Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*

Mark Briffa*, Simon D. Rundle and Adam Fryer

Marine Biology and Ecology Research Centre, School of Biological Sciences, The University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

Many phenotypic traits show plasticity but behaviour is often considered the ‘most plastic’ aspect of phenotype as it is likely to show the quickest response to temporal changes in conditions or ‘situation’. However, it has also been noted that constraints on sensory acuity, cognitive structure and physiological capacities place limits on behavioural plasticity. Such limits to plasticity may generate consistent differences in behaviour between individuals from the same population. It has recently been suggested that these consistent differences in individual behaviour may be adaptive and the term ‘animal personalities’ has been used to describe them. In many cases, however, a degree of both behavioural plasticity and relative consistency is probable. To understand the possible functions of animal personalities, it is necessary to determine the relative strength of each tendency and this may be achieved by comparison of statistical effect sizes for tests of difference and concordance. Here, we describe a new statistical framework for making such comparisons and investigate cross-situational plasticity and consistency in the duration of startle responses in the European hermit crab *Pagurus bernhardus*, in the field and the laboratory. The effect sizes of tests for behavioural consistency were greater than for tests of behavioural plasticity, indicating for the first time the presence of animal personalities in a crustacean model.

Keywords: animal personalities; plasticity; consistency; boldness; hermit crab

1. INTRODUCTION

Behaviour has long been considered the ‘most plastic’ phenotypic trait as it is likely to show the quickest response to temporal changes in conditions (e.g. Hazlett 1995). The ability to produce appropriate responses to changing conditions, or ‘situations’ (*sensu* Sih *et al.* 2004), should clearly be beneficial. However, it is also clear that phenotypic plasticity might be costly to produce or maintain (DeWitt *et al.* 1998). Proximate constraints that could limit behavioural plasticity include constraints on sensory capabilities (‘information gathering’), cognitive structure and learning (‘information processing’) or constraints due to morphological and physiological factors (Hazlett 1995; Dall *et al.* 2004). Such limits on behavioural plasticity appear to vary between (Brown & Braithwaite 2004) and within (Wilson 1998) populations, in some cases leading to consistent variation in behaviour between individuals. When limits on plasticity are correlated across contexts they produce ‘behavioural syndromes’ (Riechert & Hedrick 1993; Sih *et al.* 2004) or ‘clusters’ (Koolhaas *et al.* 1997). When these differences in individual behaviour are consistent, either temporally, across contexts or between situations, they have been characterized as ‘behavioural tendencies’, ‘coping styles’ or ‘animal personalities’ (Dall *et al.* 2004; Sih *et al.* 2004;

Dingemanse & Réale 2005). While it seems logical that the ability to appropriately modulate behaviour between situations would be advantageous, the observation that consistent individual differences in behaviour are often distributed in a non-random way leads to the possibility that this variation is adaptive, perhaps allowing responses that are ‘approximately appropriate’, while avoiding the potential costs of plasticity. Dall *et al.* (2004), for example, suggest that animal personalities may arise when the fitness benefits of a behavioural strategy are both frequency dependent and vary with an individual’s prior experiences.

The strength of plasticity and consistency may be the result of evolutionary or developmental trade-offs that influence the level of investment in mechanisms required for plasticity (e.g. sensory systems). Such trade-offs could be influenced by both the costs and the levels of plasticity required to cope with the environment. Thus, both behavioural plasticity and consistency may be adaptive. Indeed, an individual may modulate its behaviour to give appropriate responses in different situations but still show a consistent level of response relative to the responses of other individuals (e.g. see Johnson & Sih’s 2007 study on fishing spiders). In order to understand the direction of such trade-offs, it is necessary to investigate the balance between plasticity and consistency. An analytical framework for such an investigation is illustrated in figure 1, which shows four possible combinations of the presence or absence of consistent animal personalities and behavioural plasticity. Between situations, a population of animals

* Author for correspondence (mark.briffa@plymouth.ac.uk).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.0025> or via <http://journals.royalsociety.org>.

