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Decision rules, energy metabolism and vigour of hermit-crab fights

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Aggressive interactions between animals are often settled by the use of repeated signals that reduce the risk of injury from combat but are expected to be costly. The accumulation of lactic acid and the depletion of energy stores may constrain activity rates during and after fights and thus represent significant costs of signalling. We tested this by analysing the concentrations of lactate and glucose in the haemolymph of hermit crabs following agonistic interactions over the ownership of the gastropod shells that they inhabit. Attackers and defenders play distinct roles of sender and receiver that are fixed for the course of the encounter. Attackers perform bouts of 'shell rapping', which vary in vigour between attackers and during the course of the encounter, and are a key predictor of victory. In contrast to the agonistic behaviour of other species, we can quantify the vigour of fighting. We demonstrate, to our knowledge for the first time, an association between the vigour of aggressive activity and a proximate cost of signalling. We show that the lactate concentration in attackers increases with the amount of shell rapping, and that this appears to constrain the vigour of subsequent rapping. Furthermore, attackers, but not defenders, give up when the concentration of lactate is high. Glucose levels in attackers also increase with the amount of rapping they perform, but do not appear to influence their decision to give up. Defenders are more likely to lose when they have particularly low levels of glucose. We conclude that the two roles use different decision rules during these encounters.

Keywords: hermit crab; glucose; lactate; agonistic encounter

1. INTRODUCTION

Fights between animals are often resolved by the use of signals that are thought to advertise quality (Parker 1974). For example, red deer engage in 'roaring contests' (Clutton-Brock *et al.* 1979) and birds sing during territorial disputes (Weary *et al.* 1991). Such signals are often performed in a series of bouts but the exact functions of these repeated activities are not clearly understood. It is generally assumed that the use of signals increases fitness by increasing an individual's chance of accessing a contested resource while minimizing the risk of injury (Maynard Smith 1982), but they should be costly to perform in terms of the time and energy expended (Huntingford & Turner 1987). The costs associated with energy metabolism include the depletion of energy reserves and the accumulation of harmful products, such as lactate (Haller 1995; Thorpe *et al.* 1995; Neat *et al.* 1998; Sneddon *et al.* 1999). It has been suggested that costs such as these are the basis of the decision rules that animals use to make strategic decisions during aggressive encounters (Neat *et al.* 1998). Thus, losers should accrue higher costs than winners, and higher blood lactate levels in losers have been demonstrated for fights between cichlid fishes (Neat *et al.* 1998). When dyadic contests are settled by the use of signals, the chance of success should be related to the level at which the signal is performed.

It is often difficult to determine the decision rules that are used by senders and receivers because the two contestants usually alternate between these two roles. During shell fights in hermit crabs, however, the roles of sender and receiver are fixed throughout the encounter. The attacker is usually the larger of the two crabs, and it initiates a fight in an attempt to obtain possession of the shell occupied by a smaller defender, if this offers an improvement in quality over the shell that it currently occupies. The key activity performed by the attacker is 'shell rapping', whereas the defender remains tightly withdrawn into its shell until the encounter is resolved. During shell rapping, the attacker grips the shell of the defender with its walking legs and brings its own shell rapidly and repeatedly into contact with that of the defender in a series of bouts that are separated by pauses. The 'vigour' of rapping varies in terms of the number of raps in each bout and the duration of the pauses between bouts (Elwood & Briffa 2001). After a number of bouts of rapping, the attacker may 'give up' by releasing its grip on the defender's shell or, alternatively, the defender gives up and is pulled out of its shell. In the latter case the attacker chooses to occupy one of the two available shells and the defender occupies the shell discarded by the attacker. The vigour of rapping by the attacker has been shown to be a key predictor of success and is thought to act as a signal advertising relative resource-holding potential (Briffa *et al.* 1998; Briffa & Elwood 2000*a*,*b*). Other species, such as shore crabs (Sneddon *et al.* 1999) and cichlid fishes (Neat *et al.* 1998), which have been tested for metabolite levels during fights, have a much greater choice of activities that vary qualitatively, and do not show repeated bouts that vary quantitatively as do hermit crabs engaged in shell fights. Thus, hermit crabs are an ideal model to assess relationships between fight activity and metabolite concentrations.

We predict that lactate levels should increase in attackers during contests, and that the magnitude of the increase should be proportional to the number of raps performed but should also be moderated by the relative difference in the sizes of the crabs in the contest. Pauses

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between bouts of rapping have previously been described as periods of recovery from fatigue (Briffa *et al.* 1998; Briffa & Elwood 2000*a*), and their duration is thus likely to reflect any increase in lactate levels. Attackers are predicted to give up the contest if lactate levels become particularly high, such that there may be a threshold lactate level upon which their decision is based. These predictions are based on the finding that the agonistic behaviour of attackers is readily influenced by oxygen levels prior to fighting (Briffa & Elwood 2000*c*). In contrast, defenders are not influenced by oxygen levels prior to a contest, and we have no clear prediction as to the effect of lactate levels on this role. Both attackers and defenders are expected to mobilize glucose during the contest, as has been demonstrated during contests between shore crabs (Sneddon *et al.* 1999) and anabantid fishes (Haller 1992), and this ability might also influence decision rules.

