THE ROYAL SOCIETY

Use of energy reserves in fighting hermit crabs

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When animals engage in fights they face a series of decisions, which are based on the value of the contested resource and either their relative or their absolute fighting ability. Certain correlates of fighting ability or 'resource holding potential' such as body size are fixed but physiological correlates are expected to vary during the encounter. We examine the role of energy reserves in determining fight outcomes and parameters during 'shell fighting' in hermit crabs. During these fights, the two contestants perform very different roles of attacker and defender. We show that the balance of the total energy pool, in the form of glucose and glycogen, determines the ability of defenders to resist eviction from their shells. Low glucose in evicted defenders is not caused by depletion of energy reserves, rather mobilization of glycogen appears to be the result of a strategic decision about whether to resist effectively, based on the perceived fighting ability of the attacker. Attackers, however, always initiate the fight so such a decision for this role appears unlikely. In addition to influencing decisions and ability during fights, physiological correlates of fighting ability can in turn be influenced by strategic decisions.

Keywords: hermit crab; fight; aggression; glycogen; glucose; mobilization

1. INTRODUCTION

Animals facing a potential fight make a succession of decisions as the encounter progresses. First, they must decide whether to enter into overt fighting. This decision, in the first instance, will be taken by the initiating competitor in the form of a challenge or attack, but the non-initiator may be able to mediate the decision if it is possible to flee. Second, once the fight has been initiated, each contestant may have to decide whether to escalate the contest by employing increasingly intensive or dangerous activities. Third, one contestant will decide to end the contest by giving up. Thus, fights are resolved by a series of decisions that may differ between the two contestants. The information on which these decisions are based comes from a range of sources. Animals may base decisions only on their own known fighting ability (Bridge *et al.* 2000; Taylor *et al.* 2001; Taylor & Elwood 2003) or on their own ability relative to the perceived fighting ability of their opponent (e.g. Maynard Smith & Parker 1976). Displays observed during fights, for example, are assumed to allow such 'mutual assessment' and a large body of theoretical (e.g. Enquist & Leimar 1983; Payne & Pagel 1997) and empirical (e.g. Clutton-Brock *et al.* 1979; Thornhill 1984; Burmeister *et al.* 2002) evidence supports this idea. In particular, Payne & Pagel (1997) suggest that some contests are 'energetic wars of attrition' where the contestant that commits the greatest amount of energy to the contest will be the eventual victor.

Regardless of whether an individual's fighting ability is based on absolute measures or on measures relative to that of the opponent, it is often assumed to be primarily determined by body size (e.g. Riechert 1978; Caldwell & Dingle 1979) or by the size of the weapons it possesses (e.g. Barki *et al.* 1997; Sneddon *et al.* 1997). Such features are 'fixed' and will not vary during the fight. Furthermore,

once adulthood has been achieved, these features will be stable from fight to fight, varying only with changes in condition and the accumulation of injuries (Neat *et al.* 1998) (and in some species the degree of subsequent regeneration). Certain features that influence fighting ability, however, are expected to change during the course of a fight. First, any injuries acquired will impair fighting ability during the remainder of the fight. Second, when fighting is energetically demanding, physiological variables will influence behaviour. Such constraints may progressively reduce the level of performance until a decision to quit would pay. Physiological constraints on fighting activities have been investigated in a range of species including cichlid fishes (Neat *et al.* 1998), shore crabs (Sneddon *et al.* 1999), swimming crabs (Thorpe *et al.* 1995) and hermit crabs (Briffa & Elwood 2001, 2002).

During fighting in hermit crabs, over ownership of gastropod shells, the two contestants fight in very different roles. The initiator or 'attacker' performs bouts of vigorous 'shell rapping' where it raps its shell against the surface of the shell of the non-initiator or 'defender'. The defender, on the other hand, remains tightly withdrawn into its shell until the encounter is resolved. Resolution occurs when either the defender decides to give up, by releasing its abdominal grip on its shell and allowing the attacker to evict it by pulling it out through the aperture, or the attacker decides to give up without first evicting the defender. For a full description of shell fighting, see Elwood & Briffa (2001). The chance of the defender giving up increases with the vigour of rapping employed by the attacker (Briffa *et al.* 1998, 2003; Briffa & Elwood 2000*a–c*) but the vigour with which the attacker is capable of rapping is constrained by the concentration of lactic acid in its blood, which accumulates as the fight progresses (Briffa & Elwood 2001, 2002). If the concentration becomes sufficiently high, the attacker will give up. Lactic acid concentration does not appear to influence the decision of defenders, but those that successfully defend their shells have greater concentrations of glucose in their

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blood than either those that have not fought or those that are evicted (Briffa & Elwood 2001, 2002).

