

Research article

Group size and individual 'personality' influence emergence times in hermit crabs

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Many animals benefit from aggregating due to the anti-predator effects associated with living in groups. Hermit crabs are known to form groups, or 'clusters', which may occur at sites of high shell availability. Clustering may also have anti-predator benefits, if individuals in larger clusters are able to spend less time engaging in defensive behaviours such as hiding in their shells. Here, we test the hypothesis that crabs in larger clusters will emerge faster from their shells after an elicited startle response in the European hermit crab (*Pagurus bernhardus*). We found that individuals were generally consistent in their emergence times across group sizes (displaying 'personality' in relation to emergence time), but that group size influenced emergence time in *P. bernhardus*. In contrast to the hypothesis, crabs in larger clusters had longer emergence times relative to their own emergence times in smaller clusters. Suggested explanations for this effect include intra-specific competition for the gastropod shells that hermit crabs inhabit, as well as the possible release of chemical cues by crabs in larger clusters.

Key words: hermit crabs, emergence time, personality, group size, behavioural consistency, *Pagurus bernhardus*

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Introduction

Group-living has been observed across a broad range of animal taxa (Krause and Ruxton, 2002), and group size in particular has a major influence on the outcome of predator-prey interactions, allowing group-living animals to manage their vulnerability to predation risk (Cresswell and Quinn, 2011). The major costs associated with group-living, such as higher rate of attack from predators due to increased conspicuousness, may be offset by anti-predator mechanisms (Uetz *et al.*, 2002). These mechanisms include the dilution of individual risk (Foster and Treherne, 1981), the confusion of predators, reducing attack success (Miller, 1922; Krakauer, 1995), encounter-dilution (Turner and Pitcher, 1986) and selfish herd effects (Hamilton, 1971). Grouping individuals also benefit from collective vigilance, with those in larger groups able to reduce time spent scanning and increase time engaging

in other activities (Pulliam, 1973; Cresswell and Quinn, 2011), which can also allow for cooperative warning, escape and defence behaviour (Krause and Ruxton, 2002). However, as group size increases, individuals may also be subjected to increased competition for resources, which could be a limiting factor in group size regulation (Grand and Dill, 1999).

'Clustering' has been identified as a behavioural strategy in several hermit crab (superfamily Paguroidea) species, (Taylor, 1981; Gherardi and Vannini, 1989). Hermit crabs aggregate at sites of gastropod mortality, possibly to engage in 'vacancy chain' behaviour; the sequential distribution of the acquired gastropod shells that hermit crabs inhabit (Lewis and Rotjan, 2009). When a hermit crab vacates its shell in order to occupy a more suitable one, other crabs have been observed 'lining up' in order to vacate their own shells in favour of a newly available one (De Waal, 2005). In *P. bernhardus*, the structure of these vacancy chains differs in the presence and absence of

predation risk (Briffa and Austin, 2009), but it is not known whether the size of a cluster affects predation risk. Hermit crabs in the genus *Pagurus* do exhibit alarm responses when exposed to the chemical cue of a crushed conspecific (Rittschof *et al.*, 1992), and therefore clustering may serve an anti-predator function, with individuals benefiting from dilution or detection effects. However, larger clusters may also carry increased risk of competition for shells from conspecifics.

Hermit crabs employ two major defences when exposed to potential predation: fleeing and refuging within their acquired gastropod shells (Scarratt and Godin, 1992). If, on detecting a predator, a crab decides to hide within the shell, then there is an associated second decision that determines the length of time wherein the crab will remain hidden before emerging once again (Briffa and Twyman, 2011). This decision to emerge is sensitive to the perceived risk of predation (Scarratt and Godin, 1992). For example, the presence of chemical cues in the form of effluent from the predatory rock crab, *Cancer productus*, has been shown to significantly reduce emergence times in hermit crabs; whereas exposure to effluent from the herbivorous kelp crab, *Pugettia productus*, showed no difference from a saltwater control (Rosen, Schwarz and Palmer, 2009). Withdrawal into a shell is also a response to competition: individuals are able to defend themselves from competitors in shell fights by retreating into their shells to avoid being forcibly removed (Courtene-Jones and Briffa, 2014), and thus the decision to emerge may also be sensitive to the risk of competition. Emergence from a startle is also consistent across individuals, with some showing consistently longer recovery times, while others show consistently shorter times (Briffa, Rundle and Fryer, 2008; Briffa and Twyman, 2011; Briffa, Bridger and Biro, 2013; Briffa, 2013).

