Do I stand out or blend in? Conspicuousness awareness and consistent behavioural differences in hermit crabs

Mark Briffa* and Claire Twyman
Marine Biology and Ecology Research Centre, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK
*Author for correspondence (mark.briffa@plymouth.ac.uk).

Animals titrate their behaviour against the level of risk and an individual's conspicuousness should influence decisions such as when to flee and for how long to hide. Conspicuousness will vary with variation in substrate colour. Since hermit crabs frequently change the shells they occupy, shell colour will also influence conspicuousness and to be aware of their conspicuousness would require information on both of these factors to be integrated. Reduced boldness in high-contrast shell and substrate combinations compared with situations of low contrast indicates that hermit crabs are aware of current conspicuousness. Differences between individuals remained consistent across conspicuousness levels indicating the presence of animal personalities.

Keywords: hermit crab; animal personality; conspicuousness; startle response

1. INTRODUCTION
When faced with a dangerous situation such as the presence of a predator, several factors will influence the level of risk and hence the optimal course of action. This could involve the timing of a decision to flee (e.g. [1–3]) or for animals that occupy shelters, such as hermit crabs inhabiting empty gastropod shells, the duration of a ‘startle response’ of rapidly withdrawing into the shelter before re-emerging [4]. In animals that flee to avoid attack, the decision might be influenced by the proximity and prowess of the predator [1–3]. For shelter-dwelling animals, the decision is influenced by the quality of their shelter [5]. In both animals that flee and animals that withdraw into shelters, an additional factor that might influence the level of risk is an individual's conspicuousness.

Evidence that animals can use information on their own coloration to adjust risk avoidance is provided by studies of broad-headed skinks, Eumeces laticeps [6] and rock lizards, Iberolacerta cyreni [3]. While camouflaged (‘cryptic’) colouration can reduce conspicuousness, this may still vary owing to movement over heterogeneous substrates. Therefore, the ability to make decisions that reduce risk would be enhanced if individuals are aware of their current conspicuousness. This would require the integration of information on (i) the individual’s own coloration and (ii) properties of the background.

In European hermit crabs, Pagurus bernhardus, frequent changes of gastropod shell, in addition to heterogeneous substrates, can influence conspicuousness. Littorina obtusata shells occupied by intertidal P. bernhardus occur in a range of colours but 90 per cent express one of two colour morphs, ‘dark reticulata’ or ‘citrina’ [7]. These dark brown and bright yellow shells are thought to be associated with a stable feeding polymorphism of L. obtusata, of grazing on the upper (reticulata) or lower (citrina) side of the seaweed frond [7]. Hermit crabs occupying reticulata shells are more conspicuous against a light substrate than a dark substrate whereas crabs in citrina shells are more conspicuous against a dark substrate than a light substrate ([8]; see electronic supplementary material, S1 and figure 1b). In order to titrate the duration of startle responses against current conspicuousness, hermit crabs would therefore need to use information on both background colour and shell colour.

In a previous study where risk was manipulated via the presence and the absence of a predator, startle responses were shorter under the low-risk situation when the predator was absent and longest under the high-risk situation when the predator was present [9]. Thus, if hermit crabs are aware of their conspicuousness, we would expect them to show shorter startle responses under shell–substrate combinations that provide low conspicuousness than under combinations that produce high conspicuousness. In addition to such behavioural plasticity, relative differences between individuals may persist across risk levels [9]. ‘Behavioural correlation across situations’ is a key marker for the presence of ‘animal personalities’ ([10]; see [11] for a taxonomic review) and latency to emerge from a refuge has been used as a measure of ‘boldness’ (e.g. [9,12,13]). We aim to determine (i) whether hermit crabs are capable of integrating information about the colour of the substrate and their gastropod shell and (ii) whether between-individual differences in startle responses are robust across situations that vary in two factors.