Thus, it appears clear that, in response to fighting, glucose concentration is elevated, presumably by mobilization of glycogen reserves. The cause of low glucose in evicted defenders, however, is not clear but there are two possible reasons. First, energy reserves comprising circulating glucose and stored glycogen might become depleted such that the concentration of circulating glucose is reduced. Since glucose is elevated in response to fighting, expenditure of energy is clearly required in order to resist. Defenders then might base their decision to give up on some threshold level of low glucose, in a manner similar to that used by attackers based on high lactate. The second possibility is that circulating glucose levels in evicted defenders might be low because glycogen reserves have not been mobilized. This might be the case if a high disparity in fighting ability in favour of the attacker was perceived early in the contest, leading the defender to give up. Thus, in addition to physiological constraints influencing behavioural decisions, this behavioural decision might influence a key physiological variable.

The key aim of the present study is to examine how energy resources are mobilized during a fight and what factors influence that mobilization. Specifically, we aim to distinguish between the two possibilities during shell defence by comparing muscular glycogen levels in defenders that have engaged in shell fights and in defenders that have not fought. If defenders that are evicted give up because their energy reserves are depleted below a threshold level, they would also be expected to have low glycogen in comparison with those that have not fought, and perhaps also in comparison with those that resist eviction. High glycogen in evicted defenders, of a similar level to that in defenders that have not fought, on the other hand, would indicate a decision not to mobilize glycogen reserves. We also aim to examine the timing of such a decision, to determine whether it is based on information from pre-fight displays or from shell rapping. Furthermore, in addition to examining differences in glycogen concentration between outcomes for attackers and defenders, we aim to determine whether there are relationships between the concentrations of these metabolites and the vigour of rapping.

2. MATERIAL AND METHODS

(a) *Staging encounters and measuring behaviour*

Littoral specimens of the common European hermit crab *Pagurus bernhardus*, of sufficient size (0.6–1.8 g) for collection of adequate muscle tissue, were collected weekly from Minerstown, Co. Down, Northern Ireland, between March and September 2002. They were held in groups of 40–50 in 60 cm × 30 cm plastic tanks, which were filled with aerated sea water at 10 °C to a depth of 10 cm, and fed *ad libitum* on catfish pellets. The crabs were removed from their shells by cracking the shells open in a bench vice and sexed; only males were used for staging encounters. Females were supplied with new shells and returned to the sea, thus avoiding sex differences in fighting behaviour, which have been noted in previous studies (Neil & Elwood 1985). Only male crabs that were free from: (i) obvious parasites; (ii) loss of appendages and (iii) recent moult were used. Male crabs were

allocated to pairs, such that each pair contained a small crab and a large crab.

The larger crab of each pair (potential attacker) was provided with a *Littorina littorea* shell that was 25% of its preferred shell weight, and the smaller crab of each pair (potential defender) was supplied with a *L. littorea* shell that was 100% adequate for the large crab. Preferred shell weights were determined from regression lines obtained from previous unpublished shell-choice experiments. Encounters were staged in three groups. In group A ($n = 10$ pairs), samples were taken without staging a fight between the two crabs. Group B ($n = 21$ pairs) contained fights that were stopped at the point where the attacker first made contact with the shell of the defender. The third group contained fights that were allowed to proceed until either the attacker evicted the defender (group C, $n = 38$ pairs) or the attacker gave up without first effecting an eviction (group D, $n = 16$ pairs). Thus, four groups emerged for analysis.

Fights were staged in a 120 mm crystallizing dish filled to a depth of 7 cm with aerated sea water at 10 °C and containing a 1 cm deep layer of cleaned sand. The two crabs of each pair were introduced into the dish, which was placed behind the one-way mirror of an observation chamber such that the observer could see the crabs but the crabs could not see the observer.