Rather than responding optimally across every situation (behavioural plasticity), some individuals are constrained by consistent differences in behaviour over time or across contexts (sometimes known as ‘animal personality’; Mathot and Dingemans, 2014). Startle responses may therefore be consistent between individuals, forming a component of a ‘behavioural syndrome’; which occurs when behaviours are correlated across multiple behavioural categories (Jandt *et al.*, 2014). One behaviour which is often reported as consistent is the ‘shyness-boldness’ axis, allowing for the classification of individuals as somewhere between ‘shy’ or ‘bold’ (Wilson *et al.*, 1994). A bold individual would emerge rapidly from a startle stimulus, while a shy would not (Briffa, Rundle and Fryer, 2008), and in *P. bernhardus* is correlated with each individual’s willingness to engage in ‘risky’ behaviour (Gherardi, Aquiloni and Tricarico, 2012). Behaviour however is also plastic in response to environmental conditions, and individuals can adapt their behaviour to the environment (Pigliucci, 2001). In *P. bernhardus*, this plasticity is exceeded by individual consistency in boldness in response to high- and low-predation risk scenarios (Briffa, Rundle and Fryer, 2008). These between-individual differences over an environmental gradient (context) are termed ‘behavioural reaction norms’ (Briffa, Bridger and Biro, 2013).

This study investigates whether *P. bernhardus* exhibits reaction norm variation across individuals when exposed to different degrees of clustering (i.e. different group sizes). By analyzing the variation in startle responses exhibited by individual hermit crabs across several classes of group size, this study explores whether emergence time is influenced by clustering in *P. bernhardus*. If cluster size in this species is influenced by both the anti-predator benefits and competition-associated costs of group-living, we expect to find a significant effect of group size on emergence time. If this species forms clusters as a response to predation risk, or gains anti-predator benefits from clustering, individuals are predicted to register shorter emergence times in larger groups (where individual risk is lower) relative to their emergence times in smaller groups (where individual risk is higher). Alternatively, if clustering carries increased risk of competition, we might expect individuals in larger groups to remain in their shells for longer periods, to reduce the risk of engaging in shell fights. Additionally, we predict that individual hermit crabs show significant patterns of individual consistency across different group sizes.

Methods

Data collection

Sixty *Pagurus bernhardus* were collected from South Bay, Scarborough, UK (54°16′12″N 0°23′25″W) in October 2015. They were transported back to the laboratory at the University of Hull within 4 h of collection, where they were kept in a holding tank (1.5-m circular diameter) that contained steadily filtered aerated saltwater at a constant temperature of 11°C. Crabs were given access to a large number of vacant shells of varying size (primarily common periwinkle, *Littorina littorea*; dog whelk, *Nucella lapillus*; and flat top shell, *Gibbula umbilicalis*) and left to acclimatize to their new surroundings (and occupy a new shell if required) for 72 h. Following acclimatization, 25 crabs were randomly selected, weighed within their shells and individually numbered on the shell using nail varnish, then placed inside plastic containers (18 × 10 cm; one side meshed for aeration) within the holding tank to isolate them and prevent shell-swapping (Gherardi, 2006), a behaviour observed in the holding tank among unmarked individuals. Crabs were fed twice a week on chopped mussel purchased from a local supermarket. Crabs were not sexed as previous studies have found that individual differences in startle response are independent of sex (Briffa, Rundle and Fryer, 2008).

