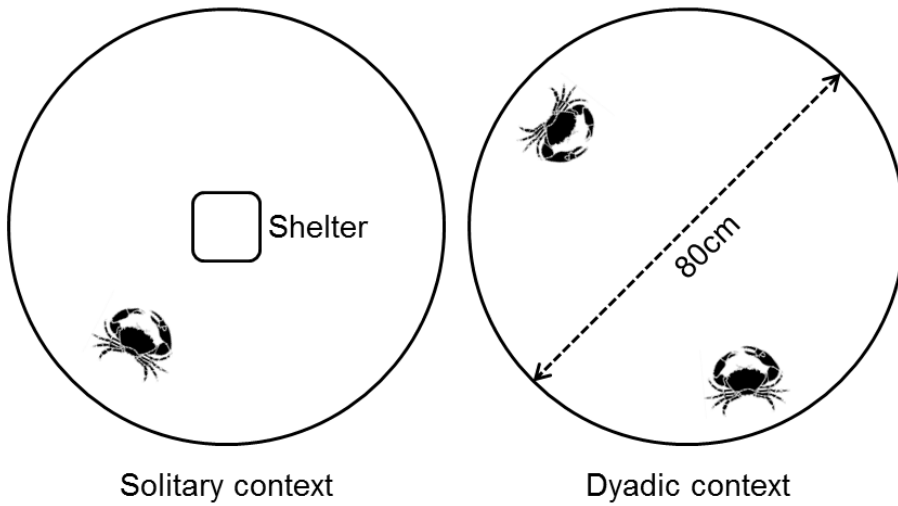
Figure 2: Experimental set-up. Behavioural trials were carried out in a circular test tank (80 cm diameter) lined with white gravel and filled with sea water up to 3 cm.
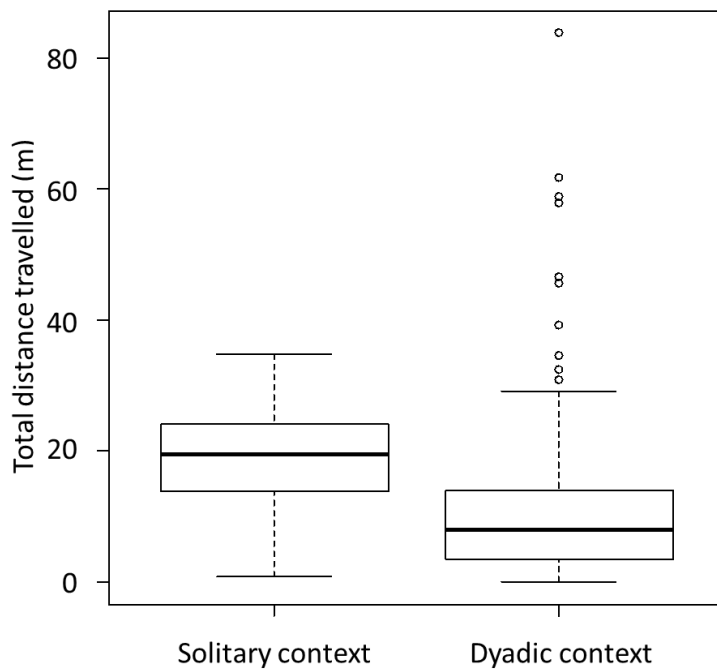

Figure 3: Shore crab (N=60) activity (i.e. total distance travelled) in solitary and dyadic contexts. The solid black line represents the median, boxes represent the upper and lower quartiles, whiskers represent 1.5 × the interquartile range and dots represent outliers.