To gain an index of the power of rapping we analysed the intensity of the rapping sound. The rapping sound was recorded, via a hydrophone suspended in the test arena, directly onto the hard disc of an Apple Macintosh personal computer. The sound data were captured and analysed using CANARY 1.2.4 BIOACOUSTIC WORKSTATION (Charif *et al.* 1995) software running on the computer. (Briffa *et al.* (2003) contains full details of the methods used to measure sound intensity.) The pattern of shell rapping was also recorded using a hand-held computer configured as a time–event recorder using 'THE OBSERVER' 3.0 observational data recording computer package.

(b) *Analysis of muscular glucose and glycogen concentrations*

Samples of abdominal muscle were used because: (i) it is present in sufficient quantity; (ii) it is easily accessible; and (iii) it is likely to be the key muscle group used by both attackers and defenders during shell fights, because these muscles are used to grip the gastropod shell. Crabs were again removed from their shells by means of the vice and frozen immediately in liquid nitrogen. Each crab in turn was removed from the liquid nitrogen and, while still frozen, the membranous abdomen was separated from the cephalothorax using a scalpel. The abdomen was carefully dissected to separate the abdominal musculature from the epithelium and internal organs (digestive tract and testes). The muscle tissue was placed in a pre-chilled porcelain mortar containing liquid nitrogen and ground, with a pestle, into a fine powder. A small amount of excess liquid nitrogen was added to the powder and used to wash it into a 1.5 ml Eppendorf tube. Once the liquid nitrogen had evaporated, via a small hole made in the Eppendorf tube's lid, the tube was weighed and the weight of muscle tissue obtained was noted. We added 0.5 ml of 0.3 M perchloric acid to the tube and, after thorough mixing, the sample was centrifuged at 13 000 r.p.m. for 10 min. The supernatant was decanted and stored on ice, and an additional 0.5 ml of perchloric acid was added to the muscle sample, which was again centrifuged for 20 min. The supernatant was decanted and combined with the original supernatant, and this final sample was neutralized by dropwise addition of 2 M potassium hydrogen carbonate, the added volume of which was noted. This

neutralized sample was chilled on ice for 10 min, and the precipitate potassium perchlorate was separated by centrifugation for 10 min. The neutralized supernatant was then stored in an Eppendorf tube at $-20\,^{\circ}$C until required for assay of glycogen concentration.

Analysis of glycogen concentration was based on the method of Keppler & Decker (1974) where amyloglucosidase is used to hydrolyse the glycosidic bonds that link together D-glucose molecules to form glycogen. Samples were removed from the freezer and allowed to thaw slowly on ice. Two 0.2 ml aliquots were taken from each sample. A 2.0 ml aliquot of amyloglucosidase solution (10 mg of amyloglycosidase per ml of distilled water) was added to the first aliquot (A), whereas the same volume of distilled water was added to the second aliquot (B). Both aliquots were incubated for 2 h at 40 °C, then assayed for glucose concentration, using a pre-prepared kit (Sigma 115) based on the method using hexokinase to catalyse the phosphorylation of D-glucose described by Carroll *et al.* (1971). The concentration of glycogen was obtained by subtracting the concentration of glucose in B from that in A, and adjusted to correct for: (i) the amount of muscle tissue obtained; and (ii) the amount of potassium hydrogen carbonate added to neutralize the sample.

(c) *Statistical analyses*

Two two-factor ANOVAs with one repeated measure were used to determine the effects of group on the concentrations of glucose and glycogen in the muscle tissue of attackers and defenders. The independent factor was 'group', the repeated measure was 'role' (attacker or defender) and the dependent variable was either glucose concentration or glycogen concentration. Initial analyses showed no significant difference in either glucose concentration or glycogen concentration between groups A and B, and the data from these groups were thus pooled into a single group containing animals that did not fight. Since the total energy pool (TEP) available to an individual is the sum of circulating glucose and stored glycogen, the proportion of this pool that is present in the form of glucose might reflect behavioural decisions more clearly than does the absolute concentration of either glucose or glycogen. We calculated this by:

proportion of TEP in the form of glucose

= [glucose]/([glucose] + [glycogen]).

A further repeated-measures ANOVA was performed to determine the effects of role and group on this measure. Since the effect of fight outcome influenced the energy pools of the two roles differently (see § 3), the effects of fight activities on the energy pool may also have been different for the two roles. To examine these effects, multiple regressions were conducted. The dependent variable was the concentration of glucose, the concentration of glycogen or the proportion of the energy pool in the form of glucose. The independent variables were the fight parameters: the average power of raps as measured by the sound intensity of the raps, the mean duration of pauses between bouts of rapping, the mean number of raps per bout and the total number of raps. The number of bouts of rapping was not included in the analysis because it was highly correlated with the number of raps ($r > 0.8$).