Startle response times for each marked individual were measured in five different group sizes (1, 2, 5, 10 and 20 individuals). A group consisted of the marked individual and an appropriate number of unmarked specimens selected haphazardly from the holding tank. A circular observation container (35 cm diameter) was filled to a depth of 10 cm with water taken from the holding tank. The focal crab and the correct number of unmarked individuals were placed onto a plate (22 cm diameter), ensuring that the focal crab was positioned

in an inverted position to ensure it withdrew fully into its shell before observations began. All crabs were then gently tipped into the observation container. This method of eliciting a startle response is both successful and non-harmful in determining response times of *P. bernhardus* (Briffa, Rundle and Fryer, 2008; Briffa, 2013).

Latency to emerge from the shell was timed to the nearest second using a digital stopwatch from the point that the crab enters the observation container until the point at which its pereopods made contact with the base of the container (Briffa, 2013), when it is considered to be fully emerged. After emergence, the focal crab was returned to its individual container, and the remaining crabs to the holding tank. The water in the observation container was changed between each trial. Each crab was given a maximum of 3 min to emerge before the trial was terminated (failure to emerge was recorded in 61/375 trials). Startle responses were induced in each crab twice a week for seven and a half weeks with each crab providing up to 15 latencies in total, with 3 at each of the 5 group sizes to evaluate consistency of emergence time within a context (group size). Crabs were assigned a group size at random during each data collection session, while ensuring that each experienced each group size a maximum of three times.

Ethical approval was obtained from the School and Faculty Ethics Committees before the study began. At the end of the experiment, the crabs were returned to the shore where they were collected from.

Statistical analyses

To assess the relationship between group size and the time that it took individuals to emerge from their shells, linear mixed-effects models were implemented using the package ‘nlme’ (Pinheiro *et al.*, 2015) in R version 3.2.3 (R Core Team, 2015). Since the nature of the data involved several group size classes (1, 2, 5, 10 and 20), group size was treated as a categorical variable during analysis. Group sizes were compared to a reference level of group size 2, as this was the group size with the lowest mean emergence time (pairwise

comparisons with all reference levels can be found in Appendix I). Body size was included as an additional fixed effect, and the identity of the crab was included as a random effect to account for multiple measures on each individual both within and between group sizes. Data were log-transformed to meet the assumptions of normality for statistical analysis, and non-significant interactions between body size and group size were removed.

To investigate whether different individuals had predictably different emergence times, an ANCOVA model was used on data from across all group sizes. This included the emergence time of the crab as the independent variable, the crab’s identity as a dependent variable, and the group size that the emergence time was obtained from as a covariate. A series of regression analyses were then used to further assess whether an individual’s emergence time in one group size was a significant predictor of their respective emergence time in another group size. A total of 10 linear regressions were used in this manner, with the mean emergence time of each crab in a given group size being regressed against their mean emergence time in another group size, until each group size had been compared against every other condition. To quantify individual consistency, repeatability was calculated using the intraclass correlation coefficient (r_{IC}); a measure of test–retest reliability (Uher, 2011). This was achieved using the R package ‘ICC’ (Wolak, Fairbairn and Paulsen, 2012).

Results

Does group size affect emergence time?

Accounting for individual variation in startle response, emergence time increased with group size (Table 1, Fig. 1). There was no significant effect of body size on emergence time (Table 1). Treatment groups were compared against a group size of 2 as this was the group with the lowest mean emergence time (Fig. 2). Crabs emerged faster in groups of 10 and 20 than they did in groups of 2 (Table 1). All other pairwise comparisons can be found in Appendix I.

Table 1. Linear mixed-effects models assessing the relationship between group size, body size and emergence time with individual identity as a random effect. Significant *P*-values are highlighted in bold.