Figure 1. Cross-situational testing for the presence (+) and absence (-) of behavioural plasticity and behavioural consistency. Grey bars represent an average behavioural response from three individuals under three different situations, A–C. The measure from each individual is represented by circles in different shades. (a,b) Significant differences in the average response between the situations indicate the presence of behavioural plasticity whereas (c,d) the absence of a significant difference would suggest that this behaviour is not plastic between the situations. (a,c) Significant concordance between the ranks of individual responses between the three situations would indicate the presence of animal personalities whereas (b,d) a lack of concordance between individual responses between the situations would indicate that animal personalities are not present. In this scheme, there are four hypothetical extremes of the presence or absence of plasticity and consistency, but it is possible for both to be present, such as in (a), indicated by significance in tests for both difference and consistency. In such cases, the relative strength of plasticity and personality can be gauged by comparing effect size estimates for tests of difference (e.g. repeated measures ANOVA) and tests of consistency (e.g. Kendall's coefficient of concordance) between situations. The effect size for an ANOVA is ' η^2 ', and the effect size for concordance is Kendall's coefficient, ' W '.

could show (a) plasticity in average responses but with individuals showing consistent levels of response relative to one another, (b) plasticity in average responses without consistency in individual responses, (c) consistency in individual responses without any average plasticity, and (d) no individual consistency and no plasticity.

These four possibilities represent hypothetical extremes of the presence or absence. In reality, possibility (a), where there is a degree of both behavioural consistency and plasticity, appears to have the greatest level of support from empirical studies where both possibilities have been tested for (e.g. Johnson & Sih 2007). Nevertheless, where both behavioural plasticity and consistency are detected, there may still be a trade-off between the tendency for plastic and consistent behaviours. One way to determine the direction favoured in this trade-off is to compare effect size estimates for tests of average differences in behaviour between situations (plasticity) with those obtained for tests of stability in ranks of individual responses between situations (consistency). Comparison of effect size estimates is a technique that underpins meta-analysis, where it is often necessary to make comparisons between different statistical tests. As noted by Johnson & Sih (2007), the correct test for *variation* in behaviour where measures are taken from individuals on multiple occasions is repeated measures ANOVA. A suitable test for *consistency* in differences in behaviour between individuals across multiple occasions is

Kendall's coefficient of concordance (e.g. Bremner-Harrison *et al.* 2004; alternatively, in studies where tests of behavioural consistency or 'correlation' between only two situations have been conducted, Pearson's product-moment correlation was used; Brown & Braithwaite 2004; Johnson & Sih 2007). Kendall's coefficient of concordance compares the level of agreement between ranks of two or more variables (Sokal & Rohlf 1995) and is often used to determine the temporal stability of dominance hierarchies. For both types of test, estimates of effect size that scale to a maximum of 1 can be calculated allowing a direct comparison between the extent of behavioural plasticity and consistency. An explanation of the appropriate effect size estimates is given in the electronic supplementary material. If the effect size for average variation between situations is greater than the effect size for consistency between situations, this indicates that selection has favoured the costly trait of behavioural plasticity. If the effect size of the test for consistency between situations is greater than the test for difference, this indicates that selection has favoured the less costly approximately appropriate responses to different situations associated with animal personalities.

A key axis of animal personality, which has been investigated in several taxa, is variation in the 'shyness–boldness axis' (Wilson *et al.* 1993) often simply referred to as 'boldness'. A bold individual will typically show high levels of exploratory behaviour in a new environment,

readily investigate novel objects and when disturbed show a 'startle response' of short duration. A number of studies of boldness have identified either consistent responses (Budaev 1997; Coleman & Wilson 1998; Fraser *et al.* 2001; Dingemanse *et al.* 2002) or average differences between situations and locations (Brown & Braithwaite 2004; Brown *et al.* 2005). However, relatively few have attempted to compare the extent of behavioural plasticity and consistency across situations. In studies by Sih *et al.* (2003), the boldness of laboratory-reared larval salamanders, *Ambystoma barbouri*, was examined by measuring their propensity to emerge from refugia in two situations, the presence and absence of predatory green sunfish *Lepomis cyanellus*. On average, salamanders spent more time out of their refuges in the absence of the predator but individual responses were also correlated between the two situations. Similar results were obtained in studies of an arachnid, the fishing spider *Dolomedes triton* (Johnson & Sih 2007). Although these studies revealed both behavioural plasticity and consistency between situations, the two patterns were not formally compared by examination of statistical effect sizes.

