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Published in:
Behavioral Ecology

DOI:
[10.1093/beheco/aru085](https://doi.org/10.1093/beheco/aru085)

Publication date:
2014

Link:
[Link to publication in PEARL](#)

Citation for published version (APA):
Courtene-Jones, W., & Briffa, M. (2014). Boldness and asymmetric contests: role- and outcome-dependent effects of fighting in hermit crabs. *Behavioral Ecology*, 25(5), 1073-1082. <https://doi.org/10.1093/beheco/aru085>

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Boldness and asymmetric contests: Role and outcome dependent effects of fighting in hermit crabs.

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Acknowledgements: We are grateful to Gareth Arnott and an anonymous reviewer for their insightful comments on this manuscript.

This is a pre-copyedited, author-produced PDF of an article accepted for publication in *Behavioral Ecology* following peer review. The version of record [Courtene-Jones W & Briffa M. 2014. Boldness and asymmetric contests: Role and outcome dependent effects of fighting in hermit crabs. *Behavioural Ecology* **25**, 1073-1082] is available online at: <http://beheco.oxfordjournals.org/content/25/5/1073.full?sid=caaab932-f89b-4495-9e10-e3ef69094844>.

Consistent-between individual differences in behavior have been demonstrated in an array of species from diverse taxa and variation in boldness may be associated with variation in aggressiveness. However, little is known about how boldness is linked with the ability to win fights (resource holding potential, RHP) or about how the experience of fighting may alter subsequent boldness. Animal contests often involve role-asymmetries, where the two opponents fight in different ways. Here we investigate boldness before and after fighting in attacking and defending hermit crabs during contests over the ownership of gastropod shells. Although pre-fight boldness did not influence the chance of winning for attackers, successful defenders had longer startle responses (less bold) than those that that gave up. Post-fight changes in boldness also differed between roles. For defenders there was a significant decline in consistency of startle responses after fighting, coupled with outcome-dependent plasticity in mean boldness. Furthermore, post-fight boldness in defenders varied with the intensity of agonistic behavior inflicted upon them by attackers. In contrast boldness in attackers was stable across the before and after-fighting situations. Links between internal state and agonistic behavior are known to vary between roles in asymmetric contests. It now appears that similar role-specific links are present between aggression and animal personality.

Introduction

Intraspecific contest behavior occurs when two or more individuals directly interact during competition over the ownership of an indivisible resource unit (Hardy & Briffa 2013). In many cases the contest involves the use of non-injurious agonistic signals and is resolved when one individual makes a decision to withdraw. The ability to persist and win a contest is referred to as an individual's resource holding potential (RHP). This trait is known to emerge from a number of attributes that vary between individuals. The roles of physical attributes such as body size, weapon size, strength and endurance have been studied in a great deal of detail (see Briffa & Sneddon 2007). An attribute that has received far less attention with respect to resource holding potential is an individual's location on an axis (or axes) of consistent between individual variation in behavior, in other words an individual's behavioral type or personality. The potential for contest behavior to act as a selective agent for consistent between individual differences (henceforth 'consistency') has long been recognized, such that there are clear reasons for predicting a link between personality and aggressive prowess. The Hawk-Dove game (Maynard Smith & Parker 1976), for example, shows how natural selection can result in a mixture of evolutionarily stable strategies comprising aggressive 'hawks', who always attack with injurious consequences, and placid 'doves' who's agonistic repertoires are limited to displays and retreats. Similarly, negative frequency-dependent selection has been invoked as an explanation for the presence of animal personality both in a general sense (Dall et al. 2004) and in the specific context of sexual selection (Schuett et al. 2010).

In addition to these theoretical links between personality and intraspecific aggression, there is increasing empirical evidence that aggressiveness, the propensity to initiate, escalate or persist in an agonistic encounter, can be a personality trait. In insects (Clarke & Moore 1995, Brown et al. 2006) and vertebrates (Bakker 1986, Riddell & Swain 1991, Garamszegi

et al. 2006, Kralj-Fiser et al. 2007, Pavlova et al. 2007, Wilson et al. 2011, 2013) for example some individuals are consistently more aggressive than others. Consistent aggressiveness may also extend beyond the context of intraspecific contests to interspecific conflict as in the case of aggression directed towards brood-parasites (Trnka et al. 2013). Aggression may also co-vary with other traits to form behavioral syndromes (as defined in Sih et al. 2004, Mowles et al. 2012). Consistently bold fiddler crabs, *Uca mjoebergi*, engage in more fights than consistently shy individuals (Reaney & Backwell 2007) and a recent study of water-striders shows that hyper-aggressive males have high activity rates in comparison with normally aggressive males (Chang & Sih 2013). In addition to crustaceans and insects, correlations between aggression and behaviors measured in other contexts have been demonstrated among other taxa, including teleosts (Huntingford et al. 1976, Westerberg et al. 2004, Bell 2005, Ruiz-Gomez & Huntingford 2012) and arachnids (Riechert and Hedrick 1993). A study on European hermit crabs, *Pagurus bernhardus*, where boldness, exploration and aggression were measured twice in each individual, demonstrated behavioral syndromes of boldness and aggression, and boldness and exploration that were both stable across risk levels (Mowles et al. 2012). Crabs that had short startle responses had consistently lower latency to attack another crab and to investigate a novel object. The startle responses themselves show repeatable duration over time (Stamps et al. 2012, Briffa 2013a) and across situations (Briffa et al. 2008, Briffa & Bibost, 2009, Briffa et al. 2013). Thus, in the case of hermit crabs, this behavioral syndrome involving startle responses and aggression appears to be a personality trait.

