



# Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*

M. Briffa\*, R. W. Elwood and J. T. A. Dick

School of Biology and Biochemistry, The Queen's University of Belfast, 97 Lisburn Road, Belfast BT9 7BL, UK

Shell exchanges between hermit crabs may occur after a period of shell rapping, when the initiating or attacking crab brings its shell rapidly and repeatedly into contact with the shell of the non-initiator or defender, in a series of bouts. There are two opposing models of hermit crab shell exchange and the function of shell rapping. The negotiation model views shell exchange as a mutualistic activity, in which the initiator supplies information about the quality of its shell via the fundamental frequency of the rapping sound. The aggression model views shell rapping as either detrimental to the defending crab, or as providing it with information about the initiator's ability or motivation to continue, or both. The negotiation model makes no predictions about the temporal pattern of rapping, but under the aggression model it would be expected that crabs that rapped more vigorously would be more likely to effect an exchange. Repeating the signal could be expected under either model. Crabs that achieve an exchange rap more vigorously, rapping is more persistent when a clear gain in shell quality may be achieved, and the vigour is greater when the relative resource-holding potential (or 'fighting ability') is high. These findings support the aggression model rather than the negotiation model. Contrary to the predictions of game theory, crabs that do not effect an exchange appear to signal that they are about to give up. The data suggest that rapping is performed repeatedly because the accumulation of all of the performances acts as a signal of stamina.

**Keywords:** hermit crab; shell fighting; repeated signals; aggression; communication; negotiation

## 1. INTRODUCTION

Hermit crabs interact in pairs in apparently agonistic encounters, at the end of which there may be an exchange of shells. During the encounter, the initiating crab hits its shell, in a series of bouts, against that of the non-initiator ('shell rapping'). These bouts of rapping are interspersed with pauses, during which the initiator pulls at the chelipeds of the non-initiator and the latter may then evacuate its shell. These encounters are unusual in involving two resources and there is the possibility that both crabs could gain shells more suited for their size (see Dowds & Elwood (1983) for a full description of shell fighting). For example, a large crab in a shell that is too small may exchange with a small crab in a shell that is too large (Hazlett 1978). The possibility of mutual gain has given rise to the hypothesis that crabs 'negotiate' over the ownership of shells (Hazlett 1978, 1983, 1987, 1989, 1996). This possibility requires that the non-initiating crab assesses the quality of the initiating crab's shell. Hazlett (1987) suggested that shell rapping conveys this information in the fundamental frequency of the individual raps, but the non-initiating crab must discriminate between the frequency of its own shell and that of the initiator. The fundamental frequency of each shell is assumed to be determined by its volume. After comparing the quality of the initiator's shell with the quality of its own shell, the non-initiating crab would be able to decide

whether to allow an exchange of shells to proceed, by releasing its uropodal grip on its current shell.

An alternative view of shell fights is that they are agonistic encounters over ownership of limited resources. This aggression model (Elwood & Glass 1981; Dowds & Elwood 1983, 1985) could support three different functions for shell rapping, which are not mutually exclusive. First, Elwood & Neil (1992) suggested that shell rapping is in some way detrimental to the non-initiating crab. Rapping could incur a cost for the non-initiator while it retains its shell, either by disrupting the functioning of sensory organs, causing disorientation, or by disrupting the respiratory current of water through the gill chambers, causing an oxygen debt to build up. Second, the rapping might signal the motivational state of the initiating crab for persisting with the attack. Thus, shell rapping would signal the initiator's 'willingness' to expend future time and energy in the contest. Third, it is possible that rapping is primarily determined by the attacking crab's condition and size, rather than by its level of motivation for obtaining the shell of the non-initiator. The initiating crab would in effect be signalling its ability to continue the contest. Thus, either an actual inflicted cost on the defender (i.e. injury or discomfort: possibility 1), or anticipated time costs (possibility 2 or 3) influence the defender's decision to vacate the shell.

Under both models it is reasonable that these encounters involve a series of repeated signals (raps), structured in bouts. The function of repeatedly performing the same signal during aggressive interactions in general has been

\*Author for correspondence (m.briffa@qub.ac.uk).

Table 1. *Percentages of fights and exchanges*( $\chi^2$  tests quoted in the text were performed on raw data.)

group (by large crab)	fights as % of observations	exchanges	no exchange	exchanges as % of observations	exchanges as % of fights
50% <i>Gibb.</i>	100	23	8	74.19	74.19
80% <i>Gibb.</i>	82.75	17	7	58.62	70.83
50% <i>Litt.</i>	77.42	19	5	61.29	79.17
80% <i>Litt.</i>	68.97	15	5	51.27	75.00
total	—	74	25	—	—

reviewed by Payne & Pagel (1996*a,b*, 1997) and the present study provides a test of their conclusions using hermit crab shell fighting as a model.