	Value	SE	df	<i>t</i>	<i>P</i>
Group size as a categorical variable (intercept: group size = 2)					
(intercept)	2.150	0.493	285		
Group size = 1	0.225	0.161	285	1.391	0.165
Group size = 5	0.231	0.158	285	1.456	0.147
Group size = 10	0.400	0.160	285	2.492	0.013
Group size = 20	0.426	0.164	285	2.595	0.010
Body size	0.156	0.120	23	1.309	0.234

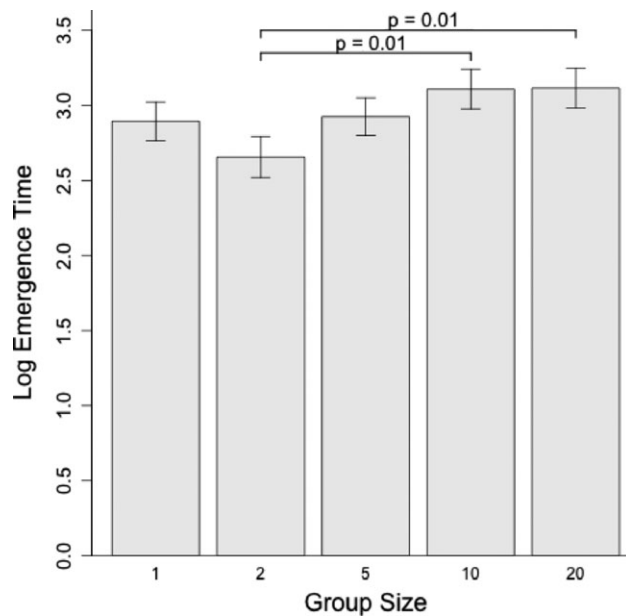


Figure 1. Bar graph showing mean responses of all crabs across group sizes with standard error represented as error bars. Significant effects of group size on emergence time are shown between a group size of 2 and 10, and 2 and 20.

Do hermit crabs exhibit personality?

Emergence times differed between crabs, even when accounting for variation caused by the different group sizes (group size effect, $F = 4.28$, $df = 1288$, $P = 0.03$; individual effect, $F = 5.67$, $df = 24\ 288$, $P < 0.001$; Fig. 3). In 8 out of 10 group size comparisons, the emergence time registered by a crab in one group was found to be a significant predictor of how that crab would respond in other group sizes (Fig. 2; Table 2); this shows consistency in the behaviour of crabs between treatments. No significant correlation was observed between emergence times in group sizes of 1 and 10 ($t = 1.67$, $P = 0.11$), and 5 and 20 ($t = 1.86$, $P = 0.08$).

Across all groups, emergence time was found to be generally repeatable when measured with the intraclass correlation coefficient ($r_{IC} = 0.26$; Fig. 4). However, considering each group size alone, significant repeatability was only found in a group size of 2 ($r_{IC} = 0.56$) and a group size of 20 ($r_{IC} = 0.51$). All other treatment groups returned an r_{IC} value which had a 95% confidence interval inclusive of zero (Fig. 4), indicating non-significant repeatability despite the overall result.

Discussion

The results suggest that both individual consistency and group size affect emergence time in hermit crabs. Individual crabs were consistent in their behaviour across group sizes: those with shorter emergence times ('bolder' individuals)

consistently emerging rapidly from their shells, while those with longer emergence time ('shy' individuals) having consistently longer emergence times. The positive relationship between larger group size and longer emergence times suggest that competition with conspecifics, rather than the anti-predator benefits of grouping, are the key determinant of emergence decisions. Two related factors may explain this relationship: direct competition for gastropod shells and exposure to 'fighting cues' from conspecifics.