Despite these studies of aggressiveness as a personality trait, relatively little is known about how an individual's personality will contribute to its RHP. One approach is to investigate the consistency in aggressiveness itself and determine whether individuals that show consistently high levels of aggression are also consistently likely to win contests. The

link between the agonistic behavior of a focal individual relative to that of its opponent and the focal individual's chance of winning is well established for pair-wise contests (e.g. Hardy & Briffa 2013). In a study on the swordtail *Xiphophorus birchmanni*, Wilson et al. (2013) show how the link between aggressiveness (itself a stable suite of co-varying agonistic behaviors) and dominance is repeatable across several contests. Aggressiveness in fish may even be stable across major life history transitions such as sex-change in the sequentially hermaphroditic reef fish *Parapercis cylindrica* (Sprenger et al. 2012). Another approach is to determine whether a repeatable behavior measured in a different (i.e. non-agonistic) context co-varies with the chance of victory during a contest. Reaney and Backwell (2007) assessed boldness in *U. mjoeberti* males by recording the latency to re-emerge from burrows after being startled by a simulated predator. In subsequent contests over burrow ownership bold males were more likely than shy males to evict other males from their burrows (although shy males evicted more females). Similarly, in the sea anemone *Actinia equina*, individuals showing consistently short startle response durations prior to a contest were the most likely to win the contest (Rudin & Briffa 2012). Re-measurement of startle responses after contests indicated outcome-dependent plasticity in this behaviour, with losers that had been injured showing an increase in startle response duration. Furthermore, in losers the correlation between individual startle responses measured across occasions interrupted by a fight was reduced. Although only a few studies have examined post-fight behavioural change from an animal personality perspective, a number of studies have demonstrated how the experience of engaging in a fight can influence the outcome of subsequent encounters. The 'winner and loser effect' occurs when contest outcomes predict an individual's chance of victory in subsequent contests (Hsu & Wolf 1999, Hsu et al. 2006). Studies on the mangrove killifish, *Kryptolebias marmoratus*, show how hormonal changes contingent on fight outcomes can promote changes in agonistic behavior (Chang et al. 2012, Earley et al. 2013), and that the

effect of these changes in endocrine status may interact with the individual's prior dominance status (Lan & Hsu 2011). On the other hand, little is known about functional aspects of post-fight behavioral change. Understanding how such changes carry-over into other behavioral contexts might further explain why winner and loser effects emerge. For example, in contests where both opponents fight in the same way, high boldness and aggression are typically associated with a greater chance of winning (e.g. Rudin & Briffa 2012, Wilson et al. 2013). Thus in the case of *A. equina*, we hypothesized that the post-fight changes in boldness might promote further victories for winners and further losses for losers (Rudin & Briffa 2012). Many contests, however, are asymmetrical with each opponent adopting a different role and utilizing a different set of agonistic behaviors. This type of contest is common whenever one opponent attempts to wrest a resource unit away from the current owner. In these cases a given personality trait might differentially affect the ability to perform each role. Equally, post-contest behavior might be subject to different levels (or types) of change for each role.

Shell fights in *P. berhnardus* provide such an example of contest behavior where there is a clear role-asymmetry with each opponent performing very different agonistic behaviors. These encounters begin with a pre-fight period where both roles assess one another's cheliped displays (Elwood et al. 2006) but during the subsequent escalated phase the role-asymmetries become apparent. Escalated shell fights are initiated when one individual (the attacker) lunges at an opponent (the defender). The attacker grasps the defender's shell with its walking legs and inserts its chelipeds into the defender's shell. Meanwhile, the defender withdraws tightly into its own shell. Shell fights are characterized by repeated bouts of rapid shell rapping signals, where the attacker strikes its shell against that of the defender in a demonstration of stamina (see Briffa et al. 1998, Briffa & Elwood 2000, Briffa & Elwood 2002, Mowles et al. 2009, 2010). These bouts are separated by pauses and the vigor of shell rapping can be quantified in terms of the total number of raps, the total

number of bouts, the mean number of raps per bout and the mean duration of pauses. Shell fights can end in one of two ways. First, the attacker may decide to give up without first evicting the defender. Second, the defender may decide to give up, releasing its abdominal grip on the shell and allowing the attacker to evict it by pulling it out through the aperture. In this case the attacker will usually discard its own shell and enter the shell that the defender has been evicted from.

In previous studies of shell fighting it has been shown that different proximate mechanisms drive the agonistic behavior of each role during shell rapping and that post-fight physiological state varies between roles and outcomes (Briffa & Elwood 2000, 2004). Analyses of these physiological constraints and agonistic behaviors indicate that during this escalated phase of the encounter attackers and defenders may also use different assessment activities. Defenders seem to monitor the activity of attackers and this information influences their persistence time (Briffa & Elwood 2002, 2004). Attackers on the other hand have only limited information about the defender, and they give up on the basis of an individual cost threshold. These two modes of assessment are equivalent to the mutual and self-assessment discussed by Briffa & Elwood (2009) (see also Arnott & Elwood 2009), attackers switching from mutual assessment before shell rapping to self-assessment during shell rapping. Thus the two roles in shell fights are subject to asymmetries in information and in the effects of internal state. Since personality may be related to stable differences in underlying state there is the potential for personality to show different relationships with RHP for each role during and following asymmetric contests. The aim of this study is to determine whether startle responses in *P. bernhardus* are predictive of RHP for attackers and defenders, both in terms of their ability to win fights and in terms of the vigor of shell rapping performed by attackers upon which their chance of victory is highly dependent (Briffa et al. 1998). Furthermore, we ask whether startle responses are subject to changes (in mean level and in the consistency of

between individual differences), according to the role adopted during the contest and to its eventual outcome. If boldness is predictive of RHP then we expect to see significant correlations between startle response durations measured before fights and subsequent performance in a fight. If startle responses change as a result of engaging in a fight, then we would expect to see correlations between these fight parameters and post-fight startle response durations.

Methods

Animal collection and maintenance

We collected crabs inter-tidally from Hannaford Point, Cornwall, U.K. between February and March 2013, and immediately transported them back to the laboratory and held them in groups of approximately 100 individuals in 125L of constantly filtered and aerated seawater at 15°C. We removed the crabs from their shells by carefully cracking the shell in a bench vice, and then sexed and weighed the naked crabs. To avoid known sex differences in shell preference (Neil & Elwood, 1985) and agonistic behavior (Briffa & Dalloway 2007) we discarded females from the experiments and provided them with new shells before returning them to the sea. We only used males free from missing appendages, obvious parasites and recent molt in the experiments.