Laboratory studies are necessary for conducting the manipulations required to produce the differences in situation (e.g. the presence or absence of a predator) and in the case of the study on spiders (Johnson & Sih 2007) to investigate patterns through ontogeny. However, it is also useful to know how behaviour varies in the animal's natural environment as this might be different to behaviour in the laboratory. This is particularly important if comparisons of boldness between populations or locations are to be made. Few such *in situ* studies of animal personality (Wilson *et al.* 1993; Brown *et al.* 2005) have thus far been conducted and these have been restricted to bony fishes (Osteichthyes). It is also possible to conduct experiments where responses are examined both *in situ* and in a laboratory context, allowing both an assessment of responses in a natural setting and experimental manipulation of situations. Typically, studies of *in situ* boldness use the duration of a startle response, of withdrawing into a shelter when confronted with a novel stimulus, as the measure of boldness. In most *in situ* studies, it is necessary to place animals in artificial shelters (e.g. Brown *et al.* 2005) or to present stimuli that would not normally be experienced in a natural setting (e.g. Coleman & Wilson 1998; although the use of realistic models can provide a more natural stimulus, e.g. Krause *et al.* 1998 and Dowling & Godin 2002) in order to elicit a startle response. This is because studies using natural shelters are often impractical and could be complicated by factors such as the chemical presence of owners. This complication can be avoided during investigation of the startle response of hermit crabs (Crustacea: Anomura) such as *Pagurus bernhardus*. They are obligate occupants of portable refugia in the form of empty gastropod shells. The shells protect the soft uncalcified abdomen from attack by predators (Vance 1972) and also play a role in buffering against environmental extremes (Shumway 1978; Young 1978; Taylor 1981). When threatened, they show a startle response of rapid withdrawal into the shell (Briffa & Elwood 2001). This response can be elicited in the field and laboratory by means of a simple handling protocol. While this procedure does not remove the necessity of handling the animal (although in this case it

is the gastropod shell rather than the crab *per se* that is handled), it does mean that the animal is not placed into an artificial structure or subjected to a stimulus that is far beyond its normal experience (e.g. when being handled by a predator). Furthermore, most crabs tend to occupy shells that are relatively well matched to their body size and shell optima can be obtained by shell selection experiments relating crab size to shell size. Therefore, in hermit crabs, the 'value' of the refuge can be accurately determined and any effects of refuge size on boldness measures can be accounted for (Elwood 1995).

The aim of this study is to investigate the balance between behavioural plasticity and animal personality using the startle response of *P. bernhardus* as a measure of boldness. As illustrated in figure 1, it is possible that animals can exhibit both plasticity and personality. By comparing estimates of effect size for tests of difference and concordance we aim to compare the relative strength of behavioural plasticity and animal personality. This comparison could reflect the direction of an evolutionary trade-off between the two possible means of coping with uncertainty; plastic behaviour allowing an accurate response but incurring significant costs, or consistent behaviour allowing only an approximately appropriate response but avoiding the higher costs of plasticity. Further, we aim to determine whether the direction of this trade-off could vary between sites that differ in local conditions.

2. MATERIAL AND METHODS

(a) Study locations

Crabs were studied at three rocky intertidal locations on the south west coast of England, UK, Bantham, Mount Batten and Hanafore. The three sites were chosen as *P. bernhardus* is abundant at each site. However, initial surveys suggested that there was a trend for a difference in the density of hermit crabs between sites (ANOVA on crabs m^{-2} : $F_{2,27} = 2.96$, $p = 0.06$) with more crabs at Hanafore than at Bantham or Mount Batten (Fisher's PLSD: $p < 0.05$). The abundance of intact empty shells suitable for occupation by hermit crabs (*Littorina obtusata*, *Littorina littorea*, *Gibbula umbilicalis*, *Calliostoma zizyphinum* and *Nucella lapillus*) also varied between sites, with fewer shells at Bantham than at Mount Batten or Hanafore (ANOVA on shells m^{-2} : $F_{2,27} = 3.8$, $p < 0.05$). However, there was no difference in the number of available shells per crab between the three sites ($F_{2,27} = 0.7$, n.s.). Subsequent analyses of effects of shell size, which will be presented elsewhere, show that there was no difference in average shell quality (percentage of site-specific optimal shell weight) between sites.