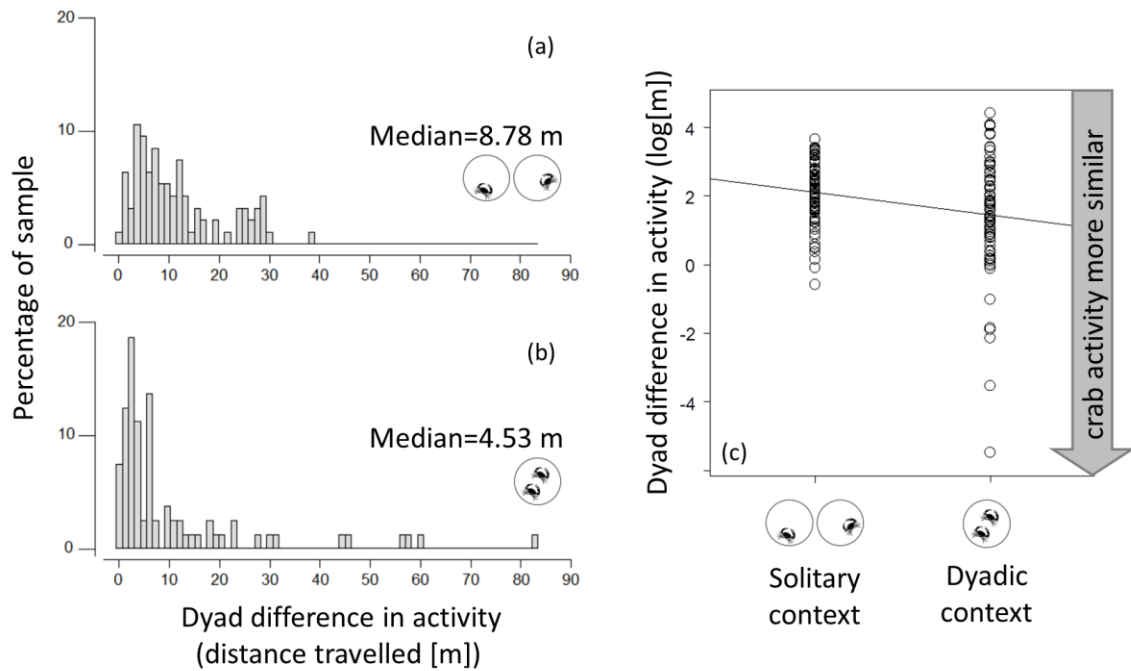
Figure 4: Dyad difference in shore crab activity (i.e. distance travelled) when tested alone (solitary context) and together (dyadic context). (a) Histogram (percentage of sample) showing the difference in crab activity when tested in a solitary context. (b) Histogram (percentage of sample) showing the difference in crab activity when tested in a dyadic context. (c) Dyad difference in activity (log[m]) within solitary and dyadic contexts, with the line representing the effect size as estimated by LMM2.
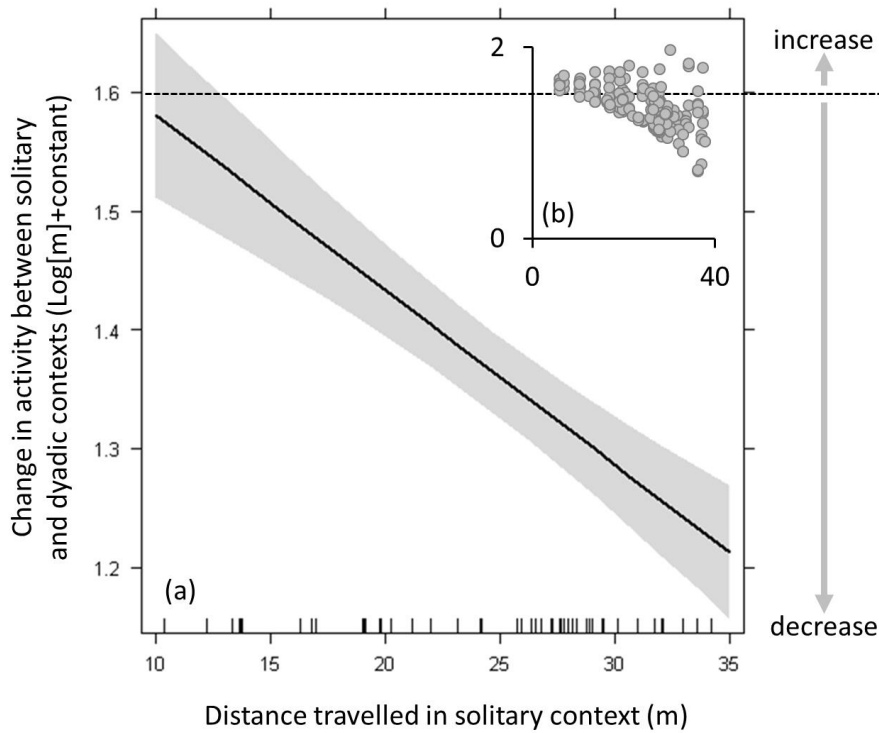
Figure 5: Relationship between average activity (i.e. total distance travelled) in a solitary context ('personality') and the change in activity between solitary and dyadic contexts. The predicted effect (solid line) and upper and lower 95% confidence limits (shaded area) from LMM3 are shown (tick marks represent the distribution of data points on the x-axis). The inset shows the actual data. The dotted horizontal line represents zero change in activity between solitary and dyadic contexts; below this line represents a decrease in activity, meaning that crabs in the bottom right of the figure (most active personalities) reduced their activity the most.