Competition for gastropod shells is well-documented in hermit crabs (Elwood and Glass, 1981; Briffa, Elwood and Dick, 1998; Caven, Clayton and Sweet, 2012). Increased emergence times in larger groups may be explained by unintentional interference between individuals as they begin to move and emerge, such as shell-to-shell hitting or knocking. This type of disturbance would cause an emerging crab to retreat into their shell (Edmonds and Briffa, 2016), regardless of group size, but is probabilistically more likely as group size, and therefore density, increased. A tap to the shell during emergence could indicate to the crab that the risk of competition was high, as it may be able to perceive whether the source of the tap was initiating a fight or not, and, given that crabs were likely to be in preferred-size shells, would have withdrawn into the shell in defence (Elwood and Glass, 1981).

Any anti-predator benefits potentially gained from clustering may have been offset by the risk of forced shell-eviction from a conspecific. Indeed, in the wild, many members of the genus *Pagurus* are known to maintain a 'rather large individual distance' instead of aggregating (Hazlett, 1968). Shell fights are often initiated by larger crabs and crabs that occupy poor quality and/or unsuitably small shells (Dowds and Elwood, 1985), although we found no effect of size on emergence time. As crabs in this study were able to select from unoccupied shells before experiments began, they may have had low motivation to initiate a fight and maximal motivation to retain their shells. As potential competition increases (increasing numbers of nearby conspecifics) motivation to remain in the shell, defending it against competitions, may have increased, as 'shy' behaviour is associated with higher chances of successful shell-defence during a fight (Courtene-Jones and Briffa, 2014). As motivation to fight in hermit crabs is dependent on the quality of their shells (Elwood and Briffa, 2001), future studies may therefore benefit from examining how individual emergence behaviour varies when crabs are housed in shells of varying size, quality and fit.

Hermit crabs are also able to use chemical cues in order to detect conspecifics and discriminate shells (Benoit, Peeke and Chang, 1997), and to distinguish between crabs that have recently fought and crabs that have not (Briffa and Williams, 2006). Exposure to these 'fighting cues' lengthens the amount of time a hermit crab spends withdrawn into its shell (Briffa and Williams, 2006). Therefore, if the unmarked crabs had been engaged in fights, the presence of fighting cues in the water may have increased time spent withdrawn in the shell