Experiment 1: Startle responses and shell fights

As in previous studies of shell fighting (Briffa et al. 1998, Briffa & Dalloway 2007, Briffa & Elwood 2000, 2002, 2004, 2007, Mowles et al. 2009) we allocated crabs to pairs ($N = 100$ pairs) comprising a larger crab (the attacker) and a smaller crab (the defender). Attackers

ranged in mass from 0.2 to 1.56g and defenders ranged from 0.13 to 1.22g, but within a pair the attacker was always larger than the defender. This size asymmetry is necessary in order to ensure that attackers initiate a contest. We housed each crab of the pair in an individual crystallizing dish containing aerated seawater at 15°C and supplied attackers with a new *Littorina littorea* shell of 50% of its preferred shell mass (calculated from a regression line obtained from a previous shell selection experiment, Briffa & Elwood 2007) and defenders were supplied with a shell that was 100% adequate for the larger crab. We allowed the crabs to enter their new shell and two startle response durations were then obtained. As described in previous studies (e.g. Briffa et al. 2008), to obtain a startle response, we lifted a crab out of the seawater by hand and held it in an inverted position. This causes the crab to withdraw into its gastropod shell. After 5s the crab is replaced into the dish in this inverted position with the aperture facing upwards. We timed the duration of the startle response from when the crab was replaced in the dish until the walking legs first touched the floor of the tank. We obtained the first startle response 2 hours after the crab entered its shell and the second after another 16h. This was timed so that the end of the second startle response occurred at least 10 minutes before the two crabs were induced to engage in a shell fight.

To induce a shell fight, we transferred the two crabs of each pair to a third dish, placed behind the one-way mirror of an observation chamber, such that the observer was unseen by the crabs. When shell fights ensued, we recorded the pattern of shell rapping and the eventual outcome of the encounter (eviction; $n = 76$, or non-eviction; $n = 24$) using a Psion Workabout handheld computer configured as a time-event recorder using The Observer XT 7.0 event recording software (Noldus IT). From this we calculated the total number of raps, the total number of bouts, the mean number of raps per bout and the mean duration of pauses (Briffa et al. 1998). When the fight was resolved, we returned the crabs to their individual dishes and in this ‘after fighting situation’, we obtained startle responses from each

crab on two further occasions, the first immediately after the fight. Due to time constraints, we obtained the second startle response 2 hours later, so the time period separating the two post-fight startle responses was shorter than the period separating the two pre-fight startle responses. While a shorter inter-observation period could potentially elevate the strength of behavioral consistency, this was unlikely to have occurred in this study as we only found reduced correlations between startle responses post-fight, rather than increased correlation coefficients (see below).

Experiment 2: Startle responses in the absence of shell fighting

Since shell fighting may result in an exchange of shells (i.e when fights end with an eviction) and shell size influences the startle responses of hermit crabs (Briffa & Bibost 2009) we conducted a second experiment to assess the effects on startle response duration of removing hermit crabs from their original shells and supplying them with new shells, and of shell changing behavior, in the absence of a fight. We allocated crabs to pairs and provided them with new shells, as described above for Experiment 1, so as to provide a nominal attacker and a nominal defender. We again obtained two initial startle response durations for each crab. We then subjected the crabs to one of two treatments. In the first group ($n = 25$ pairs) each crab remained isolated in its crystallizing dish for 16h. In the second group each crab also remained isolated but we provided it with an alternative empty *L. littorea* shell, equivalent in mass to that which the crab would have occupied if had it engaged in a shell fight that ended in an eviction. Of the 25 pairs used in group 2, 17 nominal attackers and defenders chose to change shells during the 16h isolation period. For crabs in both groups we then obtained two final startle response durations from each crab on two further occasions, separated by another 2 hours isolation period. Thus group 1 (no shell change) and group 2 (shell change) are

analogous to the non-eviction and eviction outcomes in Experiment 1 and the initial and final situations are equivalent to the before fight and after fight situations in Experiment 1.

Statistical methods

In order to determine the individual consistency of startle responses for attackers and defenders, before and after fights, we calculated a series of Pearson correlation coefficients. These provide an appropriate measure of consistency for data obtained across two occasions (Nakagawa & Schielzeth 2010). By comparing the 95% confidence intervals of the correlation coefficients, we can then determine whether there are significant differences between consistency estimates obtained in different situations. For experiment 1, we calculated before and after-fight correlation coefficients for attackers and defenders. These analyses were performed for all shell fights combined, and then separately for shell fights that ended in evictions and non-evictions. Since sample sizes differed between outcomes, we did not compare correlation coefficients between evictions and non-evictions. We do, however, make comparisons between correlation coefficients obtained before and after fights within each outcome. For experiment 2 we calculated correlation coefficients across occasions one and two for the initial and final situations (as defined above) for nominal attackers and nominal defenders.

In order to determine the effect of engaging in a fight, and the outcome of the fight, on startle response duration, for attackers and defenders, we used a three-within, one between repeated measures ANOVA (Briffa & Elwood 2010). For Experiment 1, the between-group factor was the outcome of the fight (eviction or non-eviction). The three within-observation factors were specified with a nested structure that reflected the hierarchical nature of the data. Each fight involved two roles, attacker and defender. For each attacker and defender, startle responses were obtained in two situations, prior to the fight and after the fight. And within

each situation, startle responses were obtained on two occasions. Therefore, the within-observation factors were occasion (one or two), which was nested within situation (before or after fighting), which in turn was nested within role (attacker or defender). A similar analysis was conducted for data from Experiment 2, but here the levels for situation were ‘initial’ or ‘final’ and the levels for the between-observation factor, outcome, were called ‘shell change’ or ‘no shell change’. Although significant interaction effects are superseded by lower order effects, understanding the direction of main effects and lower order interaction effects can assist with the interpretation of higher order interactions. Therefore, as in previous studies, we prefer to report all of the results from the ANOVA tables, prior to describing the highest order interactions. Finally we used Pearson correlation coefficients to determine whether startle responses varied with the duration of fights and the performance of shell rapping, and we compared the vigor of shell rapping between outcomes using unpaired t-tests. Data were not normally distributed and we therefore $\text{Log}_{10} + 1$ transformed the data prior to analysis.