2. MATERIAL AND METHODS

(a) *Staging fights and recording behaviour*

Crabs were collected from rock-pools at Minerstown, County Down, Northern Ireland, between January and April 2000. They were held in 100 cm × 60 cm × 10 cm plastic tanks filled with aerated seawater at 10 °C, in densities of approximately 50 crabs per tank, and fed *ad libitum* on catfish pellets. Crabs were used within one week and any unused crabs were returned to the sea. Each crab was removed from its shell by cracking it open in a bench vice and carefully removing the shell fragments from the crab's abdomen. Only male crabs that were free from obvious parasites, had not lost any appendages and had not recently moulted were used in the experiment. The crabs were allocated to pairs comprising a large crab (weight, mean ± s.e.m. = 1.5 ± 0.06 g) and a small crab (weight, mean ± s.e.m. = 0.97 ± 0.04 g). The relative weight difference (RWD) was calculated as:

$$\text{RWD} = 1 - (\text{weight of small crab}/\text{weight of large crab}). \qquad (2.1)$$

After being removed from its shell, each crab was provided with a new shell and isolated for 16 h in an 11 cm diameter crystallizing dish filled with 5 cm of aerated seawater. Males of the size used in this experiment typically occupy *Littorina littorea* shells (Elwood *et al.* 1979), and the preferred weight of shell for each crab was determined from a regression line relating crab weight to preferred shell weight, calculated using data from a shell-selection experiment ($n = 30$). The larger crab of each pair was provided with a *L. littorea* shell that was 50% of its preferred shell weight, whereas the smaller crab of each pair was provided with a shell that was the preferred shell weight for the corresponding larger crab. Thus, the attacker would always improve its shell quality by evicting the defender. The change in shell suitability that an exchange of shells would entail for the defender will co-vary with the size difference between the crabs (Briffa *et al.* 1998). However, defenders have little or no information about the attacker's shell, so this should not affect their motivation to resist (e.g. Dowds & Elwood 1983). The crabs were placed in an arena consisting of an 11 cm crystallizing dish filled with a 1 cm-deep layer of washed sand and 5 cm of aerated seawater. This was placed behind a one-way mirror so that the crabs were not able to see the observer. The rapping sound was recorded using an Ultravox sound-analysis system (Noldus Information Technology b.v., Wageningen, The Netherlands) that recorded the timing of each rap on a computer. The data for both the behavioural and the physiological measurements were not normally distributed and thus were $\log_{10}$ transformed prior to analysis.

(b) *Analysis of lactate concentration*

Fights were staged between pairs of crabs in two groups. In the first group, the larger crab of each pair was allowed to initiate a fight but the crabs were separated as soon as the attacker's chelipeds contacted the defender's shell ($n = 21$). In the second group, each fight was allowed to continue until it was resolved, either by the defender being evicted from its shell ($n = 33$) or by the attacker giving up ($n = 20$). Thus, three groups of crabs emerged for analysis: crabs that had just started to fight; crabs that had engaged in fights where the defender gave up and was evicted; and crabs that had engaged in fights where the attacker gave up without evicting the defender. After each observation the crabs were again removed from their shells, and a 50 μl sample of haemolymph was taken from each crab by piercing the arthroidal membrane at the base of the third pereiopod with a 21 G hypodermic needle attached to a 1 ml disposable syringe. This procedure took *ca.* 2–4 min for each crab and, although complete recovery from high lactate levels would be expected to take a number of hours (Gleeson 1996), it is possible either that some of the lactate would be metabolized during this period or that further lactate production would be induced by stress. To compensate for these possibilities the first sample was taken from attackers and defenders on alternate observations. Each sample was immediately deproteinized with perchloric acid and the neutralized supernatant was stored at −20 °C until the assay for lactate (Gutmann & Wahlefeld 1974; Engle & Jones 1978) was conducted.

(c) *Analysis of glucose concentration*

Again, fights were staged between two groups of crabs, the first group consisting of fights that were stopped as soon as the attacker initiated contact with the defender ($n = 15$). A further 69 fights were staged, of which 48 resulted in the defender giving up and 21 ended with the attacker giving up. After each encounter had been resolved, haemolymph samples were taken as described in § 2b, and we assayed the concentration of glucose using a standard kit (Sigma Diagnostics Ltd, Poole, UK) for the enzymatic analysis of glucose concentration (Raabo & Terkildsen 1960).