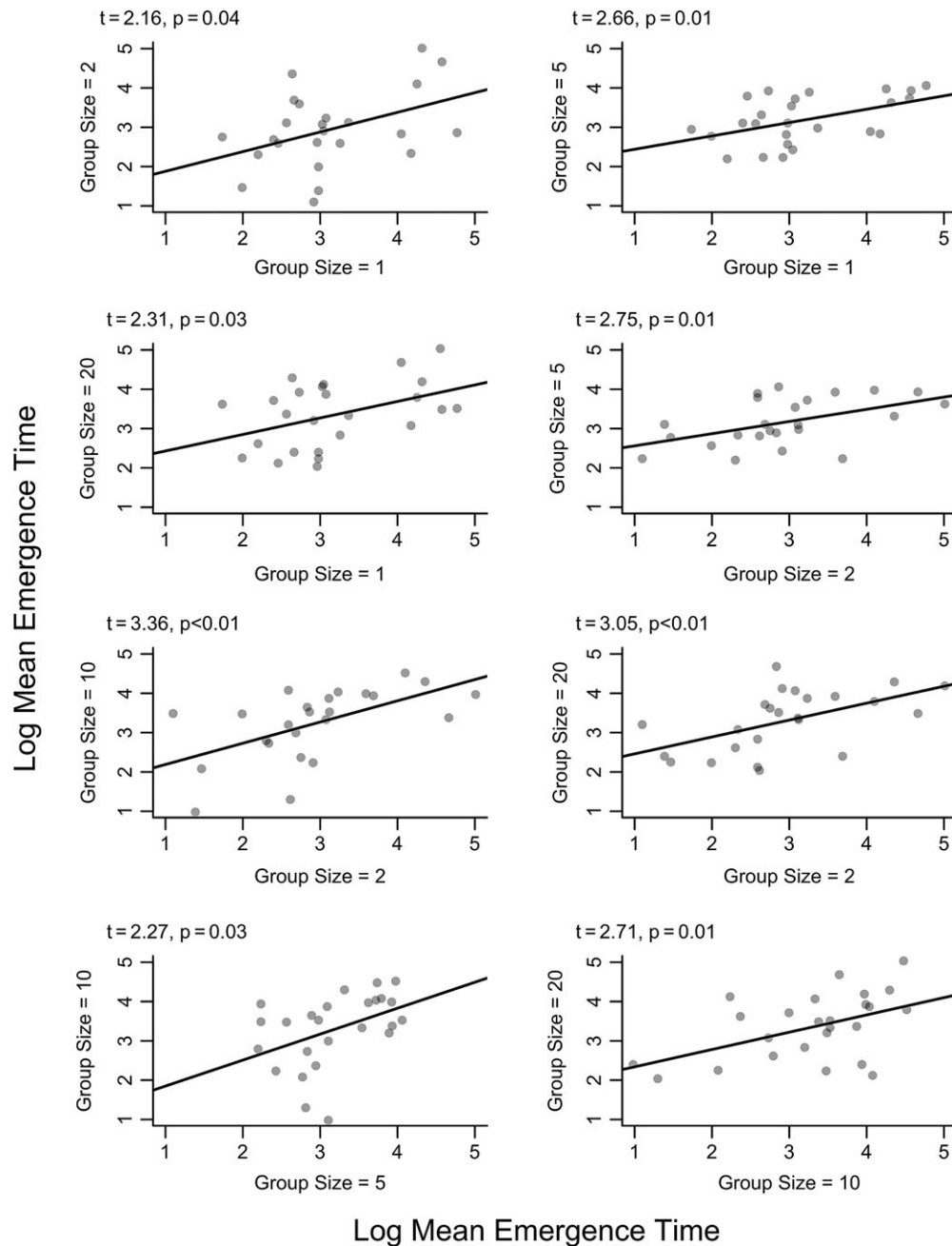


Figure 2. Significant positive correlations between crab emergence times in two group sizes; one larger than the other. Significance in these regressions represents predictability of an individual's behaviour across treatments. Each data point represents an individual crab's mean log emergence time at the specified group size. Group sizes are indicated on the axes of the graphs.

in larger groups, where the probability of any one crab having recently engaged in a fight would be increased, particularly as crowding is associated with increased aggression (Hazlett, 1968). In the green swordtail (*Xiphophorus helleri*), 'eaves-dropping' on fights reduces a bystander's propensity to engage in aggressive behaviour with the winning combatant post-fight (Earley and Dugatkin, 2002).

The degree in which hermit crabs are able to detect discrete differences in conspecific group size is not known, forming a potentially enlightening area for future investigation. The suggestion that animals are able to discriminate quantity through the mental representation of numbers (counting)—as opposed to through non-numerical perceptible variables which differ with numerosity—has traditionally been restricted to mammalian