Apart from the fundamental frequency of individual raps, there are two probable ways in which shell rapping could vary between fights; these are in the physical force of the individual raps, and in the pattern of rapping. The pattern of rapping refers to the temporal spacing of raps, and the number of raps performed. The aggression model, but not the negotiation model, predicts that (i) vigorous, more frequent rapping would be more likely to result in an eviction; (ii) potential gain and, hence, motivation of the initiator would influence the vigour of rapping; and (iii) relatively larger crabs should rap more frequently and vigorously. Furthermore, the aggression model predicts that the potential gains to the non-initiator that a shell exchange would facilitate should not influence the duration of the fight. Under the negotiation model it would be expected that non-initiators that stood to gain would allow an exchange to take place relatively quickly; but when an exchange would only lead to a small gain, or to a decrease in shell quality for the non-initiator, it would be expected that fights would last longer. Here, we determine how the key factors of potential value of resource and the relative size of the contestants influences the fine temporal structure and outcome of fights, and how the structure compares with the predictions of Payne & Pagel (1996*a,b*, 1997).

## 2. METHODS

Littoral specimens of the common European hermit crab, *Pagurus bernhardus*, were collected weekly from Ballywalter, on the coast of the Ards peninsula, Northern Ireland, between February and September 1996. They were held in groups of 75–100 in 60 cm × 30 cm plastic tanks, filled with aerated seawater to a depth of 10 cm, and fed twice weekly on chopped whitebait. Crabs were used within one week and then returned to the sea. The crabs were removed from their shells by cracking the shells open in a bench vice. Males only were used in the experiments, thus avoiding sex differences in behaviour that arise during the breeding season (Neil & Elwood 1985), which encompasses the time of the experiment. Only crabs between 0.12 g and 0.53 g in weight, which were free from (i) obvious parasites, (ii) loss of appendages and (iii) recent moult, were used.

Crabs of the size used in the present experiments show a strong preference for *Littorina obtusata* shells over *Gibbula cineraria* shells and, for both species, particular size shells relative to the size of the crab (Jackson 1988). These preferences have marked fitness consequences (Elwood *et al.* 1995) and have been shown

to influence the probability of initiating a shell fight and engaging in shell rapping (Dowds & Elwood 1983). These preferences are thus used in the present study to vary the potential gain that might be made from a shell exchange.

Four groups of crabs were used, which were defined by the shell supplied to the large crab. In each group, the small crab was supplied with a *Littorina obtusata* shell of optimal weight for the large crab. Large crabs were either supplied with a preferred *L. obtusata* shell, or an unpreferred *G. cineraria* shell, of 50% or 80% of the preferred shell weight for the crab. In group 1 ( $n=31$ ), the large crab was supplied with a 50% of preferred shell weight *G. cineraria* shell, whereas in group 2 ( $n=29$ ), the large crab was supplied with an 80% of preferred shell weight *G. cineraria* shell. In groups 3 ( $n=31$ ) and 4 ( $n=29$ ), the large crabs were supplied with 50% and 80% of preferred shell weight *L. obtusata* shells, respectively. The crabs were isolated in crystallizing dishes and left with their new shells for *ca.* 16 h before any observations were made. Individual raps were recorded using a Psion Organiser hand-held computer (model LZ 64), configured as a time-event recorder using The Observer software package.

Large crabs in group 1 would have had the greatest potential for gaining in shell quality by effecting an exchange, and would therefore be expected to have the greatest motivation for shell acquisition, whereas large crabs in group 4 would have the least potential gain. Large crabs in groups 2 and 3 would have an intermediate potential gain, but it is not clear in which of these two groups the motivation would be higher.

Large crabs weighed between 0.20 g and 0.53 g (mean  $\pm$  s.e. =  $0.308 \pm 0.021$  g) and small crabs weighed between 0.12 g and 0.31 g (mean  $\pm$  s.e. =  $0.206 \pm 0.027$  g). The size differences between large and small crabs ranged from 0.01 g to 0.32 g (mean  $\pm$  s.e. =  $0.109 \pm 0.006$  g). This provided a range of relative weight differences (RWDs), calculated by

$$\text{RWD} = 1 - (\text{weight of small crab} / \text{weight of large crab}),$$

of 0.038 to 0.603 (mean  $\pm$  s.e. =  $0.321 \pm 0.126$ ).

## 3. RESULTS

A total of 120 observations were made, which resulted in 101 fights. Two observations were discarded from the analysis (one each from groups 2 and 3) because the smaller of the two crabs initiated the shell fight and proceeded to rap.