(d) *Statistical methods*

We used repeated-measures analyses of variance (ANOVAs) to determine the effect of fighting on lactate and glucose concentrations in attackers and defenders. The role of the crab (attacker or defender) was a repeated measure, and the between-group factor was whether the fight was allowed to proceed or was prevented. Similar analyses were used to determine the effect of fight outcome on lactate and glucose levels for those fights that were allowed to proceed, role again being a repeated measure and with outcome (defender evicted or defender not evicted) as the factor. Since repeated-measures analysis does not allow the application of *post hoc* tests within ANOVA, when interaction effects were encountered we made pairwise comparisons by means of paired *t*-tests. Pearson's product–moment correlation coefficients were calculated in order to determine levels of association between physiological and behavioural variables. One-tailed tests of significance were used where there were specific

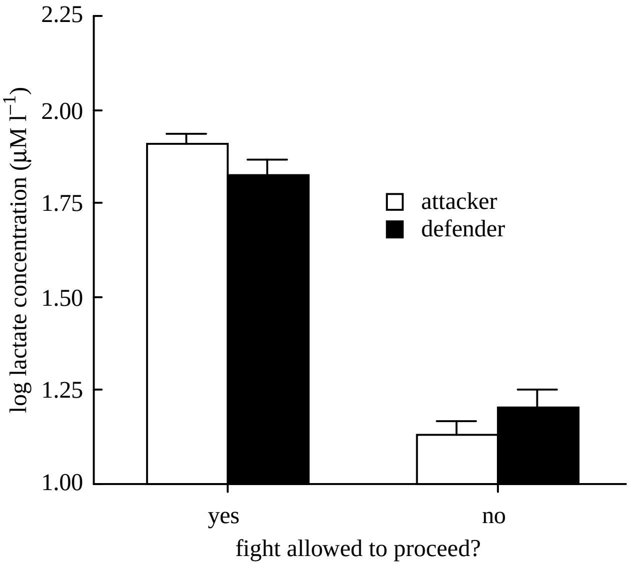

Figure 1. The increase in haemolymph lactate concentration in crabs that had been prevented from fighting and those that had fought. When the fight was allowed to proceed there was a substantial increase in lactate levels compared with those in crabs that had not fought, for both attackers and defenders. Note, however, that there was no interaction effect between the role and whether the fight was allowed to proceed. Error bars show standard errors.

predictions about the direction of any association. Since neither physiological nor behavioural data were normally distributed, the data were $\log_{10}$ transformed prior to analysis.

3. RESULTS

(a) *Effect of fighting*

The haemolymph lactate concentration of crabs (both attackers and defenders) that had fought was substantially higher than that of crabs prevented from fighting (fight completed: mean ± s.e.m. = 83.0 ± 3.4 μM l^{-1}; fight prevented: mean ± s.e.m. = 16.5 ± 1.0 μM l^{-1}) ($F_{1,72} = 214.5$, $p < 0.0001$) (figure 1). The haemolymph glucose concentration of crabs that had fought was also greater than those that were prevented from fighting; however, the difference was not significant ($F_{1,82} = 3.1$, $p < 0.1$).

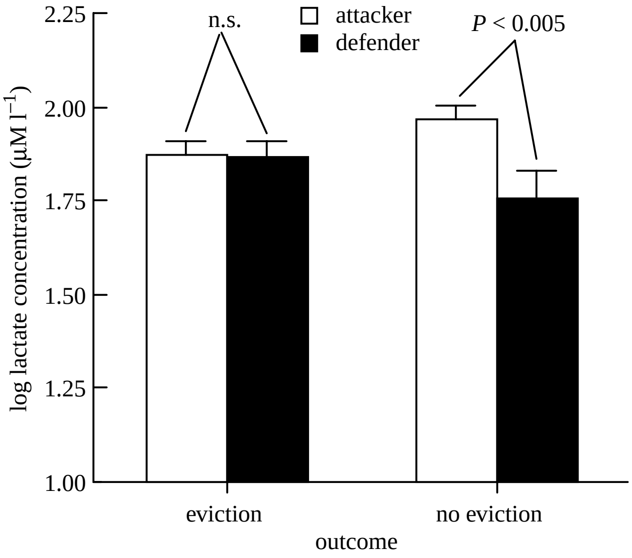

Figure 2. The interaction effect between the role of the crab (attacker or defender) and the outcome of the encounter on haemolymph lactate concentration. Lactate concentrations were high in attackers that failed to evict the defender and low in defenders that resisted eviction. Error bars show standard errors.