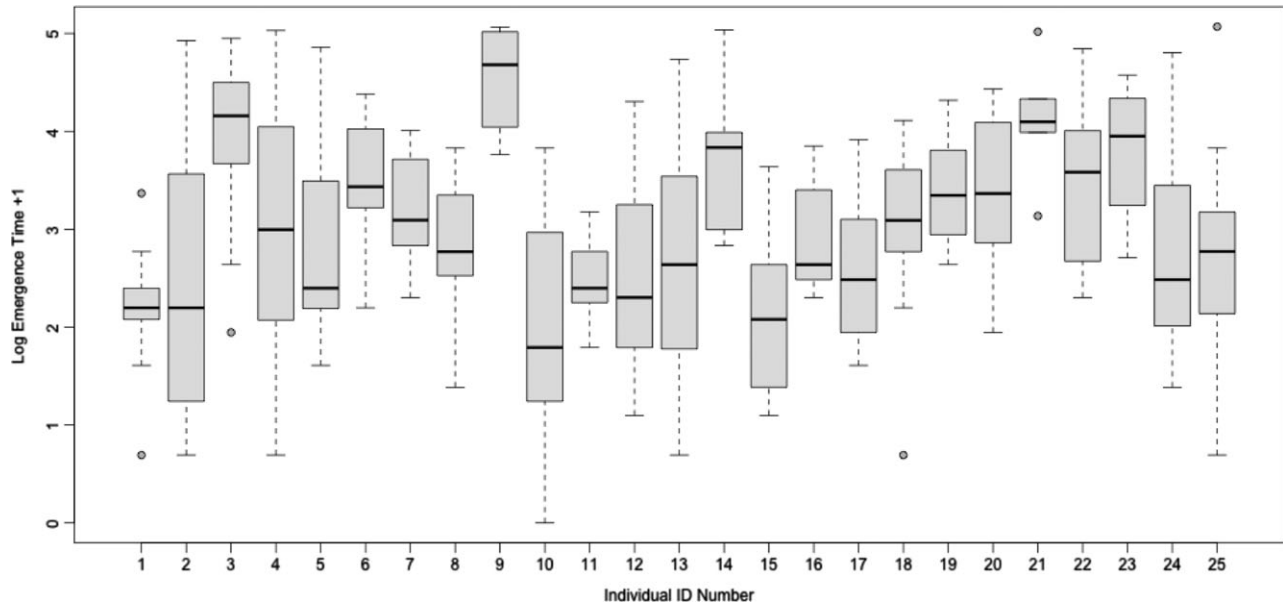


Figure 3. Box and whisker diagrams for each crab showing variation in emergence time across all treatments. Grey box represents interquartile range with black line representing the median emergence time; outliers are represented as grey circles.

Table 2. Pairwise comparisons of emergence time in five different group sizes. Significance (indicated by bold) represents predictability of an individual's behaviour across treatments.

Group size comparison	<i>t</i>	<i>P</i>	<i>n</i>	<i>R</i> ²
1 and 2	2.16	0.04	24	0.18
1 and 5	2.66	0.01	25	0.26
1 and 10	1.67	0.11	25	0.11
1 and 20	2.31	0.03	25	0.19
2 and 5	2.75	0.01	24	0.26
2 and 10	3.36	<0.01	24	0.34
2 and 20	3.05	<0.01	24	0.30
5 and 10	2.27	0.03	25	0.18
5 and 20	1.86	0.08	25	0.13
10 and 20	2.71	0.01	25	0.24

models (Agrillo *et al.*, 2009). However, previous studies have documented counting of conspecifics in mosquitofish (*Gambusia holbrooki*; Agrillo *et al.*, 2008), as well as the counting of landmarks in honey bees (*Apis mellifera*; Chittka and Geiger, 1995). The relationship between group size and emergence time discovered in this study therefore presents a novel opportunity to explore quantity discrimination in a crustacean model.