Fights were most likely in group 1 and least likely in group 4 ( $\chi^2_3=11.42$ ,  $p < 0.02$ ; table 1). A similar, although non-significant trend was seen when the number of exchanges in each group is expressed as a percentage of the total number of observations for that group

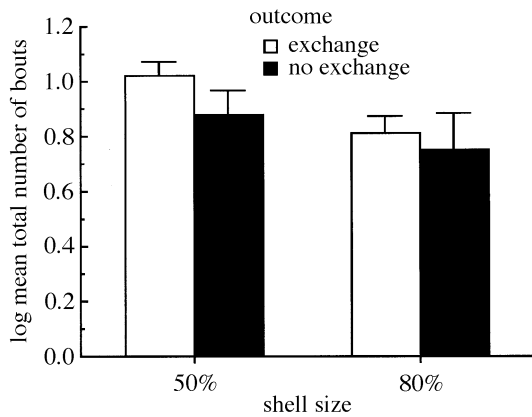


Figure 1. The interaction effect between outcome and shell size on the mean total number of bouts performed by initiators.

( $\chi^2_3=5.293$ ,  $p<0.1$ ; table 1), but not when that number was expressed as a percentage of the number of fights that were initiated in each group ( $\chi^2_3=0.449$ ,  $p$  was n.s.; table 1). The RWD was greater in crabs that effected an exchange (mean  $\pm$  s.e. =  $0.40 \pm 0.02$ ) than in those that did not (mean  $\pm$  s.e. =  $0.28 \pm 0.02$ ) (unpaired, two-tail  $t$ -test,  $t_{97}=2.55$ ,  $p<0.02$ ).

Three-factor ANCOVAs were performed on the  $\log_{10}$ -transformed data for each dependent variable (total bouts, total raps, mean raps per bout and mean time between bouts). The three factors were the outcome of the encounter ('outcome'), the percentage of preferred shell weight of the shell originally occupied by the large crab ('shell size') and the species of the shell originally occupied by the large crab ('shell species'), and the regressor was RWD. The degrees of freedom vary between the different measures because (i) different numbers of non-significant interaction effects were removed from the different measures during calculation of the ANCOVAs, and (ii) because there were fewer replicates for the mean duration of pauses than for the other measures because not all crabs performed more than one bout of rapping. ANCOVA was done using SuperANOVA v. 1.11 (Sibley *et al.* 1991).

Initiators that effected an exchange performed more bouts of rapping than those that did not exchange ( $F_{1,86}=4.03$ ,  $p<0.05$ ; figure 1), and crabs in smaller shells also performed more bouts ( $F_{1,86}=9.35$ ,  $p<0.005$ ; figure 1). Shell species and RWD had no effect on the total number of bouts performed. There was a significant interaction between outcome and shell size, with the difference due to the outcome being more marked when the attacker was in a small shell (50%) than in a large shell (80%) ( $F_{1,86}=5.09$ ,  $p<0.05$ ; figure 1). There were no other significant interaction effects.

Crabs that effected an exchange of shells performed more raps than those that did not effect an exchange ( $F_{1,86}=4.39$ ,  $p<0.05$ ; figure 2), and initiators occupying the smaller shells performed more raps than those occupying the larger shells ( $F_{1,86}=10.58$ ,  $p<0.002$ ; figure 2). The shell species, however, had no significant effect. Again there was a significant interaction between outcome and shell size ( $F_{1,86}=6.82$ ,  $p<0.02$ ; figure 2), but no other significant interaction effects.

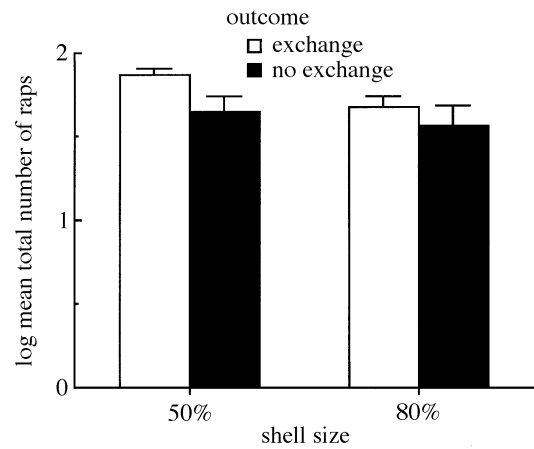


Figure 2. The interaction effect between outcome and shell size on the mean total number of raps performed by initiators.

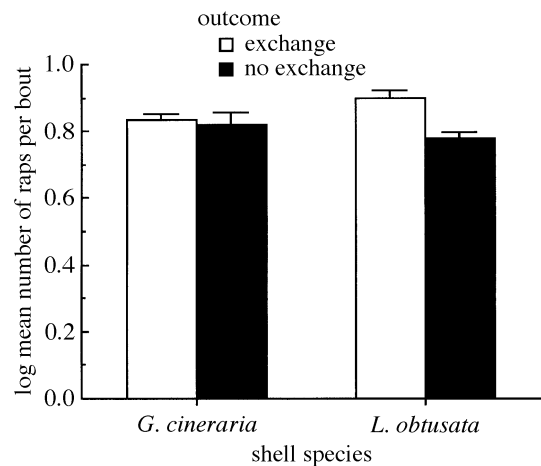


Figure 3. The interaction effect of outcome and shell species on the mean number of raps per bout by initiators.