Results

Experiment 1- Shell fighting

Pre and post-fight correlations among startle responses

For all attackers and defenders, regardless of the outcome, there was a significant correlation between the startle responses obtained on the two occasions before fighting and between the startle responses obtained on the two occasions after fighting. When attackers only were included, there was no difference between the two correlation coefficients, but for defenders comparison of 95% confidence intervals indicates that the consistency of startle response duration after fighting was lower than that before fighting (Table 1a). For those fights that

ended in an eviction only, startle responses were again significantly repeatable in both situations for each role. However, in the case of evicted defenders, the correlation coefficient was significantly lower after the fight compared to before the fight (Table 1b, Figure 1). In fights that ended in a non-eviction, there was a significant correlation before fights for both roles. However, the correlation was not significant for either role after the fight. Nevertheless, there was no significant difference in the correlation between situations for either attackers that gave up or for defenders that retained their shell (Table 1c).

Pre to post-fight plasticity in startle responses

Overall, startle responses were of greater duration in crabs that engaged in fights that ended with a non-eviction ($F_{1,98} = 6.67, P = 0.011$) and of shorter duration for attackers compared to defenders ($F_{1,98} = 13.32, P = 0.0004$). Startle responses were shorter after fights than before fights ($F_{1,98} = 7.86, P = 0.006$) and for occasion 2 compared to occasion 1 ($F_{1,98} = 6.5, P = 0.012$). There were highly significant interactions between situation and outcome ($F_{1,98} = 12.92, P = 0.0005$) and occasion and outcome ($F_{1,98} = 9.99, P = 0.002$). These outcome-dependent effects of situation and occasion led to a significant three-way interaction effect ($F_{1,98} = 8.25, P = 0.005$). Before fights, there was little difference between startle responses in Occasions 1 and 2, regardless of the eventual outcome of the fight. After fights that ended in a non-eviction startle responses in Occasion 1 were greater than in Occasion 2. For fights that ended in an eviction, startle responses were of shorter duration after the fight compared to before the fight, but there was little difference between the two post-fight occasions (Figure 2). There was no significant interaction between role and situation ($F_{1,98} = 0.012, P = 0.91$) or between role and occasion ($F_{1,98} = 0.3, P = 0.58$) but there was a non-significant trend for a three-way interaction between role, situation and occasion ($F_{1,98} = 3.57, P =$

0.062). For attackers, startle responses tended to be shorter after fights than before, and longer for Occasion 2 compared to Occasion 1. For defenders, initial startle responses were longer than for attackers, but the decline in duration during the post-fight stage of the experiment was absent (Figure 2). There were non-significant trends for interactions between role and outcome ($F_{1,98} = 3.4, P = 0.07$) and between role, situation and outcome ($F_{1,98} = 3.57, P = 0.062$) but there was no interaction between role, occasion and outcome ($F_{1,98} = 1.51, P = 0.27$). There was, however, a significant four-way interaction between outcome, role, situation and occasion ($F_{1,98} = 5.05, P = 0.027$) (Figure 2). For successful attackers that evicted the defender, startle responses were shorter after the fight than before. But for attackers that failed to evict the defender, startle responses were similar before and after the fight; furthermore, for these unsuccessful attackers, startle responses were always of greater duration on Occasion 1 than on Occasion 2. A different pattern was seen in crabs adopting the defender role. Startle responses were longer in successful defenders that resisted eviction compared to those that gave up; after the fight startle responses increased on Occasion 1 but on Occasion 2 had declined to pre-fight levels. For unsuccessful defenders that had been evicted, the post-fight startle responses were of lower duration compared to the pre-fight duration, with post-fight Occasion 1 responses being of lower duration than post-fight Occasion 2 responses (Figure 2).

Startle responses, shell rapping and fight duration

There was no correlation between the mean before-fight startle response of attackers and the number of raps that they performed ($r_{93} = -0.07, P = 0.5$), the number of bouts ($r_{93} = -0.035, P = 0.7$), the mean number of raps per bout ($r_{93} = 0.09, P = 0.4$) or the mean duration of pauses ($r_{83} = 0.1, P = 0.4$). There were no significant correlations between the mean after-fight

startle response of attackers and the total number of raps ($r_{93} = 0.14$, $P = 0.18$), total number of bouts ($r_{93} = 0.11$, $P = 0.26$) or mean number of raps per bout ($r_{93} = 0.06$, $P = 0.55$) that they had performed during the fight. However, attackers that left longer pauses between bouts had longer startle response durations after the fight ($r_{83} = 0.22$, $P = 0.04$) (Figure 3). Defenders that had long startle response durations before the fight received more raps ($r_{93} = 0.321$, $P = 0.001$) (Figure 4) and more bouts of rapping ($r_{93} = 0.312$, $P = 0.002$) during the fight, but there was no correlation between the mean startle response of defenders before the fight and the number of raps per bout performed by attackers ($r_{93} = 0.05$, $P = 0.62$) or the duration of pauses that they left ($r_{83} = 0.13$, $P = 0.22$). These positive correlations between startle response duration and the number of raps ($r_{93} = 0.23$, $P = 0.023$) and bouts ($r_{93} = 0.25$, $P = 0.014$) remained for the defender's startle responses after the fight and again there was no correlation between the startle responses of defenders after the fight and the number of raps per bout that they had received ($r_{93} = -0.02$, $P = 0.82$). After-fight startle response duration in defenders, however, was strongly correlated with the duration of pauses left by attackers ($r_{83} = 0.50$, $P < 0.0001$) (Figure 5). Attackers that evicted the defender performed more raps per bout than those that gave up ($t_{98} = 2.68$, $P = 0.009$) and left shorter pauses between bouts ($t_{83} = 4.1$, $P < 0.0001$).

The number of raps ($r_{97} = 0.46$, $P < 0.0001$) and number of bouts of rapping ($r_{97} = 0.76$, $P < 0.0001$) performed by attackers increased with the duration of the shell fight. The mean startle response durations of defenders before ($r_{97} = 0.34$, $P < 0.0006$) and after the fight ($r_{97} = 0.46$, $P < 0.0001$) the fight also increased with fight duration. These trends remained significant when we consider only evictions, the fights that were terminated by the defender's decision to give up (before $r_{74} = 0.37$, $P < 0.0009$; after; $r_{74} = 0.31$, $P < 0.006$).