The data (glucose and glycogen concentrations in attackers and defenders, and the behavioural measures) were not normally distributed and thus were $\log_{10}$-transformed prior to analysis. To test whether this transformation attained normality in each case, the ideal normal value of each datum point was calculated
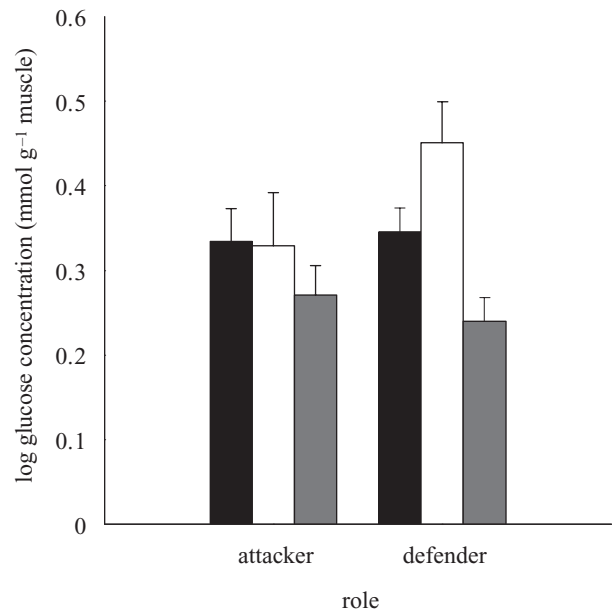

Figure 1. The effect of the outcome of the fight on glucose concentrations in attackers and defenders. (Black bars, eviction; open bars, no eviction; grey bars, no fight.)

from a frequency distribution with the same mean and standard deviation as the variable in question, and a Kolmogorov–Smirnov test was used to test for differences between the actual and ideal frequency distributions. In each case, the *p*-value was greater than 0.05, indicating that the transformation was effective. To determine whether metabolite levels varied with size, correlation coefficients were calculated using data from all crabs that did not fight ($n = 62$). There was no association between crab weight and log-glucose concentration ($r_{60} = -0.05$, n.s.) or log-glycogen concentration ($r_{60} = -0.14$, n.s.) using a one-tailed test ($r_{crit} = 0.21$). Thus, no size correction was applied to the measures of metabolite level prior to analysis.

3. RESULTS

Glucose concentration varied between the three groups (eviction, no eviction and no fight) ($F_{2,82} = 5.02$, $p < 0.01$), but there was no difference between attackers and defenders (figure 1). *Post hoc* analysis (Fisher's protected least significant difference (PLSD)) shows that those crabs that did not fight had lower glucose than those that engaged in fights resulting in an eviction ($p < 0.05$) and those that engaged in fights where the defender retained its shell ($p < 0.005$). The effect of group on glucose concentration was analysed further, separately for each role, by means of one-factor ANOVAs. In the case of attackers there was no difference between outcomes, whereas for defenders glucose concentration did vary significantly between outcomes ($F_{2,82} = 8.7$, $p < 0.0005$). *Post hoc* analysis (Fisher's PLSD) shows that glucose concentration in defenders that were not evicted was greater than in defenders that were evicted ($p < 0.05$), and that glucose concentration in evicted defenders was greater than in defenders that had not fought ($p < 0.01$; figure 1).