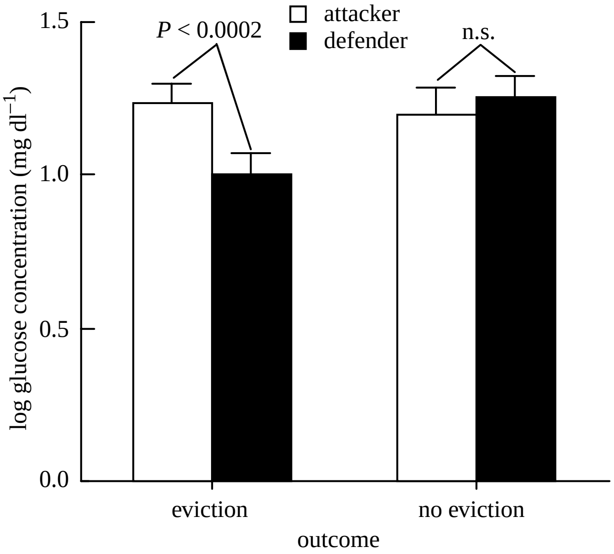

Figure 3. The interaction effect between the role of the crab (attacker or defender) and the outcome of the encounter on haemolymph glucose concentration. Glucose concentrations were low in defenders that were evicted. Error bars show standard errors.

(b) *Differences between attackers and defenders*

Analysis of just those crabs that had fought showed that the concentration of lactate in attackers was greater than that in defenders ($F_{1,51} = 5.9$, $p < 0.02$), and that there was a non-significant trend for attackers to have a greater glucose concentration than defenders ($F_{1,67} = 2.8$, $p < 0.1$). Overall, however, there were no differences in the mean lactate or glucose concentrations between fights that resulted in an eviction and those that did not. For lactate, there was an interaction effect; lactate was higher in attackers than in defenders when the attacker gave up but there was no difference when the defender was evicted ($F_{1,51} = 5.8$, $p < 0.02$) (figure 2). These differences were confirmed by separate paired t-tests: when the attacker gave up lactate was higher in attackers than in defenders ($t_{19} = 3.3$, $p < 0.005$), but when the defender gave up there was no difference in lactate concentrations ($t_{32} = 0.06$, not significant). For glucose, an interaction effect showed that when attackers won they had higher glucose concentrations than the losing defenders, but when there was no eviction the glucose concentrations of both crabs were similar ($F_{1,67} = 7.7$, $p < 0.01$) (figure 3). These differences were again confirmed by separate paired t-tests: when the attacker gave up there was no difference in glucose concentration ($t_{20} = 0.6$, not significant), but when the defender gave up defenders had lower glucose concentrations than attackers ($t_{47} = 4.1$, $p < 0.0002$). Further ANOVAs indicated that, overall, losers had higher lactate concentrations ($F_{1,51} = 5.8$, $p < 0.02$) and lower glucose concentrations ($F_{1,67} = 7.7$, $p < 0.01$) than winners.

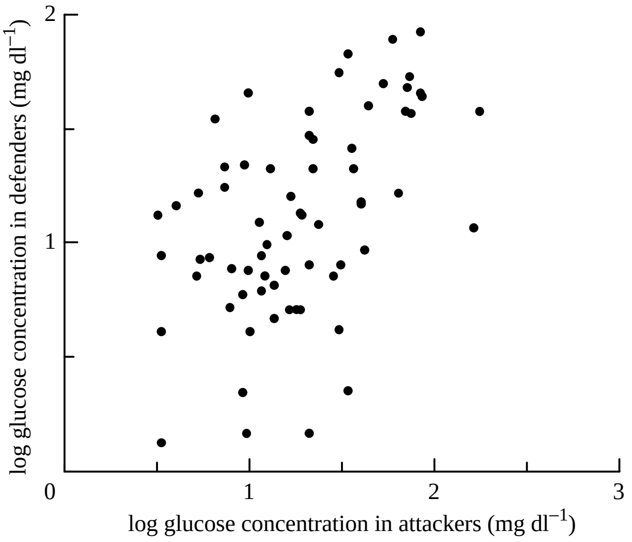

Figure 4. The positive relationship between the concentrations of glucose in the haemolymph of attackers and defenders.

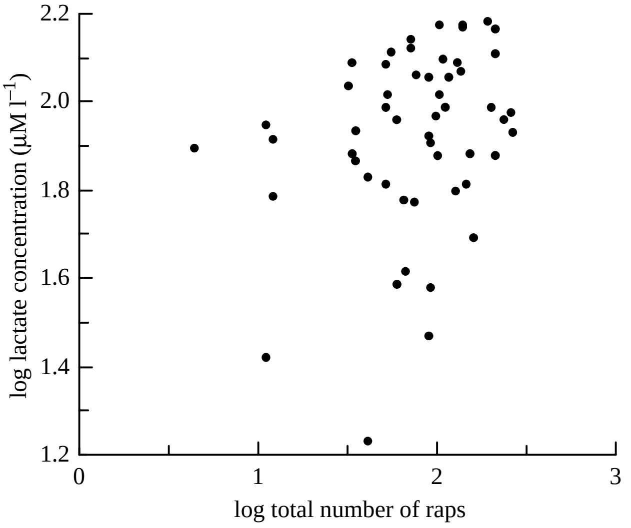

Figure 5. The relationship between the total number of raps performed by the attacker and the haemolymph lactate concentration. Lactate concentration increases with the number of raps performed.