2. MATERIAL AND METHODS
Hermit crabs occupying L. obtusata shells were collected from Hannaford point, Cornwall, UK during September–November 2009. At the laboratory, they were transferred to 125 l tanks containing aerated 15°C sea water and fed ad libitum on white fish. Crabs were removed from their shells (by cracking in a vice), sexed, examined for obvious parasites and loss of appendages and weighed. Only male crabs free from parasites or appendage loss were used. Each crab was placed into a 12 cm dish containing sea water as above and supplied with a new reticulata or citrina shell, of the preferred shell weight for the weight of the crab, established from previous shell selection experiments [14]. There was no variation between crabs in shell fit. The dish contained a 1 cm layer of yellow or black aquarium substrate (Aquatic Gravel, Pettex Ltd, UK). After a 24 h acclimation period, a startle response was induced by removing the crab by hand, inverting for 5 s and returning to the substrate with the aperture facing upwards, enabling us to time the duration of the startle response [8]. Crabs were moved into a new dish containing the alternative substrate colour and the procedure, including the 24 h settling period was repeated. Each crab was then removed again from its shell and supplied with a new shell of the alternative colour, and the process was repeated. Responses were obtained for each crab under four combinations: reticulata shell + black substrate (RB), reticulata shell + yellow substrate (RY), citrina shell + black substrate (CB) and citrina shell + yellow...
0.54) but there was a significant interaction between shell colour and substrate colour (F(1, 36) = 2.6, p = 0.06) resulted from shorter startle responses on black than on yellow sand by crabs in group C. There were no main effects (shell: F(3, 36) = 0.07, p = 0.83, substrate: F(1, 36) = 1.5, p = 0.23, group: F(2, 36) = 1.4, p = 0.25). An interaction (F(1,16) = 1079.4, p < 0.0001) between shell and substrate colour indicated that 

citrina shells contrasted more with black substrate than did reticulata shells (t = 23.5, p < 0.0001), whereas reticulata shells contrasted more with yellow substrate than did citrina shells (t = 29.7, p < 0.0001; figure 1b). Significant concordance (W = 0.61, p < 0.0001) indicated that differences between individuals persisted across the four situations. To illustrate this we calculated the Pearson correlation between mean responses in the two low and high-conspicuousness situations (r = 0.76, p < 0.0001; figure 2).

4. DISCUSSION
Startle responses were shorter when crabs were less conspicuous. Crabs also gave shorter responses in the shells they received first (groups A and B, reticulata; groups C and D, citrina). This was most marked in group B, reticulata-yellow combination; group D, citrina-black combination). These differences could be caused by a cumulative stress response to being removed from their shell twice and there may also be carryover effects between different levels of conspicuousness that were experienced. These interactions,
however, were weak compared with the interaction between the substrate and shell colour, indicating that the main driver for startle responses was the current level of conspicuousness.

Several studies show that animals adjust decisions according to their coloration (e.g. [3,6]). In some animals, physiological colour change maintains crypsis against background colours that vary spatially (e.g. chameleons Chamaeleo chamaeleon, [16]) or with season (e.g. mountain hares Lepus timidus, [17]). Similarly, hermit crabs can change their shell to provide a better match with the background but this is constrained by availability and exposure while changing [8]. Therefore, hermit crabs encounter situations where there is a mismatch between shell and substrate colour. In addition to using information on predators [9] and shell size [5], hermit crabs adjust their behaviour (figure 1a) using information on both of these variables (figure 1b). This plasticity, however, is nested within a pattern of consistent differences between individuals. While average responses were greater when crabs were more conspicuous, they were consistent relative to other individuals.

Thus, hermit crabs appear to be aware of their current level of conspicuousness. Crabs may remember information about the visual properties of their shells gained prior to their decision to occupy the shell. Alternatively, the stalked eyes may allow the crabs to see their current shell in addition to the substrate.

The capacities of crustaceans for information processing and decision making have been described in a number of gastropod shells [18]. Here, we show that similar abilities demonstrated when assessing the morphology of gastropod shells [18]. This plasticity, however, is nested within a pattern of consistent differences between individuals. While average responses were greater when crabs were more conspicuous, they were consistent relative to other individuals.

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