Crabs that effected an exchange performed more raps per bout of rapping than those that did not effect an exchange ( $F_{1,90}=5.55$ ,  $p<0.05$ ; figure 3), but there was no effect of shell size or shell species. There was an unexpected significant interaction between shell species and outcome, the effect due to outcome being much more marked in crabs occupying *L. obtusata* than those occupying *G. cineraria* shells ( $F_{1,90}=4.15$ ,  $p<0.05$ ; figure 3). There were no other significant interaction effects.

Crabs that effected an exchange of shells left shorter pauses between bouts of rapping than did crabs not achieving an exchange ( $F_{1,87}=15.46$ ,  $p<0.0002$ ; figure 4). There was no significant effect of shell species or shell size. There was a significant effect of RWD, with relatively large crabs leaving shorter pauses than relatively small crabs ( $F_{1,87}=9.15$ ,  $p<0.005$ ; figure 5).

To determine whether the duration of the encounter was affected by the potential change in shell quality that an exchange would facilitate for the non-initiator, the percentage change in deviation from optimal shell quality that would be caused by an exchange was correlated with (i) the total number of bouts and (ii) the total number of raps performed by initiators. The percentage change in deviation ('%CD') was calculated by the following formula:

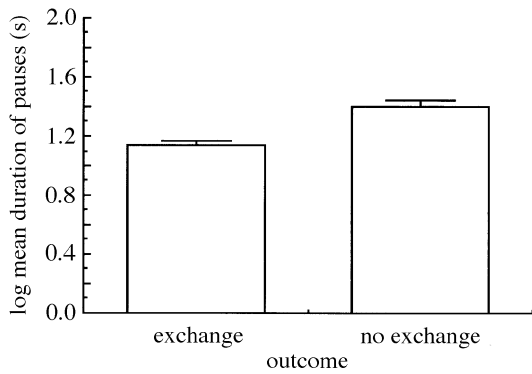


Figure 4. The mean duration of pauses between bouts of rapping for initiators that effected an exchange and those that did not.

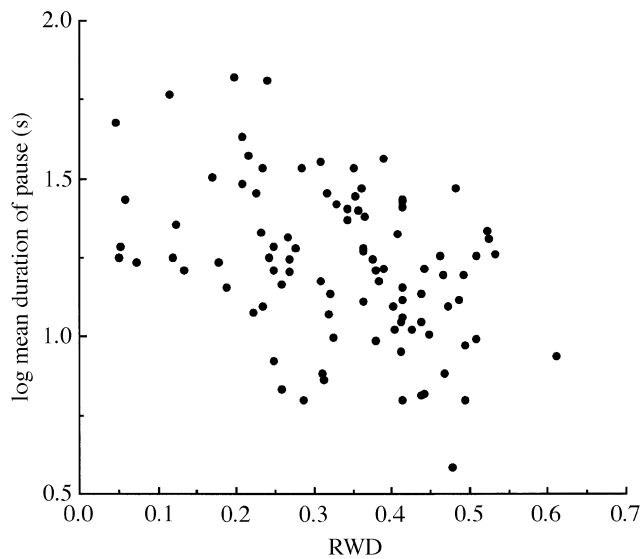


Figure 5. The relationship between relative weight difference (RWD) and the mean duration of the pauses between bouts of rapping.

$$\%CD = \left( \left| 1 - \frac{S_i}{P_n} \right| - \left| 1 - \frac{S_n}{P_n} \right| \right) \times 100,$$

where  $S_i$  is the weight of the shell supplied to the initiator,  $S_n$  is the weight of the shell supplied to the non-initiator, and  $P_n$  is the preferred shell weight of the non-initiator. When calculating the deviations from preferred shell weight before and after an exchange, the sign of the deviation was ignored, such that the magnitude, but not the direction of the deviation was calculated. The %CD was calculated only for non-initiators that were supplied with either 50% adequate or 80% adequate *L. obtusata* shells. The %CD ranged from -58.3% (i.e. the deviation of the weight of the initiator's shell from its preferred shell weight was decreased by 58.3% by the exchange) to +45.8% (i.e. the deviation of the weight of the initiator's shell from its preferred shell weight was increased by 45.8% by the exchange). The mean per cent change in deviation after an exchange was -0.8% ( $\pm 4.3\%$  s.e.) such that, on average, non-initiators made a very small improvement in shell quality (less than 1%) after an exchange had been made. Twenty exchanges resulted in a decrease in the deficit, and 23 resulted in an increase in

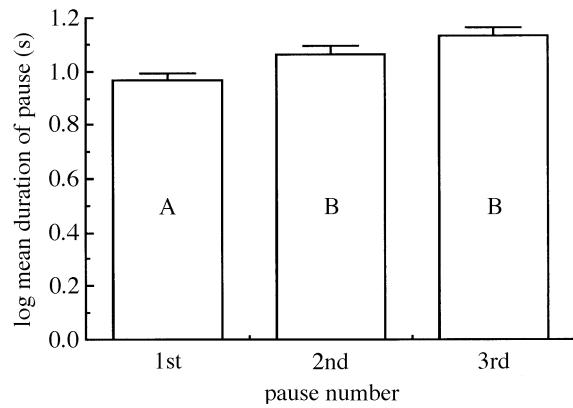


Figure 6. The mean duration of each of the first three pauses, for all initiators regardless of the eventual outcome. Means bearing different letters are significantly different.