Experiment 2 – Non-fighting crabs

In both treatment groups the initial correlation for attackers was unexpectedly low and non-significant. The final correlation for attackers, however, was significant and there were significant correlations within both situations for the defenders in each treatment group (table 1 d-e). Comparison of 95% confidence intervals indicates that for attackers that chose to exchange shells between the initial and final situations, there was an increase in the correlation (table 1d), but for all other groups of crabs there was no change in correlation between situations. In contrast to the situation with crabs that fought there was no significant between-occasion or between-situation plasticity in startle response duration and there was no effect of treatment group (see Supplement 1 for results table).

Discussion

A link between measures of boldness, such as recovery from a startling stimulus, and agonistic behavior has now been demonstrated in several species. This includes hermit crabs where in low risk situations there is a correlation between startle response durations and latency to initiate a contest (Mowles et al. 2012). In the current study we investigated the potential correlation between these repeatable startle responses, fight performance and the outcome of fights for each role. As with previous studies (Briffa et al. 2008, Briffa & Bibost 2009, Briffa & Twyman 2010, Stamps et al. 2012, Mowles et al. 2012, Briffa 2013a, b, Briffa et al. 2013), startle response durations in hermit crabs were generally repeatable in the absence of a fight. Nevertheless, for crabs adopting the attacker role, there is no evidence that boldness is an RHP-linked trait. Startle responses obtained before the contest are not associated with any measure of the vigor of shell rapping and they do not differ between attackers that go on to evict the defender and those that fail to evict the defender. Although

startle response duration is not predictive of RHP in attackers, it is associated with shell fighting in a number of other ways.

The number of raps (and bouts) performed by attackers varied with the pre-fight startle response durations of defenders, defenders with long startle responses receiving more raps than those with shorter responses. A possible explanation for this is that the behavior of attackers is influenced by the personality of defender. Of course, attackers did not have the opportunity to assess the defender's startle responses prior to the fight, but they do have the opportunity to assess the defender during pre-fight chelar displays, which occur before the contest is initiated by the attacker (Elwood et al. 2006). Thus, the prefight period of mutual assessment might reveal some information that carries over to influence the attacker's behavior during the shell rapping phase of the encounter, when attackers are assumed to rely on self-assessment. Another possibility, however, is that defenders that have a tendency to remain withdrawn into their shell for long periods following a perturbation are also more difficult for attackers to evict from their shell during a fight. Indeed, we found that defenders that were not evicted from their shells had longer startle response durations prior to the fights than did those that were evicted. Moreover, long prefight startle responses in defenders were associated with fights of longer duration, which in turn contained more raps.

Perhaps then, bold crabs are at a disadvantage when adopting the defender role, because re-emerging more readily makes them easier to evict. It has been suggested that boldness relates to a fast pace of life and is driven by high metabolic rate, because individuals with high energy demands need to allocate more time for foraging and thus show a lower latency of emergence from a shelter (Biro & Stamps 2008, Réale et al. 2010). If, however, the shelter restricts respiration as in the case of a hermit crab's shell, there is another reason why boldness could be associated with metabolic rate. Individuals with high resting metabolism may need to re-emerge sooner than those with lower metabolic rates because they will

accumulate an oxygen debt more rapidly under restricted access to well aerated seawater. Thus, it seems that repeatable startle response duration is more likely to represent an RHP trait in terms of ability to carry out the defensive role than that of attacker. This result is perhaps counter-intuitive, because in other studies (Rudin & Briffa 2012), boldness is associated with high RHP. On the other hand, this result is less surprising, when we consider that the defender role essentially entails remaining withdrawn into the shell for as long as possible. As well as being influenced by information about the attacker (Briffa & Elwood 2002), the current data indicate that physiological costs and persistence time in defenders might also be influenced by a general (i.e. across contexts) capacity for remaining withdrawn in their shell when startled, threatened or attacked.

Behavioral plasticity and consistency are not mutually exclusive in hermit crabs (e.g. Briffa et al. 2008). Thus behavior at the sample mean level can change while the responses of individuals remain consistent in relative terms. However, contest behavior might disrupt this pattern of temporal or cross-situational consistency. In sea anemones, for example, consistency is reduced after a contest (Rudin & Briffa 2012), indicating that individuals differ in how they respond to the experience of engaging in a fight. In the current study, while startle response duration seems only to be an RHP trait for defenders, there were post-fight changes in mean levels and in consistency for both roles. Startle responses were correlated on the two occasions prior to fights for both attackers and defenders, regardless of the eventual outcome of the subsequent shell fights. For fights that ended in an eviction this pattern of significant correlation remained after the fight was resolved, but for fights that ended without an eviction the degree of correlation was reduced to the point where it was not significant for either attackers and defenders. Note that for this group of crabs, there were significant correlations before the fight. Thus, although fewer contests ended in non-evictions compared to evictions, it is unlikely that this reduction in consistency after fighting is simply due to a

relatively low sample size, given that the number of individuals was sufficient to reveal strong correlations in startle responses before fighting.

Although the correlations were no longer significant after fights that ended in a non-eviction, there was no significant difference in consistency before and after fighting for successful defenders (Table 1c). In fights that ended in an eviction, however, there was a significant change in the correlation for defenders but not attackers (Table 1b). Thus, crabs that receive shell rapping were more likely to undergo a change in startle response duration than those that performed it. Indeed, mean-level changes in startle response duration following a fight appeared to be much more marked in defenders compared to attackers, especially during the first occasion after fighting. Overall, startle responses were greater for defenders than for attackers, but on the first occasion after fighting the duration for defenders only was dependent on the outcome. Evicted defenders were less cautious, showing a marked decrease in duration compared to the pre-fight situation, while defenders that successfully resisted eviction showed a clear increase in startle response duration. Again, this result is somewhat counterintuitive. Without considering the possible constraints on withdrawal duration, we would perhaps have expected victorious defenders to be emboldened, and show shorter startle responses after the fight, similar to the pattern seen in sea anemones (Rudin & Briffa 2012). On the other hand, remaining hidden in the shell entails physiological costs due to the inherent restriction of aerobic respiration, and in the absence of any benefit this behavior should be minimized. For defenders that were evicted, the lower startle response durations immediately after fighting are likely to reflect physiological changes that occurred during the fight. Indeed, for evicted defenders the recovery in startle responses between the first and second occasions after fighting is consistent with post-fight recovery from these effects. Victory for defenders on the other hand may either be dependent on a high capacity for remaining withdrawn, or alternatively might promote this costly hiding behavior for a

limited post-fight period. Overall, the post-fight loss of significant correlations in defenders can be attributed to two causes; the outcome dependent nature of the mean startle response duration immediately after the fight (after fight occasion 1) combined with the relatively short lived nature of these mean level changes as evidenced by the return of pre-fight startle response durations seen in the second occasion after fighting.