There was no difference in glycogen concentration between groups or between attackers and defenders, but a significant interaction effect suggested that differences between groups were more marked in defenders than in
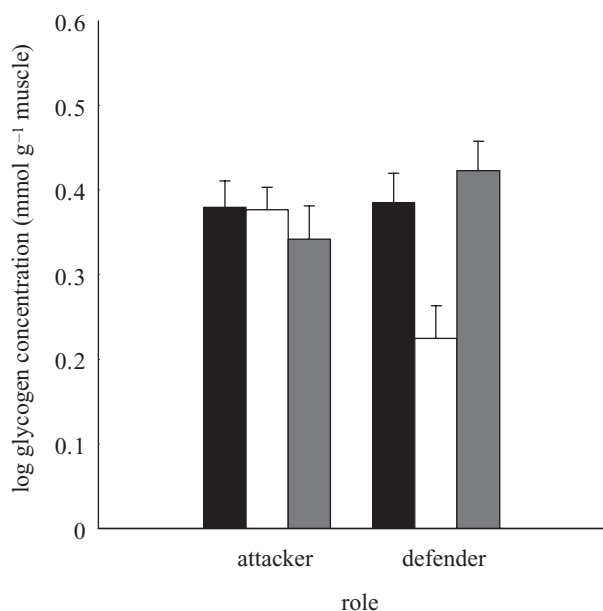
Figure 2. The effect of the outcome of the fight on glycogen concentrations in attackers and defenders. Key as in figure 1.
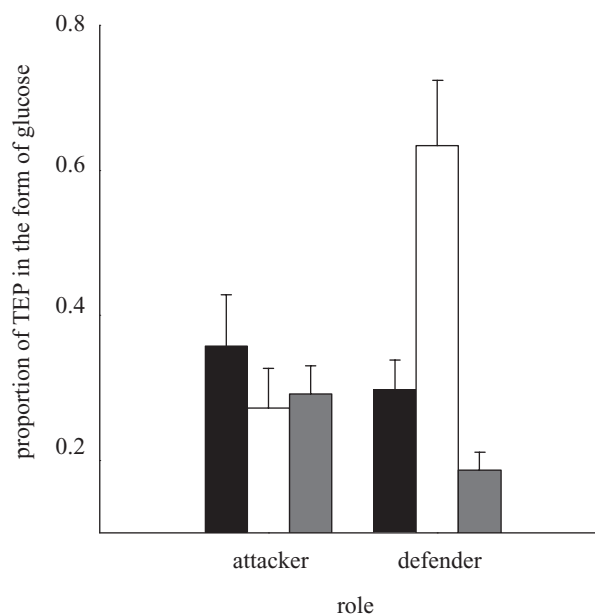

Figure 3. The effect of the outcome of the fight on the proportion of the TEP obtained from abdominal muscle tissue found in the form of glucose in attackers and defenders. Key as in figure 1.

attackers ($F_{2,82} = 4.4$, $p < 0.02$; figure 2). The effects of outcome on the concentration of glycogen in each role were examined further by means of a one-factor ANOVA. In defenders, glycogen concentration varied between the three outcomes ($F_{2,82} = 5.6$, $p < 0.005$) and *post hoc* analysis showed that the concentration was greater both in defenders that were evicted ($p < 0.01$) and in those that did not fight ($p < 0.002$) than in defenders that resisted eviction (figure 2). There was no effect, however, for attackers.

Both group ($F_{2,82} = 5.0$, $p < 0.01$) and role ($F_{1,82} = 4.0$, $p < 0.05$) had a significant effect on the proportion of the TEP in the form of glucose, but a highly significant interaction effect suggests that these differences are primarily caused by the particularly high proportion of glucose in those defenders that retained their shell ($F_{1,82} = 8.0$, $p < 0.001$; figure 3). To examine this further, single-factor ANOVAs were used to determine the effect of group on the proportion of glucose in attackers and defenders separately. In attackers there was no difference between groups but in defenders the proportion of glucose in those that retained their shell was greater than in both those that were evicted and those that did not fight ($F_{2,82} = 14.6$, $p < 0.0001$).

In attackers, the independent variables had no effect on the concentration of glucose ($R^2 = 0.06$, $F_{4,50} = 0.7$, n.s.) or glycogen ($R^2 = 0.13$, $F_{4,50} = 1.7$, n.s.) or on the proportion of the TEP in the form of glucose ($R^2 = 0.07$, $F_{4,50} = 0.8$, n.s.) when all fights were examined together. In fights where the attacker failed to evict the defender, however, there was a significant relationship between the independent variables and the concentration of glucose in attackers ($R^2 = 0.62$, $F_{4,15} = 4.5$, $p < 0.02$). Glucose concentration and the total number of raps were positively associated ($t_{15} = 4.1$, $p < 0.02$). Similarly, the proportion of the TEP in the form of glucose was related to the independent variables in these attackers ($R^2 = 0.42$, $F_{4,15} = 3.7$, $p < 0.05$). Again, there was a positive association with the total number of raps ($t_{15} = 3.4$, $p < 0.01$)

and also with the mean number of raps per bout ($t_{15} = 2.3$, $p < 0.05$). When attackers were successful, however, the fight parameters were not related to any of the dependent variables.