There was no correlation between lactate concentrations in attackers and defenders overall, but in fights where the attacker gave up there was a positive association between the lactate concentrations of the two roles ($r_{18} = 0.51$, $p < 0.05$). Glucose concentrations in attackers and defenders were positively correlated (figure 4) ($r_{67} = 0.5$, $p < 0.001$), but when the data for fights resulting in evictions and non-evictions were examined separately the association remained significant only for fights where the defender gave up ($r_{46} = 0.6$, $p < 0.0005$).

(c) *Associations between physiology and fighting behaviour*

There was a positive correlation between the total number of raps performed by attackers during the fight and both the concentration of lactate ($r_{51} = 0.31$, $p < 0.05$) (figure 5) and the concentration of glucose ($r_{67} = 0.28$, $p < 0.05$) (figure 6) in attackers. The number of bouts performed by attackers was also positively correlated with the concentration of lactate ($r_{51} = 0.37$, $p < 0.01$) (figure 7), but not with the concentration of glucose. There was no relationship between the mean number of raps performed in each bout over the entire fight and either lactate or glucose concentration. The mean duration of the pauses between bouts (calculated as a mean over the entire fight), however, increased with attacker lactate concentration ($r_{51} = 0.35$, $p < 0.01$) (figure 8) and decreased with attacker glucose concentration ($r_{64} = -0.30$, $p < 0.01$) (figure 9).

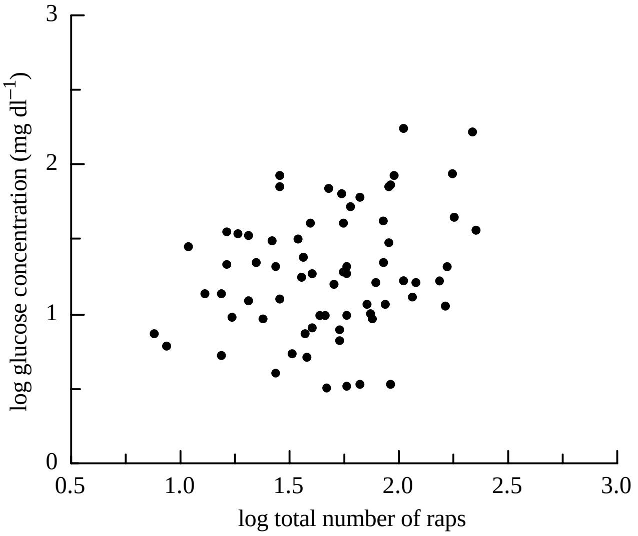

Figure 6. The relationship between the concentration of glucose in the haemolymph of attackers and the total number of raps that they performed. Glucose concentration increases with the total number of raps.

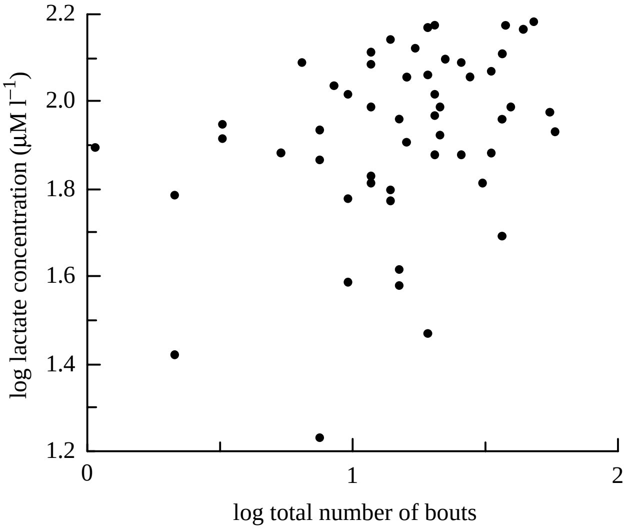

Figure 7. The relationship between the total number of bouts of rapping performed by attackers and the haemolymph lactate concentration. Lactate concentration increases with repeated performances.