deficit. The data for the total number of bouts and the total number of raps were  $\log_{10}$ -transformed. There was no significant difference between fights where the non-initiator would have increased its shell quality and fights where the non-initiator would have decreased its shell quality by exchanging shells in either the total number of bouts (two-tailed, unpaired  $t$ -test,  $t_{41}=1.44$ ,  $p > 0.05$ ) or in the total number of raps ( $t_{41}=0.87$ ,  $p > 0.05$ ) performed by initiators.

To determine whether the measures varied during the course of the shell fight, the number of raps performed during the first four and last four bouts of rapping, and the times between each of the first and last four bouts, were examined. Only crabs that performed at least four bouts of rapping were used in the analysis, which reduced the sample size to 82. Four-factor ANCOVAs were performed. Where the dependent variable was the number of raps performed in each bout, the factors were 'outcome', 'bout number' (repeated measure), 'shell size' and 'shell species'. Where the dependent variable was the duration of the pauses between the bouts, the factors were 'outcome', 'pause number' (repeated measure), 'shell size' and 'shell species'. In both cases, RWD was the regressor. Contrasts (comparison of means) were specified to determine whether there were differences between the number of raps performed in particular bouts or the duration of particular pauses.

The total number of raps performed during the first four bouts of the encounter as a whole was not affected by the eventual outcome of the encounter, shell size or shell species. Bout number had no effect on the number of raps performed in each bout. However, crabs performed more raps per bout when RWD was high ( $F_{1,73}=5.97$ ,  $p < 0.02$ ). There were no significant interaction effects.

The outcome of the encounter, shell size and shell species had no effect on the duration of pauses between the first four bouts. However, the duration of pauses increased over the first three pauses ( $F_{2,148}=8.73$ ,  $p < 0.0005$ ; figure 6). A comparison of means shows that pause 1 was shorter than pauses 2 ( $F_1=5.467$ ,  $p < 0.02$ ) and 3 ( $F_1=10.388$ ,  $p < 0.002$ ), but pause 2 was not significantly shorter than pause 3. Crabs left shorter pauses between bouts when the RWD was high ( $F_{1,73}=6.34$ ,  $p < 0.02$ ). There were no significant interaction effects.

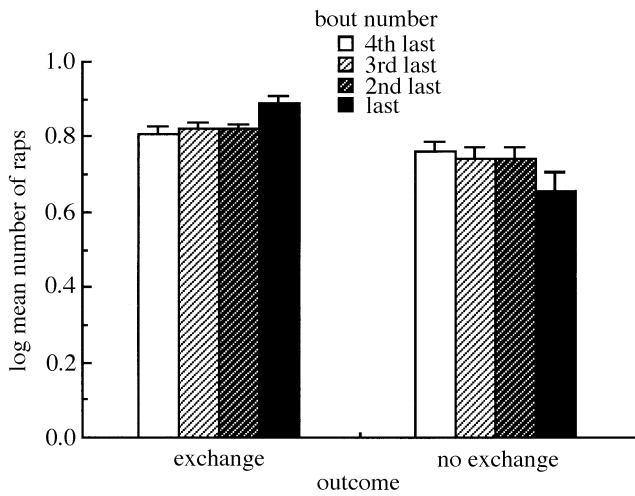


Figure 7. The mean number of raps performed in each of the last four bouts by initiators that effected an exchange and those that did not effect an exchange.

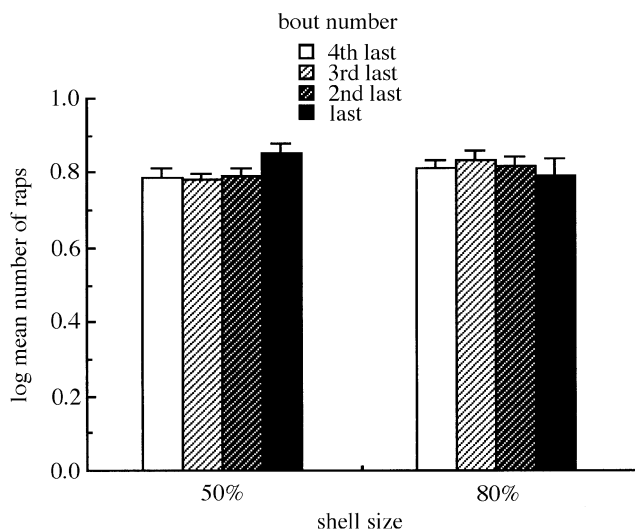


Figure 8. The mean number of raps performed in each of the last four bouts by initiators supplied with 50% adequate and 80% adequate shells.