An important driver of plasticity in startle response duration in hermit crabs is shell quality in terms of characteristics including color (Briffa & Twyman 2010) and size with crabs showing longer startle responses in shells that were 75% compared to 100% optimal (Briffa & Bibost 2009), attributed to elevated risk when shells are too small. By definition, shell fights have the potential to result in a change in shell optima, with both opponents typically experiencing an improvement in shell quality if shells are exchanged. Therefore, post-fight changes in mean level startle responses or indeed in the consistency of startle responses could be influenced by changes in shell optima. Similarly, for successful attackers in this experiment that changed from a 50% adequate shell before the fight to a 100% adequate shell after the fight, startle responses decreased in the larger shell. Smaller shells provide less protection, which might explain why crabs in small shells appear to be relatively risk-averse. Conversely, another feature of smaller shells may act counter to longer startle responses. When crabs withdraw into shells that are too small the aperture becomes crowded by the chelipeds and cephalothorax, while the coxae of the walking legs, through which the inhalant respiratory current is drawn, remain within the shell, distal to the blocked aperture. Therefore, due to the low aperture diameter, in addition to providing poor protection, small shells may place a respiratory constriction on the crab (Doake & Elwood 2011), potentially placing a limit on the duration of withdrawal. Thus, it appears that perception of risk overrides any physiological effects of small shell size. Nevertheless, interactions between risk level and physical constriction might contribute to the effects of shell size on startle response

duration. These effects of having a small shell might explain why defenders had longer startle responses before fights compared to attackers. Such shell-optima dependent changes, however, are less likely to explain the changes observed after fighting. First, the pattern of seen in the fighting experiment differs from that seen in experiment 2 that did not involve fights. Here there was no change in startle response following a change of shell that represented a 50% increase in shell size for attackers and decreases in shell size for defenders. Second, the most marked changes as a result of fighting were seen in fights that ended in a non-eviction, where crabs did not change shells.

What seems clear is that while startle responses in hermit crabs can be stable temporally and stable across situations, engaging in agonistic behavior can significantly disrupt the pattern of consistent between-individual differences in behavior. In this regard the overall relation between aggression and personality seen in hermit crabs is similar to other species where this question has been addressed, although the direction of these role and outcome specific effects differs. In sea anemones, *Actinia equina*, startle responses (tentacle retraction following a squirt of sea water aimed at the oral disc) showed significant individual consistency both in the animal's natural habitat and in the laboratory (Rudin & Briffa 2012). However, after a fight consistency is reduced (again to non-significant levels) in losers that received stings from the opponent (Rudin & Briffa 2012). Taken together this previous result on anemones and the current data on hermit crabs suggest that recipients of agonistic behavior may be particularly liable to a change in the stability of their behavior. This possibility warrants further investigation and with sufficient data on post-fight behavior it would be possible to test this idea directly by quantifying the amount of intra-individual variation in behavior (IIV), as described by Stamps *et al.* (2012). The potential for IIV to influence contest behavior has already been quantified in fights in male fallow deer, *Dama dama* (Jennings *et al.* 2013). Here, individual residual variance in the propensity to escalate

the contest was investigated, but as yet little is known about how the experience of an agonistic encounter could carry-over into other behavioral contexts in the longer term. Post-fight changes in behavior may be linked to contest outcomes (Rudin & Briffa 2012, Stevenson & Rillich 2013), as a result of contest intensity (Garcia et al. 2012) or the need for post-conflict reconciliation (Aureli et al. 2002). Various mechanisms such as injury (Rudin & Briffa 2012) and endocrine changes (Earley et al. 2006) can be involved in promoting this behavioral plasticity, which in turn could contribute to the winner and loser effects that have been reported in several species (Hsu et al. 2006). Understanding how agonistic behavior spills over into other contexts, and how permanent or short-lived these changes might be, has the potential to improve both our understanding of the consequences of fighting, such as winner and loser effects, and of the underlying causes of the consistent between individual differences in behavior referred to as animal personality. In particular, further studies linking fighting and personality with metabolic rate are warranted. Furthermore, it is interesting to note that defenders, which show behavioral plasticity in terms of adjusting their agonistic behavior according to their perception of the attacker (Briffa & Elwood 2002, 2004) also show plasticity in post-fight startle responses. Attackers on the other hand, which rely on self-assessment do not show this post fight plasticity. Therefore differences in assessment mode, as well as in physiological costs, may be linked to the different effects of fighting for each role. Overall, the current study demonstrates that in asymmetric contests boldness is not necessarily associated with high RHP. Pre-fight startle responses in attackers did not influence the chance of winning but for defenders those with longer startle responses were more likely to win. These role specific links between personality and fighting also extend to post fight changes in startle response duration, the direction and magnitude of these changes depending on the role adopted during the contest.