(b) In situ startle responses and laboratory manipulation of predator cues

Hermit crabs weighing between 0.1 and 0.71 g were collected from the three locations and an *in situ* startle response was obtained for each crab in the field. The crab was lifted out of the water by hand, held in an inverted position for 10 s and then replaced on the substrate with the aperture of the shell facing upwards. This manipulation caused the crabs to tightly withdraw into their shell, such that the aperture was occluded by the major cheliped. The duration of the response was timed from when the crab was replaced on the substrate until it had re-emerged to the point where both pairs of walking

legs were outside the aperture. Any crabs that emerged before they were replaced onto the substrate, or did not fully withdraw, were discounted from the analysis. The duration of the startle response was recorded and the crab was placed in an individually labelled screw-top container filled with fresh seawater to transport back to the laboratory in Plymouth. In the laboratory (day 1), each crab was placed in an individual 12 cm diameter crystallizing dish containing aerated seawater at 15°C and food items consisting of excess catfish pellets, such that they were fed *ad libitum*. On the afternoon of day 3, the water was replaced with either fresh aerated seawater as above (–cue) or aerated seawater at 15°C that had been taken from a 20 l tank containing 30 *Carcinus maenas* of 50–80 mm carapace width (+cue). Previous studies show that hermit crabs respond to the chemical presence of these crabs (Rotjan *et al.* 2004; Briffa *et al.* *in press*). On the morning of day 4, the startle response was elicited as above and its duration recorded. This procedure was repeated 6 hours later on the afternoon of day 4. Following the behavioural observations on day 4, the water was again changed as above, but on this occasion the treatments were reversed between groups such that crabs that initially received the ‘–cue’ treatment now received the ‘+cue’ treatment. On day 5, the duration of the startle responses were again measured on two occasions, in the morning and afternoon. This design thus yielded startle durations for crabs in the field, in the laboratory in the absence and presence of predator cues, avoiding the possibility that the effects of each cue could be confounded by time since collection. After the final observations on day 5, the crabs were removed from their shells by cracking with a bench vice, weighed and sexed. Any crabs that moulted during the laboratory phase of the experiment, or at this stage were found to have missing appendages or obvious parasites were excluded from the analysis. Thus, a series of five startle durations were obtained for $N=45$ crabs from Bantham, $N=47$ crabs from Hannafore and $N=26$ crabs from Mount Batten. At the end of the experiment, each crab was supplied with a new shell and returned to the sea, within two weeks of collection.

3. RESULTS

(a) Initial analyses of weight and sex effects

An initial analysis of size differences in the crabs from the three sites show that crabs from Bantham were heavier than those from Hannafore (Fisher's PLSD, $p<0.05$) and Mount Batten (Fisher's PLSD, $p<0.005$; one-way ANOVA: $F_{2,114}=5.6$, $p<0.005$). However, there was no correlation between crab weight and startle duration either overall ($r_{116}=0.13$, n.s.) or for any single site (Bantham: $r_{45}=0.25$, n.s.; Hannafore: $r_{45}=0.22$, n.s. and Mount Batten: $r_{24}=-0.29$, n.s.). Since weight had no effect on startle response, it was not factored into the models below. Furthermore, an unpaired *t*-test indicated that there was no difference between males and females in the duration of the startle response ($t_{118}=1.6$, n.s.), so sex was also omitted from the models below.

(b) Plasticity between situations

Repeated measure ANOVAs were conducted in order to investigate the effects of location (Bantham, Hannafore or Mount Batten), and trial type (repeated measure; *in situ*, +cue occasion 1, +cue occasion 2, –cue occasion 1, –cue occasion 2) on the duration of the startle response.