Crabs that effected an exchange performed more raps during the final four bouts of the encounter than those not achieving an exchange ( $F_{1,73}=11.66$ ,  $p<0.001$ ). Shell size, shell species, bout number or RWD had no effect on the mean number of raps. There was, however, a significant interaction between bout number and outcome, with crabs that effected an exchange performing more raps in each successive bout, with a sharp increase between the second last and the last bout, whereas those that did not exchange shells performed gradually fewer raps in each successive bout ( $F_{3,219}=6.31$ ,  $p<0.0005$ ; figure 7). There was a similar interaction effect between bout number and shell size, with initiators supplied with the smaller shells increasing the number of raps performed in each successive bout during this part of the encounter ( $F_{3,219}=3.56$ ,  $p<0.02$ ; figure 8). There were no other significant interaction effects.

Crabs that effected an exchange left shorter pauses between the last four bouts of rapping than did those not achieving an exchange ( $F_{1,73}=9.61$ ,  $p<0.005$ ), but there

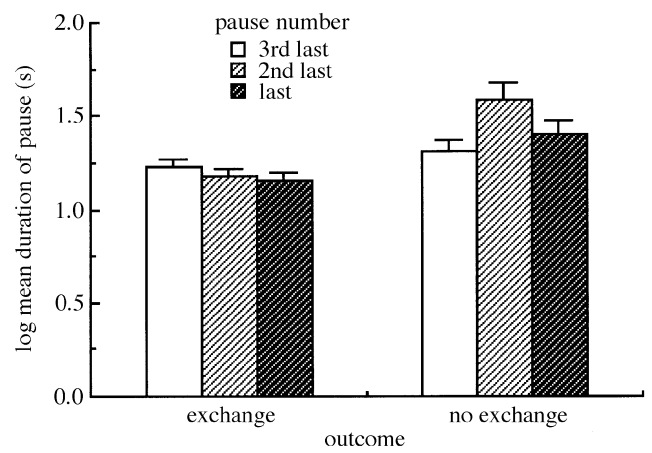


Figure 9. The mean duration of each of the last three pauses for initiators that achieved an exchange and those that did not achieve an exchange.

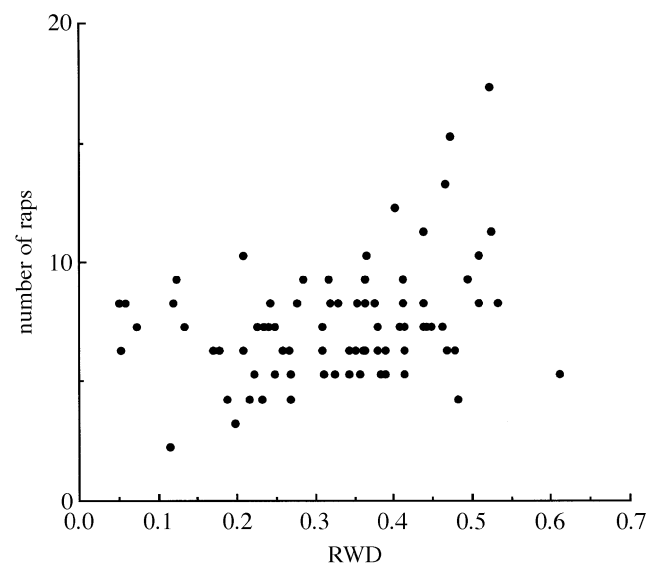


Figure 10. The relationship between relative weight difference (RWD) and the number of raps performed in the fourth bout.

was no effect of shell size or of shell species. Crabs left shorter pauses between bouts when RWD was high ( $F_{1,73}=5.835$ ,  $p<0.02$ ). In crabs that effected an exchange, the duration of the last three pauses gradually decreased, whereas for crabs not achieving an exchange, the duration increased, resulting in a significant interaction effect between bout number and outcome ( $F_{2,146}=5.23$ ,  $p<0.01$ ; figure 9). There was an interaction effect between pause number and shell species ( $F_{2,146}=3.899$ ,  $p<0.05$ ), but no other significant interaction effects.

To determine more accurately when RWD started to affect the vigour of rapping, separate three-factor ANCOVAs were performed on each of the first four bouts and the first three pauses. During the first three of these bouts, RWD had no effect on the number of raps performed in each bout, but in the fourth bout relatively large initiators performed a greater number of raps ( $F_{1,73}=5.26$ ,  $p<0.05$ ; figure 10). Similarly, RWD had no effect on the duration of the first two pauses, but the duration of the third pause was lower for relatively large crabs ( $F_{1,73}=6.27$ ,  $p<0.02$ ; figure 11).