To determine whether the fight vigour became increasingly influenced by physiological condition as the interaction progressed we examined the relationships between final lactate (table 1) and glucose (table 2) concentrations and both the number of raps per bout and the duration of the pauses, separately for each of the first six bouts and

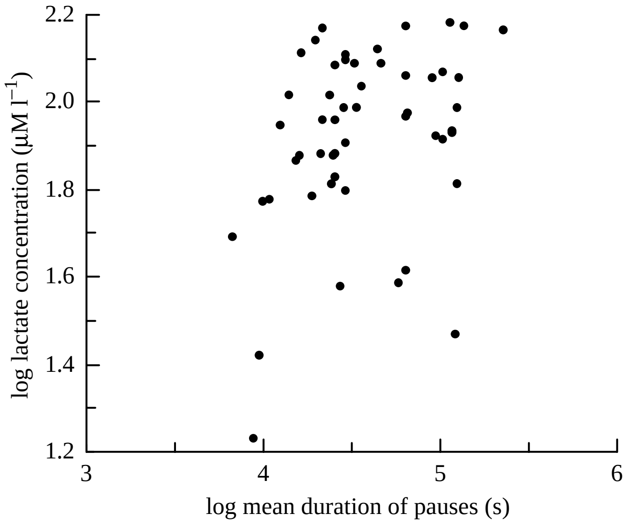

Figure 8. The relationship between the concentration of lactate in the haemolymph of attackers and the mean duration of the pauses that they left between bouts of rapping. Attackers with high lactate levels leave relatively long pauses.

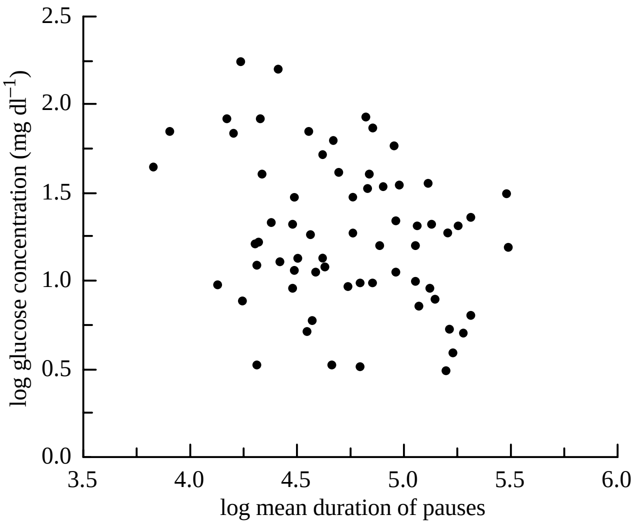

Figure 9. The relationship between the concentration of glucose in the haemolymph of attackers and the mean duration of the pauses that they left between bouts of rapping. Glucose concentration decreases with increasing duration of pauses.

Table 1. The associations between the concentration of lactic acid in the haemolymph of attackers at the ends of fights and the number of raps they performed in each of the first six bouts and the duration of each of the first five pauses.

lactate concentration versus number of raps per bout				lactate concentration versus duration of pauses			
bout number	*r*	*n*	*P*	pause number	*r*	*n*	*P*
1	0.13	53	ns	—			
2	0.09	52	ns	1	0.18	52	ns
3	−0.20	50	ns	2	0.23	50	< 0.1
4	−0.27	48	*	3	0.29	48	< 0.05
5	−0.26	47	*	4	0.37	47	< 0.01
6	−0.13	45	ns	5	0.38	45	< 0.01

P values are for two-tailed tests; 'ns' denotes non-significant results for two-tailed tests; * denotes significance ($P < 0.05$) where one-tailed tests are applied.

Table 2. The associations between the concentration of glucose in the haemolymph of attackers at the ends of fights and the number of raps they performed in each of the first six bouts and the duration of each of the first five pauses.

glucose concentration versus number of raps per bout				glucose concentration versus duration of pauses			
bout number	*r*	*n*	*P*	pause number	*r*	*n*	*P*
1	0.130	69	ns	—			
2	0.223	66	ns	1	−0.089	66	ns
3	0.171	63	ns	2	−0.068	63	ns
4	0.178	57	ns	3	0.057	57	ns
5	0.245	55	*	4	0.099	55	ns
6	0.240	49	*	5	−0.055	49	ns

P values are for two-tailed tests; 'ns' denotes non-significant results for two-tailed tests; * denotes significance ($P < 0.05$) where one-tailed tests are applied.

the first five pauses. Attackers performed variable numbers of bouts, but by limiting our analysis to the first six bouts we were able to maintain a sufficient sample size while including the part of the fight that contains a significant variation in fight parameters (Briffa & Elwood 2000*a*). The number of raps per bout was not significantly associated with lactate concentration in any of the first six bouts when two-tailed tests were applied; however, one-tailed tests were significant for the predicted negative relationship for the fourth and fifth bouts (table 1). One-tailed tests showed significant positive correlations between the concentration of glucose and the number of raps performed in the fifth and sixth bouts (table 2). Pause duration was not related to lactate concentration for the first and second pauses, but there were significant positive relationships for each of the subsequent pauses and the correlations became greater as the fight progressed (table 1). There were no correlations between glucose concentration and the durations of any of the first five pauses.