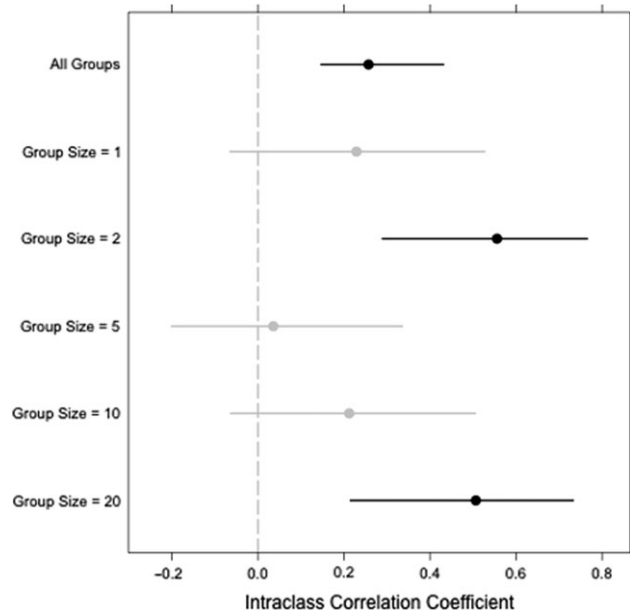


Figure 4. Intra-class correlation coefficients for all treatments and each group size separately, represented by data points and lines indicating the 95% confidence intervals. Grey dashed line represents zero. *r*_C values with intervals not crossing zero are considered significant (black data points and lines) whereas intervals crossing zero are considered non-significant (grey data points and lines).

In line with previous work (Briffa, Rundle and Fryer, 2008; Briffa and Twyman, 2011; Briffa, Bridger and Biro, 2013; Briffa, 2013), hermit crabs showed significant individual consistency in

behaviour across group sizes, yet adjusted that behaviour in response to their environment. This supports previous research which has found that although *P. bernhardus* modulates its behaviour to show measurable behavioural plasticity, this effect is exceeded by the degree of behavioural consistency observed in this species (Briffa, Rundle and Fryer, 2008). The results presented here suggest that investment in mechanisms required for behavioural plasticity and accurate modulation of responses is relatively low, with behavioural consistency and approximate modulation of responses favoured instead. Both the costs associated with the production and maintenance of sensory and information processing systems, and variation in the level of environmental heterogeneity, have been suggested as factors that could explain the balance between plasticity and consistency (Briffa, Rundle and Fryer, 2008). Previous research has remarked on the limited extent of behavioural plasticity in hermit crabs (Hazlett, 1995). As consistent individual differences in behaviour—as well as patterns of appropriate adjustment in boldness across situations—have previously been used to suggest the presence of animal personalities (Brown, Jones and Braithwaite, 2005; Mowles, Cotton and Briffa, 2012; Rudin and Briffa, 2012), this limited behavioural plasticity may be due to the presence of personality in hermit crabs, previously reported by Briffa, Rundle and Fryer (2008).

Further work is needed to elucidate the function of increased emergence times in larger groups, and the mechanisms by which individual crabs determine their emergence time across group sizes. We suggest that both immediate threat of competition for shells and the detection of cues from previous fights may influence this decision. Clustering may still be associated with reduced predation risk, as grouping carries anti-predator benefits across species (Krause and Ruxton, 2002) although larger groups may be more likely to attract predators, particularly if predators use movement to detect their prey. Future studies examining the potential anti-predator benefits of clustering in *P. bernhardus* may therefore benefit from exploring locale-dependent variation in boldness between sites with measurable differences in predation risk. Extended emergence times in hermit crabs have previously been observed with the presence of predatory cues (Scarratt and Godin, 1992), and therefore the role of predation risk in determining emergence behaviour across group sizes would shed light on whether this factor too plays a role in determining emergence times. Finally, how hermit crabs determine the size of the cluster and relative risk is another route for further research.

Supplementary Data

Supplementary data are available at *BIOHOR* online.

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Author biography

Harvey graduated from the University of Hull in 2016 with a BSc (Hons) in Zoology. Specializing in evolutionary biology and behavioural ecology, his most accomplished work ranged from a field project on the symbiotic mutualisms of clownfish and sea anemones, to a presentation on the evolution of the foot in early hominids. Harvey is currently working within the technology communications industry, conducting media relations for startups and high-growth tech companies. Eventually, he would like to develop a career in science communication, promoting novel research in the field of zoology.

Statement of responsibility

Designing the study—L.J.M. and H.E.B., conducting experiments—H.E.B., analyzing the data—H.E.B., writing the manuscript—H.E.B. with feedback and input from L.J.M., technical support—see acknowledgements, conceptual advice—L.J.M.

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