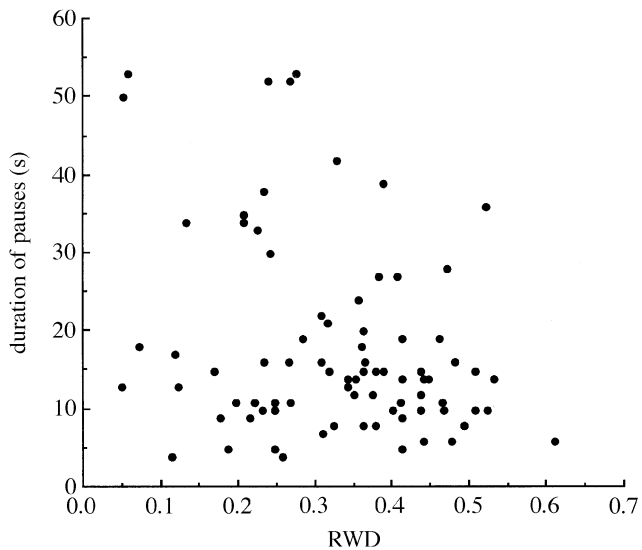


Figure 11. The relationship between relative weight difference (RWD) and the duration of the third pause.

#### 4. DISCUSSION

The aggression model of shell rapping contrasts with the negotiation model in that the latter makes no predictions about the pattern of shell rapping, and how that might influence the decision of the defender. It is clear from the present data, however, that the pattern of shell rapping has a marked effect on the decision of the defender. Initiators that effected an exchange performed more bouts of rapping (figure 1), performed more raps in total (figure 2), more raps in each bout (figure 3) and left shorter pauses between bouts (figure 4). This finding that persistent, vigorous attackers are more likely to effect an exchange, is thus consistent with the aggression model. Attackers that were in shells that were too small (50% adequate) also performed more bouts of rapping (figure 1) and more raps overall (figure 2), and relatively large initiators left shorter pauses between bouts (figure 5), suggesting that persistence and vigour of the fighting is influenced by increased motivation due to high potential gain, and by high relative resource-holding potential (RHP). Again, this is consistent with the aggression model but not the negotiation model. However, there was no effect of shell species on any single parameter of rapping, which is surprising given previous studies showing that crabs in the unpreferred *G. cineraria* shells are more likely to enter into fights and more likely to win into contests than those in *L. obtusata* shells (Dowds & Elwood 1983). The lack of effect of shell size on the mean number of raps performed per bout is also unexpected; it is curious that the number of raps per bout appears to have a clear effect on the decision of the non-initiator to evacuate and yet, apparently, not reflect the motivational state as determined by this measure of potential gain to the initiator.

RWD affects the mean duration of pauses over the whole fight, but not the mean number of raps per bout, when the fight is examined as a whole. Again, this is surprising because this measure appears to have a clear effect on the decision of the non-initiator. When the first four bouts and the pauses between them are examined

separately, however, it can be seen that RWD only has significant effects on the fourth bout (figure 10) and the third pause. This suggests that RWD is only assessed accurately by initiators as the fight progresses, and in this respect is congruent with the 'sequential assessment game' (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist *et al.* 1990). The finding is also consistent with recent attempts to probe motivational state before the commencement of shell rapping as, again, this indicated no effect of RWD at this early stage (Elwood *et al.* 1998). It thus seems that crabs assess which is the larger of the two to determine roles at the start of the encounter (Dowds & Elwood 1983), but that accurate information on relative size difference is only gathered during the fight. The effect of RWD on the duration of pauses persists for the whole fight and is still apparent during the last four bouts. The effect on the mean number of raps per bout appears to deteriorate as the fight progresses, and is not significant over the last four bouts. This could be a result of fatigue, and suggests a trade-off between performing bouts containing a high number of raps against leaving short pauses between bouts.

The negotiation model predicts that the duration of a shell fight is determined primarily by the potential change in shell quality to the non-initiator that would result from an exchange, such that when the potential gain in shell quality is high, exchanges should take place quickly, after relatively few bouts or raps, whereas exchanges should take longer when the potential gain is low or when there would be a loss in shell quality. The present data show no evidence of a relationship between the potential change in shell quality and the duration of encounters and, thus, provide further support for the aggression model over the negotiation model.

The marked changes in the number of raps during the last four bouts of the encounter (figure 7) indicate that initiators that are about to give up reduce their effort, whereas those that are about to effect an exchange appear to increase their effort. This is also reflected in the duration of the pauses during this final part of the encounter (figure 9). This decline in effort before giving up reflects a motivational change and/or the effects of fatigue, but is not predicted by game theory (Maynard Smith 1974; Maynard Smith & Parker 1976; Krebs & Dawkins 1978). However, similar types of de-escalation on the part of the losing participant are seen in other animal contests where an activity is performed in a series of bouts, for example in roaring contests in the red deer *Cervus elephas* (Clutton-Brock & Albon 1979).