In defenders the concentration of lactate decreased with the number of raps per bout that they had received ($r_{51} = -0.29$, $p < 0.05$) (figure 10), but the concentrations of lactate and glucose in defenders were not related to any other aspect of the pattern of rapping.

(d) *Associations with the size of contestants*

Lactate concentration in attackers decreased as the size disparity of the crabs increased ($r_{51} = -0.317$, $p < 0.05$), and increased with the absolute weight of the defender ($r_{51} = 0.317$, $p < 0.05$). There were, however, no relationships between the attacker's glucose concentration and the size of the contestants. Lactate concentration in defenders was not significantly related to the attacker's size or the RWD but did increase with the defender's weight

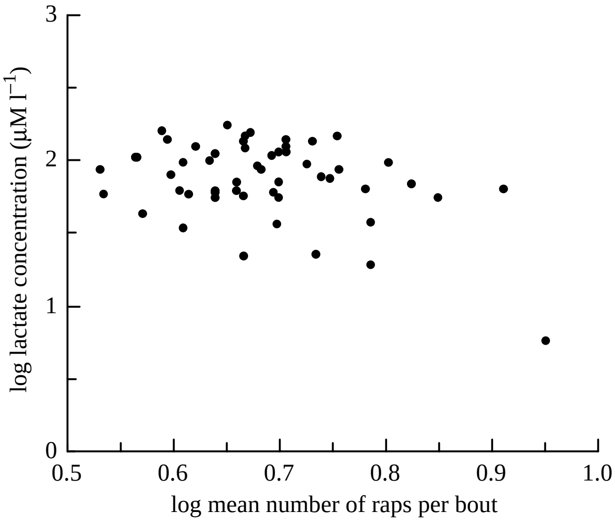

Figure 10. The relationship between the concentration of lactate in the haemolymph of defenders and the mean number of raps per bout that they received. Lactate concentration decreases with an increasing number of raps per bout.

($r_{51} = 0.279$, $p < 0.05$). The defender's glucose concentration was negatively correlated with the RWD ($r_{67} = -0.293$, $p < 0.05$).

(e) *Persistence and contestant size*

The total number of raps performed by attackers increased with the absolute size of the attacker ($r_{120} = 0.223$, $p < 0.05$) and with the RWD ($r_{120} = 0.197$, $p < 0.05$) but not with the size of the defender. Furthermore, the total number of bouts also increased with the absolute size of both the attacker ($r_{120} = 0.247$, $p < 0.02$) and the defender ($r_{120} = 0.278$, $p < 0.01$) but not with the RWD.

4. DISCUSSION

Distinct modes of fighting are common, particularly in situations where one contestant holds a resource that the opponent attempts to prize away. This occurs in fights between males for females where one male physically holds the female, for example, in damselflies (Cordero 1999), amphipods (Dick & Elwood 1996) and newts (Verrell 1986), or when one animal possesses a burrow, as in stomatopods (Shuster & Caldwell 1982). Hermit crabs also assume different roles during shell fights, attackers engaging in vigorous shell rapping and defenders remaining withdrawn in the shell; however, both roles show physiological changes as a consequence of fighting. There was a substantial increase in lactate levels, indicating the accumulation of an oxygen debt during the fight, but this was more marked in attackers than in defenders. Both lactate and glucose concentrations in attackers increased with the number of raps, and the lactate concentration increased with the number of bouts of rapping. Glycogen reserves are mobilized during fighting (Neat *et al.* 1998) and sustained activity in general (Wallace 1973; Zammit & Newsholme 1976). Accumulated lactate appeared increasingly to constrain the number of raps per bout as the fight progressed, but glucose had the opposite effect. Pauses have previously been assumed to provide periods of recovery from fatigue (Briffa *et al.* 1998; Briffa & Elwood 2000*a*,*b*,*c*), and this is supported by the finding that the duration of pauses was increasingly positively correlated with lactate concentration as the fight progresses. Furthermore, the mean duration of all pauses was positively correlated with the final level of lactate but negatively correlated with the level of glucose. Thus, fight vigour is enhanced by high glucose concentrations but reduced by high lactate concentrations. A high glucose concentration enables sustained activity, but when glycogen is metabolized anaerobically accumulated lactate inhibits sustained activity (Neat *et al.* 1998). The final level of lactate in attackers was higher when the defender was large in both absolute and relative terms. This might be because more effort is required for each rap when fighting a large defender or because large defenders persist for longer, typically receiving more bouts of rapping.