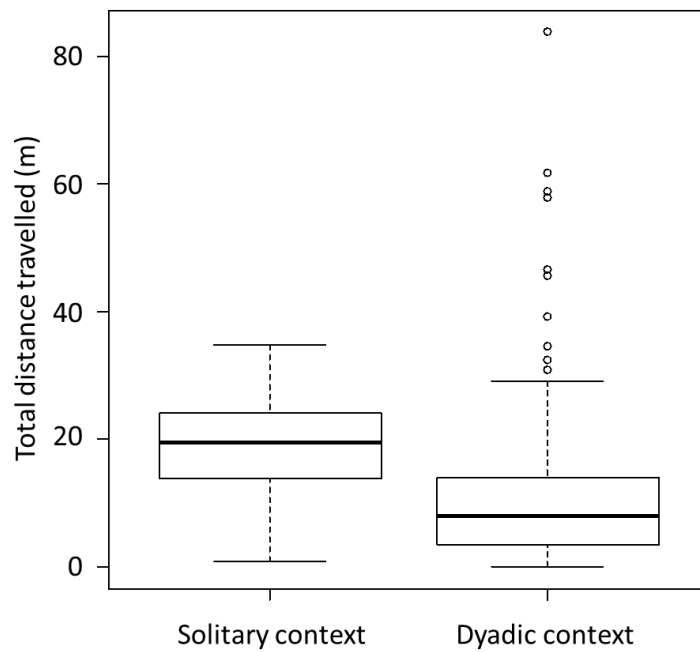
Figure A1: Shore crab activity (i.e. total distance travelled) in solitary and dyadic contexts. Data are shown for a subset of (*N*=25) crabs that were tested in a solitary context after the main experiments. The solid black line represents the median, boxes represent the upper and lower quartiles, whiskers represent 1.5 × the interquartile range and dots represent outliers.
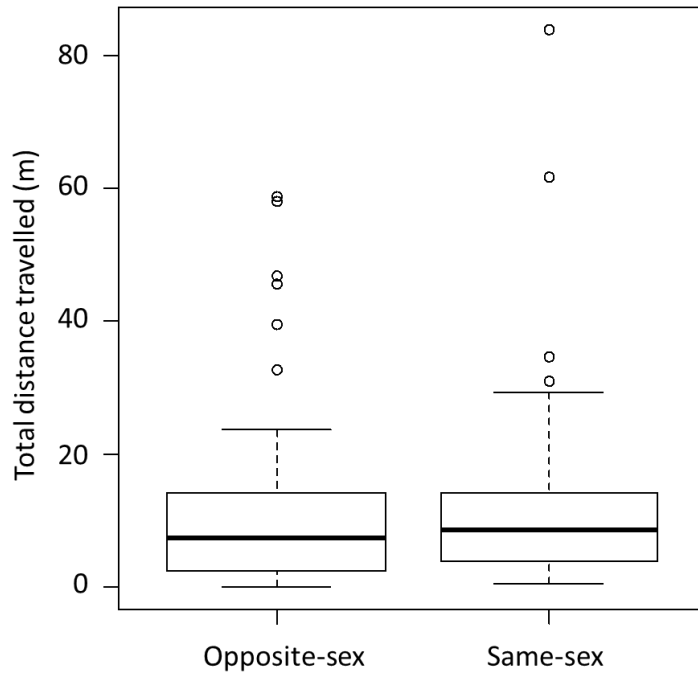
Figure A2: Difference in shore crab activity levels across solitary and opposite-sex and same-sex dyadic contexts. The solid black line represents the median, boxes represent the upper and lower quartiles, whiskers represent 1.5 × the interquartile range and dots represent outliers.