Figure 2. Plasticity in startle responses between trials in the presence and absence of predator cues. Crabs from Mount Batten (white bars) showed longer startle responses than those from Hannafore (grey bars) or Bantham (black bars).

Figure 3. The significant positive correlation between startle durations in the presence and absence of a predator cue. Startle durations were also highly concordant across the five trials. Regression line added for illustration. Since the data are not normally distributed, the Pearson product-moment correlation coefficient was calculated using log transformed data, but the raw data are presented here for illustration.

Since the data were not normally distributed, they were log transformed prior to analysis. The duration of startle responses was greater in crabs from Mount Batten than those from Bantham or Hannafore ($F_{2,113}=16.35$, $p<0.0001$). There was highly significant variation between trials, indicating that the startle response in the absence of predator cues was of shorter duration than in the field or in the laboratory in the presence of a predator cue ($F_{4,452}=11.13$, $p<0.0001$). A significant interaction effect between location and trial ($F_{8,452}=5.24$, $p<0.0001$) indicates that these differences between situations were more marked in crabs from Mount Batten than those from Bantham or Hannafore with crabs from Mount Batten showing a longer response in the laboratory than in the field (figure 2).

(c) Concordance across situations

In order to determine the degree of concordance in the duration of startle responses between different situations, Kendall's coefficient of concordance was calculated using SPSS v. 14. Individual startle responses were significantly concordant across observations with different levels of predation threat (experiment 1; $W_{117}=0.55$, $p<0.0001$).

Table 1. Effect size estimates for individual consistency and behavioural plasticity between situations. (Test statistics and effect size estimates used: consistency was tested using Kendall's coefficient of concordance, χ^2 and W . Plasticity was tested using repeated measures ANOVA, F -ratio and partial η^2 . In the case of the ANOVA, statistics and effect sizes are given for a full model containing site and for a main effects model containing trial type only. Note that for the main effects of only model, the partial η^2 values scale to a maximum of 1 and are identical to the 'classical' η^2 value.)

statistic			probability			effect size estimate		
ANOVA (F)			ANOVA (p)			ANOVA (η_p^2)		
Kendall's (χ^2)	full	main effects only	Kendall's (p)	full	main effects only	Kendall's (W)	full	main effects only
316.8	11.3	6.5	<0.0001	<0.0001	<0.0001	0.55	0.08	0.05

In order to allow comparison with previous studies where correlations between boldness measures taken on two occasions have been obtained, the Pearson product-moment correlation was calculated in Statview between log transformed data for the first instances of the two laboratory situations. There was a significant correlation between the duration in the presence and absence of a predator cue ($r_{116}=0.69$, $p<0.0001$; figure 3).

(d) Comparison of strength of plasticity and consistency in behaviour

In order to compare the relative strength of concordance and plasticity, effect size estimates were calculated for the analyses above. Summary statistics and effect sizes for analyses of concordance (' W ' values from Kendall's coefficient of concordance) and plasticity (partial ' η_p^2 ' values from repeated measures ANOVA) between trials (table 1) show that the effect sizes of tests for consistency are greater than those for variation between situations. In the repeated measure ANOVAs, an additional factor, 'site', that was not possible to incorporate into Kendall's coefficient was included. While this yields additional information about factors affecting startle response, it could alter effect sizes for the main effect of trial type, and lead to η_p^2 values that are not equal to η^2 (Levine & Hullett 2002). Therefore, to enable a valid comparison between the strength of concordance and plasticity, we also provide an analysis where the repeated measures ANOVA has been recalculated for the main effect only (table 1). Here η_p^2 is identical to η^2 (see the electronic supplementary material for a further discussion of this point).