In defenders, there was a significant relationship between the independent variables and glucose concentration ($R^2 = 0.18$, $F_{4,50} = 2.51$, $p < 0.05$). This was the result of a negative relationship between glucose concentration and the sound intensity of the raps they received ($t_{50} = -2.15$, $p < 0.05$). There was also a significant relationship between the independent variables and glycogen concentration in defenders ($R^2 = 0.31$, $F_{4,50} = 5.2$, $p < 0.002$), which was caused by a positive relationship between the concentration of glycogen and the mean number of raps per bout ($t_{50} = 3.35$, $p < 0.02$). Furthermore, the independent variables were related to the proportion of the TEP in the form of glucose in defenders ($R^2 = 0.26$, $F_{4,47} = 38$, $p < 0.01$). This resulted from a positive relationship between the duration of pauses and this measure ($t_{47} = 2.1$, $p < 0.05$).

To gain an index of the total effort employed by attackers during fights, an 'energy expenditure index' (Briffa *et al.* 2003) was calculated by multiplying the total number of raps by the average sound intensity of the raps. There was no difference in the energy expenditure index between attackers that evicted the defender and those that gave up ($t_{52} = 0.77$, n.s.) but successful attackers rapped with greater sound intensity ($t_{52} = 3.0$, $p < 0.005$), performed more raps per bout ($t_{52} = 3.79$, $p < 0.0005$) and left shorter pauses between bouts ($t_{52} = 3.83$, $p < 0.0005$). There was a negative association between the energy expenditure index during bouts 1–4 and the total number of bouts ($r_{29} = -0.4$, $p < 0.05$); that is, defenders give up early when there is high vigour early in the fight. The total energy expenditure index, however, was not related to any physiological variable in attackers or defenders, either when all fights were examined or when only fights that

ended in an eviction were examined. When attackers gave up, however, there was a positive correlation between the total energy expenditure index and the concentration of glucose in attackers ($r_{14} = 2.8$, $p < 0.005$) and the ratio of glucose to glycogen in attackers ($r_{14} = 2.5$, $p < 0.02$).

4. DISCUSSION

Fighting in animals involves demanding activity, and a contestant's ability to perform will be influenced by the availability of sufficient energy reserves. In addition to absolute levels of energy reserves, the balance between stored energy in the form of glycogen and mobilized energy in the form of circulating glucose appears to be a key factor in determining fighting success. In both swimming crabs, *Necora puber*, and shore crabs, *Carcinus maenas*, for example, circulating glucose levels are elevated in response to fighting and exercise (Thorpe *et al.* 1995; Sneddon *et al.* 1999). This increased level of glucose, however, appears not to be the result of mobilization of local glycogen reserves. Except in conditions of low oxygen, these are reduced in shore crabs only during vigorous exercise and not during fights (Sneddon *et al.* 1999). Furthermore, in these species, no difference was found in the concentration of either muscular glucose or glycogen between winners and losers. By contrast, the present data show that during fights in hermit crabs glycogen reserves are mobilized to release glucose and that the degree of mobilization depends on the role (attacker or defender), the vigour of the fight and the fight outcome.

In defenders that fought and retained their shell, for example, muscular glycogen concentration was lower than in defenders that did not fight and in those that were evicted (figure 2). These victorious defenders have greater muscular glucose levels than those that were evicted (figure 1), and higher haemolymph glucose has also been demonstrated (Briffa & Elwood 2001, 2002) such that elevated levels of glucose, mobilized from glycogen, appear necessary for an effective defence of the shell.

The comparatively low glucose levels seen in evicted defenders are not a result of depleted energy reserves. Rather, since there is no difference between the glycogen concentration in these defenders and that in those that have not fought (figure 2), it appears that their energy reserves have not been mobilized. There is, however, a slight increase in mean muscular glucose concentration in evicted defenders, in comparison with those that did not fight, although this increase is less than that seen in defenders that retained their shells (figure 1). It seems that many evicted defenders give up quickly, especially if they receive vigorous rapping in the early bouts (see below), and these individuals do not have elevated glucose levels. However, a small number of evicted defenders do attempt to resist, rather than give up early, and their glucose levels are elevated. Thus, overall, glucose is slightly elevated in evicted defenders.