Although fighting caused elevated lactate levels in defenders, these were not clearly related to the number of raps or the number of bouts of rapping. Defenders that received a high number of raps in each bout, however, had low levels of lactate, possibly because high fight vigour causes defenders to give up early (Briffa *et al.* 1998). The lactate concentration in defenders was not influenced by the size of the attacker or by the RWD, but did increase with the defender's weight. The glucose concentration in defenders was low when the defender was small relative to the attacker. Large defenders engaged in long fights during which high levels of lactate would have accumulated. Glucose also increased as a function of fight duration, and small defenders were evicted relatively early after being subjected to vigorous rapping. Thus, the relationships between physiology and size in defenders appear to be driven by the differing fight durations that defenders of different sizes endure. This might account for the positive correlation between the glucose levels of the contestants.

An alternative explanation, however, is that defenders do not mobilize their energy reserves to the same extent when engaged in a contest that they are unlikely to win. As is the case in other animals, hermit crabs appear to assess the relative size of their opponent (Dowds & Elwood 1985; Briffa & Elwood 2001). Thus, when defenders are small relative to attackers, low glucose concentrations would be expected. This possibility could also account for the positive relationship between the glucose concentrations of attackers and defenders. The mechanism of any 'decision' not to break down glycogen is unclear, however. In order to distinguish between these possibilities it would be necessary to assay both glucose and glycogen levels, but a limitation of using hermit crabs of the size used here is that it is not possible to obtain sufficient haemolymph for an assay of both compounds.

It is clear that fighting influences the physiology of hermit crabs and that the physiology constrains the subsequent vigour with which the attacker can rap. Thus, physiology influences the nature of the attack, but does it also influence the major decision of when one animal should give up? In a broad sense it appears that it does, because losers had higher lactate levels and lower glucose levels than winners. This result, however, may mask differences in the decision rules of attackers and defenders, and here we examine fights in which the attacker gave up separately from fights in which the defender gave up.

When attackers gave up, their lactate levels were high compared with those of their opponents (figure 2) but their glucose levels did not differ from those of their opponents (figure 3). Thus, a high lactate level appears to be a prime candidate for the physiological basis of the attacker's decision to give up. This suggestion is supported by the finding that a period of low oxygen prior to a fight markedly reduces the vigour of the attack and the probability of victory (Briffa & Elwood 2000*c*). The low-oxygen conditions prior to fighting would impose a period of anaerobic respiration and thus cause an accumulation of lactate.

Defenders, on the other hand, gave up when their glucose levels were particularly low (either because of low glycogen reserves or because glycogen was not broken down) (figure 3), but their lactate levels were not different from those of the attackers that won (figure 2). Thus, a low glucose level, rather than a high lactate level, appears to be a prime candidate for the physiological basis of the defender's decision. This suggestion is supported by the finding that a period of low oxygen prior to fighting had no effect on the probability of the defender giving up the fight (Briffa & Elwood 2000*c*). As in attackers, low oxygen should have caused high lactate levels, but in defenders this did not appear to influence their decisions. Nevertheless, the data show that fighting does cause elevated lactate levels in defenders (figure 1). The cause of this is somewhat unclear as defenders do not perform any obviously demanding activity during the fight. It has been suggested that defenders are prevented from ventilating effectively whilst receiving raps (Elwood & Neil 1992). Alternatively, lactate production may be a result of stress due to engaging in a fight. The absence of vigorous activity, however, might explain why the defender's decision is not based on lactate levels. Low blood glucose levels could indicate depleted glycogen reserves, and it is unlikely that crabs in this condition would initiate a fight, i.e. become attackers. Defenders, however, do not make a decision to enter into a fight because the interactions are always initiated by the attacker. Glycogen concentration might influence the decision to give up of defenders, but not of attackers, because only defenders may enter fights with depleted energy stores.

Alternatively, vigorous rapping may have a direct influence on the defender irrespective of its lactate or glucose levels. Vibration of the abdominal muscles at a particular frequency and power has been shown to induce a reflex contraction that is likely to reduce the defender's ability to maintain a grip on the shell (Chapple 1993, 1997). This agrees with the finding that defenders put less effort into resisting a vigorous attack. Presumably, the rate of mobilization of glucose is related to the effort with which defenders resist the as yet undetermined effects of rapping, and this might account for the low glucose levels in defenders that give up. It is also possible, however, that a low glucose level makes it more difficult for the defender to resist the direct effects of rapping.

Thus, this study supports the idea that depletion of energy reserves and accumulation of harmful by-products are the basis of decision rules used in fighting. Fighting affects the physiology of both attackers and defenders, but the physiological basis of the decision rule for giving up appears to be different for each role. Theoretical models of animal contests typically assume that the decisions made by each contestant are the same (Parker 1974; Maynard Smith 1982; Enquist & Leimar 1983; Payne & Pagel 1997). However, this might not be true of all contests, particularly when the animals perform distinct modes of fighting.

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