4. DISCUSSION

In this study, we examined the startle responses of hermit crabs, both *in situ* and across situations during laboratory-based manipulation of perceived predation risk. Variation in average responses between predator-cue treatments indicates that there was significant behavioural plasticity between situations. However, analysis of concordance in the ranks of individual startle durations between situations indicates that there is also a significant pattern of individual consistency in behaviour. Although hermit crabs modulate their behaviour showing a degree of behavioural plasticity between situations, this is exceeded by the extent of behavioural consistency. This indicates that there may be a relatively low level of investment in mechanisms required for behavioural plasticity and accurate modulation of responses between situations. Instead, a reliance on behavioural consistency, allowing

approximate modulation of responses, appears to be favoured over a weaker pattern of behavioural plasticity. There are two factors that can explain the balance between consistency and plasticity. First, if the costs of producing or maintaining sensory and information processing systems are sufficiently high then these costs could constrain behavioural plasticity. Second, the optimal level of plasticity may vary, for example, with the level of environmental heterogeneity. The pattern of plasticity revealed by the present data (figure 2), and illustrated in figure 1*a,b*, could still be constrained by costs if the optimal level of plasticity was greater than the level illustrated. Alternatively, an absence of plasticity (figure 1*c,d*) will not necessarily indicate a constraint if the optimal level of plasticity is zero.

In the absence of data on the heritability of a behavioural trait, it is difficult to determine whether such consistent individual differences in behaviour could be maintained by selection (Dingemanse & Réale 2005) either at the level of consistent differences within or between populations. Interestingly, however, the strength of the tendency towards behavioural consistency appeared to vary between locations. Crabs from Mount Batten showed startle responses of greater duration than those from Hannaford or Bantam particularly during the laboratory phase of the experiment. This means that these between-site differences cannot be explained by behavioural plasticity. An alternative explanation is that there may have been variation in local conditions such as food availability (e.g. Sih 1997), wave action or predation threat between different locations that caused behavioural differences that emerged during the laboratory phase of the study. Under certain circumstances, initial differences, for example in hunger, may persist as carryover effects and effectively 'lock' an individual into a risky or risk-averse way of behaving (Dall *et al.* 2004). In this study, however, variations in hunger levels are unlikely to have operated during the time scale of the experiments as the crabs were fed *ad libitum*.

In order to distinguish between these possibilities, it could be useful to investigate between-site differences in proximate factors that could influence behaviour and how they might develop through ontogeny. For example, crabs from different sites may differ in sensory acuity or cognitive structure. Interestingly, there was no variation in boldness with size, as has previously been reported for fishes (e.g. Brown & Braithwaite 2004). One explanation is that in this study, shelter size varied with the size of the crab, whereas this was not the case in the study on fishes

where a standard-sized refuge was used such that different-sized fishes could have had different perceptions of the shelter's value as a refuge. In the case of this study at least, the lack of variation with size indicates that the consistent behavioural differences between individuals from different sites do not develop during ontogeny. It is clear, however, that in order to further understand patterns of plasticity and consistency, it is necessary to gain further insights into the costs of plasticity and of variation in the optimal level of plasticity.

Startle responses have previously been used as an unambiguous measure of boldness (Wilson *et al.* 1993; Brown *et al.* 2005; Johnson & Sih 2007), and patterns of appropriate adjustment of boldness between situations coupled with consistent individual differences in behaviour (e.g. Dall *et al.* 2004; Johnson & Sih 2007) have been assumed to indicate the presence of animal personalities. On this basis, the present data strongly indicate that the surprisingly limited extent of behavioural plasticity first noted in hermit crabs by Hazlett (1995) may be due to the presence of animal personalities, which have not previously been reported in crustaceans. Indeed, the behavioural correlations between situations demonstrated for hermit crabs are of similar size to those obtained in studies of vertebrate species (e.g. $r=0.69$ in this study compared with $r=0.5\text{--}0.67$ in salamander larvae, *A. barbouri*; Sih *et al.* 2003). A review by Gosling (2001) shows that there has been a clear focus of interest on vertebrate models in research concerned with individual differences in behaviour (206 vertebrate studies and 6 studies in total on insects and cephalopods). However, there is no theoretical reason why consistent individual differences in behaviour should be restricted to one subphylum and recent studies have extended the animal personality framework to include other taxa such as arachnids (e.g. Johnson & Sih 2005, 2007). In the case of crustaceans, cross-contextual behavioural syndromes have yet to be demonstrated. However, hermit crabs offer an excellent opportunity to study such correlations as, in addition to a startle response, they show a range of readily quantifiable measures of exploratory behaviour in relation to investigating new shells (e.g. see Elwood & Neil 1992) and their agonistic behaviour may be readily and accurately quantified (Briffa *et al.* 1998; Briffa & Elwood 2000). Here, we have clearly demonstrated consistency in boldness between situations (high- versus low-predation threat) and although there was also behavioural plasticity (figures 1a and 2) comparison of effect sizes shows that the pattern of consistency is stronger than the levels of behavioural plasticity exhibited between situations. Thus, comparison of effect sizes reveals limited behavioural plasticity compared with behavioural consistency, indicating the presence of animal personalities.