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Research output: Contribution to journal › Article

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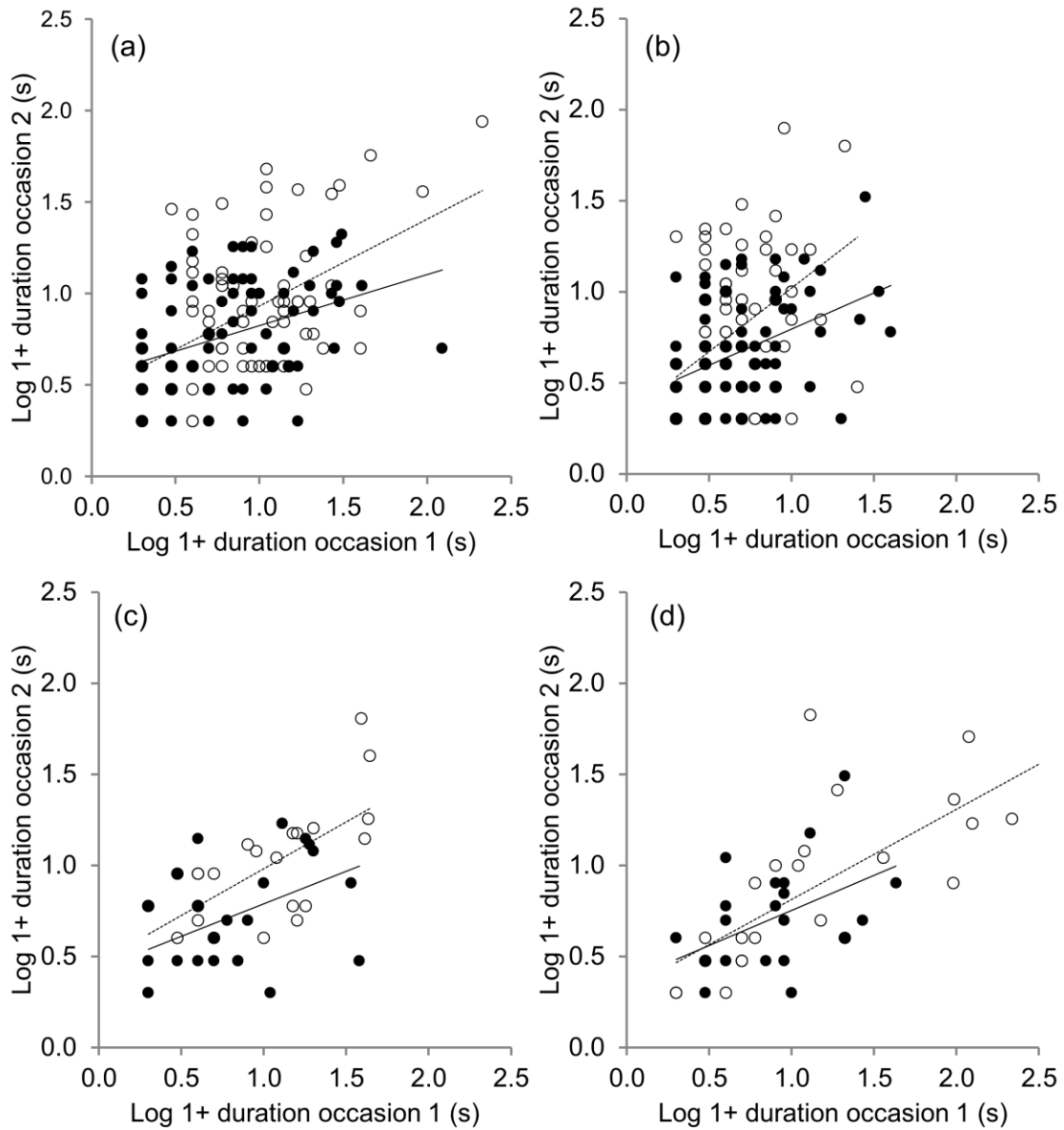


Figure 1: Correlations between startle response durations before (a, c) and after (b, d) fighting for fights that ended in evictions (a, b) and non-evictions (c, d) for attackers (filled circles, solid lines) and defenders (empty circles, dashed lines). Regression lines fitted for illustration.