There are two possible explanations for the increase in vigour immediately before the evacuation of the non-initiator from its shell. The first is that initiators that effect an exchange are able to time a period of particularly intensive rapping to coincide with the point at which they are likely to evict the non-initiator from its shell. This could be done by assessing the non-initiator's resistance to the pulling actions performed by the initiator; when the level of resistance becomes sufficiently low, successful initiators would perform a short period of relatively intense rapping in order to effect an exchange. Thus, in this case, it is a shift in motivation of the attacker that would initiate the burst of activity. Second, the intensity of rapping could be continuously escalated

and de-escalated until the non-initiator releases its shell during a period of intensive rapping, or manages to escape from the initiator's grasp during a period of low-intensity rapping. Perhaps, then, non-initiators are more likely to give up during a period of high-intensity rapping, but the shift in intensity of rapping does not reflect an assessment by the initiator of the likely persistence of the non-initiator.

It has been suggested that when a decrease in the level of aggressive signalling is exhibited by an animal after defeat in a fight, the lower-level signal inhibits aggression by conspecifics. For example, in the cichlid fish *Astronotus ocellatus*, individuals that have been defeated undergo a change in coloration which appears to serve this function (Beeching 1995). Perhaps the decrease in the vigour of rapping in non-victorious hermit crabs, before giving up, prevents grappling by the non-initiator which can occur after the initiator has released its grip on its shell (M. Briffa, personal observations).

Payne & Pagel (1997) have discussed three possible explanations as to why signals, such as shell rapping, should be repeated by the individual advertising its quality, when a single display of the signal would require less energy to be expended. The first explanation is the 'sequential assessment game' (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist *et al.* 1990). This model is based on the assumption that the assessment of the signaller's quality made by the receiver is subject to sampling error. Therefore, the accuracy of the assessment will improve each time the signal is repeated. A consequence of this is that signallers with a greater RHP are more likely to win the contest, and this is congruent with the results reported here. Furthermore, when the RWD is high, initiators performed more raps per bout and, in particular, left shorter pauses between bouts. However, signallers should also attempt to display at a constant level, such that the receiver can estimate the quality of the signaller with a high level of accuracy; the results here show that the level of intensity of rapping varies during the course of the encounter. In addition, the duration of the encounter should be negatively correlated with the relative difference in RHP, a result not found here. In fact, the negotiation model would be approximately congruent with the sequential assessment model, as a low number of repetitions would be required when a very clear increase or decrease in shell quality could be made by exchanging, whereas in cases when the affects of exchanging are less clear, a relatively high number of raps would be expected.

The second possibility is that displays are repeated because the signaller initially displays at an intentionally low level. The advantage of this would be the saving in energy expenditure that would result if the low-level signal effected a victory. Each successive display is performed at a higher level than the preceding display which it replaces (Payne & Pagel 1996a). This possibility does not match the results reported here, because at the beginning of the encounter the intensity of the signal is de-escalated (figure 6), before being escalated or de-escalated further prior to the resolution of the encounter (figures 7–9). In addition, under this model only a small number of repetitions would be expected; low-quality individuals would signal at their maximum possible level

at the start of the encounter, and high-quality individuals would be expected to be signalling at sufficiently high levels after a very low number of repetitions, to effect a victory (Payne & Pagel 1996a).

The third possibility is that the cumulative result of all of the performed repetitions acts as a signal of stamina (Payne & Pagel 1996b, 1997) or relative RHP. This allows for both the escalation and the de-escalation in the intensity of rapping reported here. De-escalation can occur if the time-associated costs of repeating the signal, such as fatigue or increased risk of predation, increase sub-linearly, that is if the duration of the encounter is doubled the costs are increased less than twice (Payne & Pagel 1996b). The key factors that contribute to the level of fatigue for the initiator are the cost of performing the raps themselves, and the defensive cheliped-flicking activities of the defender, which hinder the ability of the initiating crab to perform shell rapping (Elwood & Neil 1992). The time-associated costs of rapping alone probably increase linearly. However, as the fight progresses, defenders probably perform less cheliped flicks (as a result of oxygen deprivation from the upside-down position in which they are held or as a result of the rapping itself), which causes this component of the time-associated costs to decrease. Overall, the time-associated costs probably increase sub-linearly. De-escalation when the time-associated costs increase in this way presumably allows the signaller to continue signalling high stamina, but at a decreased cost. In the case of initiators that effect an exchange, the terminal increase in vigour could act as a signal that it still has sufficient energy reserves to continue signalling, in order to induce the defender to give up. If this is not successful the initiator could de-escalate the vigour of rapping, and continue signalling. Another feature of this explanation is that, unlike the previous model where the number of repetitions would be expected to be low, the number of repetitions would be expected to be high, as it acts as a signal of stamina. Again, this fits the encounters described here.

These data indicate that the persistence of shell rapping is determined primarily by the motivation of the initiator, whereas the vigour of rapping appears to be affected by relative RHP, such that the aggression model of shell exchange is preferred to the negotiation model. In particular, the vigour of rapping, especially in terms of the duration of the pauses between bouts, contributes to a signal of stamina.

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