We thank Sasha Dall for his comments on an earlier version of this manuscript and Joshua Padgham and Clara Lawrence for their help with data collection. We are grateful to Bob Elwood and two anonymous referees for their insightful comments and suggestions, which have helped us to improve the manuscript.

REFERENCES

- Bremner-Harrison, S., Prodohl, P. A. & Elwood, R. W. 2004 Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Anim. Conserv.* **7**, 313–320. (doi:10.1017/S1367943004001490)
- Briffa, M. & Elwood, R. W. 2000 Analysis of the finescale timing of repeated signals: does shell rapping in hermit crabs signal stamina? *Anim. Behav.* **59**, 159–165. (doi:10.1006/anbe.1999.1273)
- Briffa, M. & Elwood, R. W. 2001 Motivational change during shell fights in the hermit crab *Pagurus bernhardus*. *Anim. Behav.* **62**, 505–510. (doi:10.1006/anbe.2001.1764)
- Briffa, M., Elwood, R. W. & Dick, J. T. A. 1998 Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. *Proc. R. Soc. B* **265**, 1467–1474. (doi:10.1098/rspb.1998.0459)
- Briffa, M., Haskell, P. & Wilding, C. In press. Behavioural colour change in the hermit crab *Pagurus bernhardus*: reduced crypticity when the threat of predation is high. *Behaviour*.
- Brown, C. & Braithwaite, V. A. 2004 Size matters: a test of boldness in eight populations of bishop, *Brachyraphis episcopi*. *Anim. Behav.* **68**, 1325–1329. (doi:10.1016/j.anbehav.2004.04.004)
- Brown, C., Jones, F. & Braithwaite, V. 2005 *In situ* examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Anim. Behav.* **70**, 1003–1009. (doi:10.1016/j.anbehav.2004.12.022)
- Budaev, S. V. 1997 'Personality' in the guppy (*Poecilia reticulata*): a correlational study of exploratory behaviour and social tendency. *J. Comp. Psychol.* **111**, 399–411.
- Coleman, K. & Wilson, D. S. 1998 Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* **56**, 927–936. (doi:10.1006/anbe.1998.0852)
- Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739. (doi:10.1111/j.1461-0248.2004.00618.x)
- DeWitt, T. J., Sih, A. & Wilson, D. S. 1998 Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* **13**, 77–81. (doi:10.1016/S0169-5347(97)01274-3)
- Dingemanse, N. J. & Réale, D. 2005 Natural selection and animal personality. *Behaviour* **142**, 1159–1184. (doi:10.1163/156853905774539445)
- Dingemanse, N. J., Both, C., Drent, D., Van Oers, K. & Van Noordwijk, A. J. 2002 Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* **64**, 929–938. (doi:10.1006/anbe.2002.2006)
- Dowling, L. M. & Godin, J. G. 2002 Refuge use in a killifish: influence of body size and nutritional state. *Can. J. Zool.* **80**, 782–788. (doi:10.1139/z02-036)
- Elwood, R. W. 1995 Motivational changes during resource assessment by hermit crabs. *J. Exp. Mar. Biol. Ecol.* **193**, 41–55. (doi:10.1016/0022-0981(95)00109-3)
- Elwood, R. W. & Neil, S. J. 1992 *Assessments and decisions, a study of information gathering by hermit crabs*. London, UK: Chapman and Hall.
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. & Skalski, G. T. 2001 Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am. Nat.* **158**, 124–135. (doi:10.1086/321307)
- Gosling, S. 2001 From mice to men: what we can learn about personality from animal research? *Psychol. Bull.* **127**, 45–86. (doi:10.1037/0033-2909.127.1.45)
- Hazlett, B. A. 1995 Behavioral plasticity in crustacea: why not more? *J. Exp. Mar. Biol. Ecol.* **193**, 57–66. (doi:10.1016/0022-0981(95)00110-7)
- Johnson, J. C. & Sih, A. 2005 Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioural syndromes. *Behav. Ecol. Sociobiol.* **58**, 390–396. (doi:10.1007/s00265-005-0943-5)