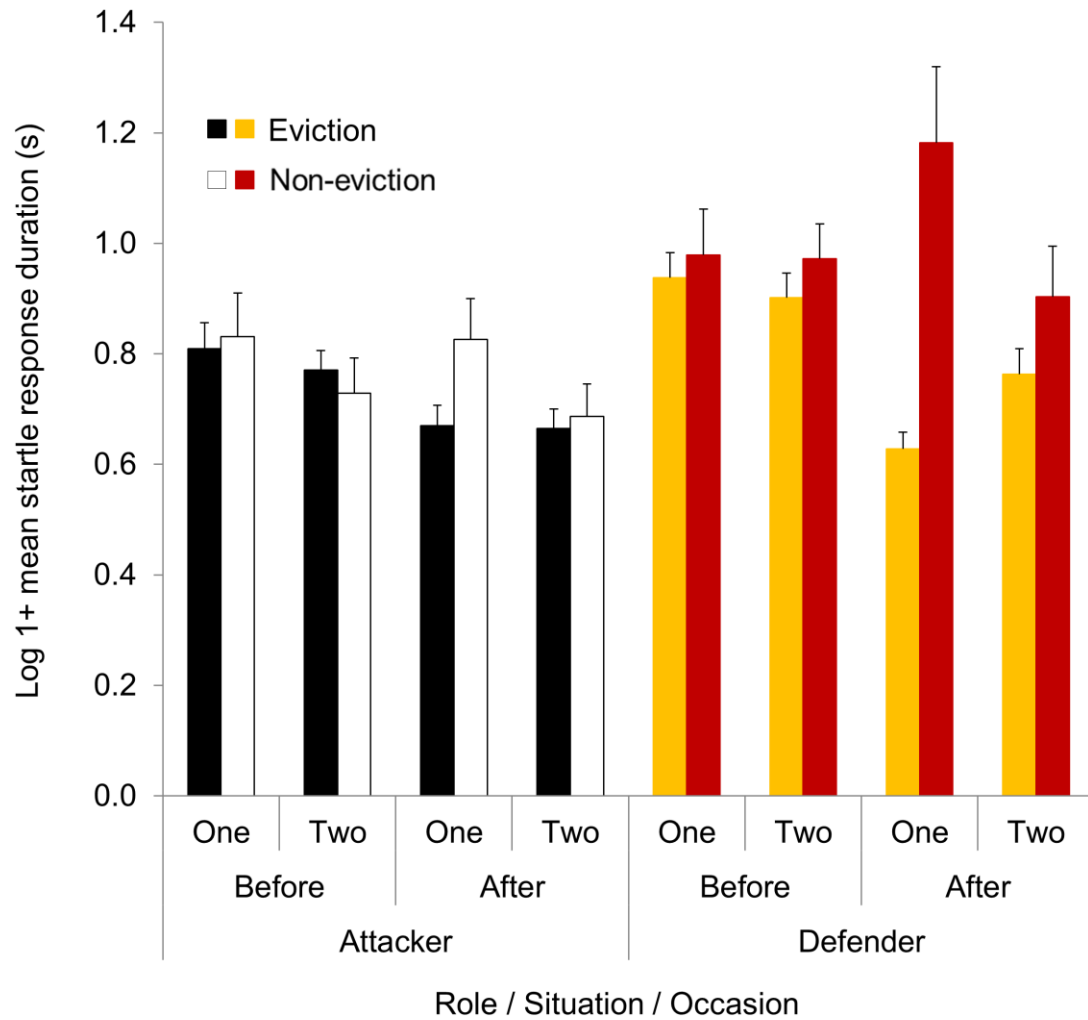


Figure 2: The interaction effect between occasion, situation, role and outcome on mean startle response duration. Black and white bars represent data for attackers and color bars show data for defenders. Error bars show standard errors.

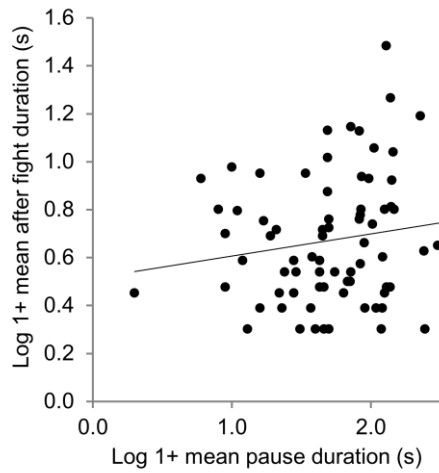


Figure 3: The positive association between mean duration of pauses during the fight and the mean after-fight startle response of attackers. Regression line fitted for illustration.

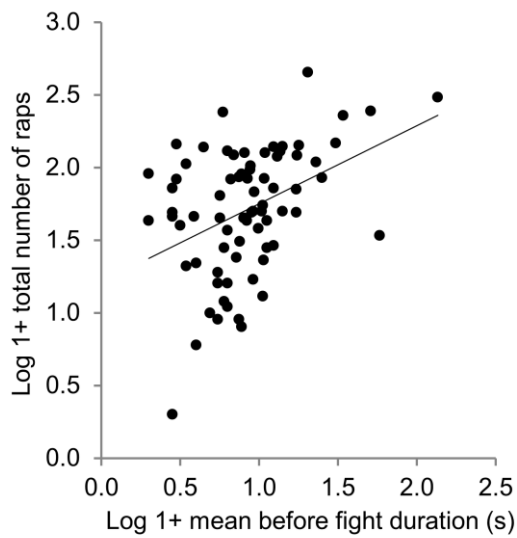


Figure 4: The positive association between the mean before-fight startle response duration of defenders and the total number of raps that they received from attackers during the fight. Regression line fitted for illustration.

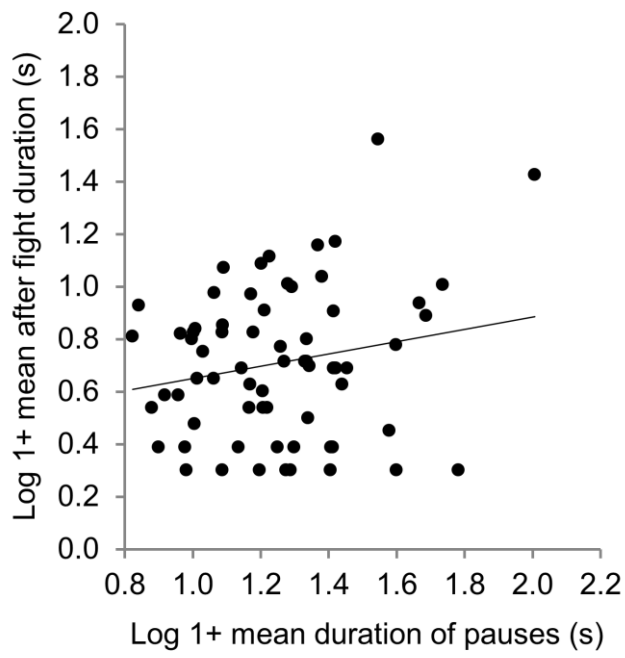


Figure 5: The strong positive association between mean duration of pauses during the fight and the mean after-fight startle response of defenders. Regression line fitted for illustration.

Table 1: Individual behavioural consistency estimates (Pearson correlation coefficient) for different roles in each situation.

Role	Correlation before fights ¹			Correlation after fights ¹		
	<i>r</i>	95% CI	<i>P</i>	<i>r</i>	95% CI	<i>P</i>
<i>(a) All fights (n= 100)</i>						
Attackers	0.393	0.213, 0.547	< 0.0001	0.375	0.192, 0.532	< 0.0001
Defenders	0.647	0.551, 0.769	< 0.0001	0.286	0.095, 0.457	< 0.004
<i>(b) Evictions only (n = 76)</i>						
Attackers	0.381	0.17, 0.559	< 0.0006	0.388	0.178, 0.564	< 0.0005
Defenders	0.685	0.543, 0.789	< 0.0001	0.381	0.17, 0.559	< 0.0006
<i>(c) Non-evictions only (n= 24)</i>						
Attackers	0.442	0.047, 0.718	< 0.03	0.353	-0.06, 0.66	< 0.1
Defenders	0.703	0.417, 0.862	< 0.0001	0.387	-.019, 0.684	< 0.1
<i>(d) No fight plus shell change (n = 17)</i>						
Attackers	0.072	-0.423, 0.53	= 0.79	0.856	0.637, 0.947	< 0.0001
Defenders	0.685	0.305, 0.877	< 0.002	0.465	-0.20, 0.773	< 0.002
<i>(e) No fight without a shell change (n = 25)</i>						
Attackers	0.251	-0.16, 0.588	= 0.23	0.571	0.227, 0.788	< 0.025
Defenders	0.570	0.225, 0.788	< 0.025	0.656	0.351, 0.835	< 0.0002

¹For rows (d) and (e) these columns contain data for initial and final startle response durations for non-fighting hermit crabs.