- Johnson, J. C. & Sih, A. 2007 Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Anim. Behav.* **74**, 1131–1138. (doi:10.1016/j.anbehav.2007.02.006)
- Koolhaas, J. M., de Boer, S. F. & Bohus, B. 1997 Motivational systems or motivational states: behavioural and physiological evidence. *Appl. Anim. Behav. Sci.* **53**, 131–143. (doi:10.1016/S0168-1591(96)01155-0)
- Krause, J., Loader, S. P., McDermott, J. & Ruxton, G. D. 1998 Refuge use by fish as a function of body-length-related metabolic expenditure and predation risk. *Proc. R. Soc. B* **265**, 2373–2379. (doi:10.1098/rspb.1998.0586)
- Levine, T. & Hullett, G. R. 2002 Eta squared, partial Eta squared, and misreporting of effect size in communication research. *Hum. Commun.* **28**, 612–615. (doi:10.1111/j.1468-2958.2002.tb00828.x)
- Riechert, S. E. & Hedrick, A. V. 1993 A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Anim. Behav.* **46**, 669–675. (doi:10.1006/anbe.1993.1243)
- Rotjan, R., Blum, J. & Lewis, S. 2004 Shell choice in *Pagurus longicarpus* hermit crabs: does predation threat influence shell selection behaviour? *Behav. Ecol. Sociobiol.* **56**, 171–176. (doi:10.1016/S0022-0981(99)00119-7)
- Shumway, S. E. 1978 Osmotic balance and respiration in the hermit crab, *Pagurus bernhardus*, exposed to fluctuating salinities. *J. Mar. Biol. Assoc. UK* **58**, 869–876.
- Sih, A. 1997 To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol. Evol.* **12**, 375–376. (doi:10.1016/S0169-5347(97)87376-4)
- Sih, A., Kats, L. B. & Maurer, E. F. 2003 Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Anim. Behav.* **65**, 29–44. (doi:10.1006/anbe.2002.2025)
- Sih, A., Bell, A. & Johnson, J. C. 2004 Behavioural syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–377. (doi:10.1016/j.tree.2004.04.009)
- Sokal, R. R. & Rohlf, F. J. 1995 *Biometry: the principles and practice of statistics in biological research*, pp. 600–601, 3rd edn. New York, NY: W. H. Freeman and Co.
- Taylor, P. R. 1981 Hermit crab fitness: the effect of shell condition and behavioural adaptations on environmental resistance. *J. Exp. Mar. Biol. Ecol.* **71**, 221–236.
- Vance, R. R. 1972 The role of shell adequacy in behavioural interactions involving hermit crabs. *Ecology* **53**, 1075–1083. (doi:10.2307/1935419)
- Wilson, D. S. 1998 Adaptive individual differences within single populations. *Phil. Trans. R. Soc. B* **353**, 199–205. (doi:10.1098/rstb.1998.0202)
- Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. 1993 Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *J. Comp. Psychol.* **107**, 250–260.
- Young, A. M. 1978 Desiccation tolerances for three hermit crab species *Clibanarius vittatus* (Bosc) *Pagurus pollicaris* say and *P. longicarpus* say (Decapoda: Anomura) in the North Inlet Estuary, South Carolina, U.S.A. *Estuar. Coast Mar. Sci.* **6**, 117–122.