These differences in the concentrations of muscular glycogen and glucose between the two outcomes appear to be the result of a behavioural decision as to whether to mount a defence of the shell. The activity involved in successful defence of the shell results in, or requires, mobilization of a relatively high proportion of the total energy reserves. Indeed, a key finding in the present study is that

successful defenders have a high proportion of their TEP in the form of glucose (figure 3). If, however, eventual eviction appears likely because of the apparent ability of the attacker, then energy reserves allocated to the contest would be wasted. In this case, it would not pay defenders to perform defensive activities that require the use of these energy reserves, instead they should give up immediately. It appears, therefore, that a major cost of mounting a defence is the mobilization and use of energy reserves.

The defender could gain information about the probable outcome from assessing the relative fighting ability of the attacker. Defenders might monitor pre-fight displays performed by the attacker and/or they could monitor the vigour of shell rapping, once this phase of the fight has commenced. There was, however, no difference in the muscular glycogen or glucose levels between defenders that had not fought and those that were allowed to engage in a period of pre-fight displays only. Thus, in this case, these pre-fight displays appear not to be associated with elevated glucose in defenders. It therefore appears that, as has been suggested by previous studies (e.g. Briffa *et al.* 1998, 2003), the decision made by defenders that leads to elevated glucose is based on the pattern of shell rapping performed by the attacker.

If the decision of defenders is based primarily on the pattern of rapping, we might expect to see relationships between measures of the energy pool available to defenders and measures of the vigour of shell rapping. Defenders that receive vigorous bouts of rapping tend to have low glucose levels and high glycogen levels. When the sound intensity of raps is high, the concentration of glucose in defenders is low, whereas defenders that receive a high number of raps per bout have relatively high glycogen levels. The duration of pauses between bouts is another feature of the pattern of rapping that predicts the success of attackers: when the pauses are short eviction of the defender is likely (Briffa *et al.* 1998). We show a positive relationship between the proportion of the TEP in the form of glucose and the duration of these pauses, such that in defenders that are unlikely to be evicted (long pauses), a high proportion of the TEP is present in the form of glucose. Thus, defenders faced with a weak attack tend to attempt to resist and mobilize their glycogen reserves, leading to elevated glucose levels.

It seems that when attackers rap with a high level of effort defenders decide not to resist and energy reserves are not mobilized. Indeed, attackers that rap with high effort, as indicated by the 'energy expenditure index', early in the fight are likely to effect an eviction after performing a relatively low number of bouts. In short, if attackers hit hard and frequently in the early stages, defenders seem to give up without mounting an effective defence. The mechanism by which an apparent 'behavioural decision' could lead to a physiological change in successful defenders is unclear. The decision to resist could simply lead to mobilization of energy reserves directly. Alternatively, the decision might be to engage in some defensive activity (obscured to the observer by the defender's shell), such as muscular contraction to 'brace' against the blows of the attacker's raps, which results in mobilization of energy reserves and hence elevated glucose levels.

Previous studies on *P. bernhardus* show how a complex combination of the temporal pattern (Briffa *et al.* 1998;

Briffa & Elwood 2000c) and power (Briffa & Elwood 2000b; Briffa et al. 2003) of rapping could advertise the fighting ability of attackers by signalling their stamina. Indeed, the pattern of rapping is related to physiological variables in both attackers and defenders. Previous studies indicate that, in attackers, levels of lactic acid, but apparently not levels of circulating glucose, vary with the pattern of rapping and that the decision to give up is influenced by levels of circulating lactate but not of glucose (Briffa & Elwood 2001). Similarly, the present data show that neither muscular glucose nor glycogen levels in attackers are related to the pattern of shell rapping that they perform when all fights are examined together or when attackers are victorious.

When only fights where attackers give up are examined, however, the muscular glucose concentration does vary with the pattern of rapping. In these fights, there was a positive association between glucose concentration in attackers and the number of raps that they performed, such that those with high glucose levels had performed a high total number of raps. Furthermore, there were positive relationships between the total energy expenditure and both the glucose concentration and the proportion of the energy pool in the form of glucose. There are two possible explanations for these relationships in unsuccessful attackers. First, it is possible that the persistence of attackers that give up is constrained by the degree to which they can mobilize energy reserves. This implies that, as we have shown here for defenders, mobilization of such reserves in attackers is dependent upon a decision to fight effectively. This seems unlikely, however, since, in contrast to defenders, all attackers choose to initiate a fight. Furthermore, there is no evidence that mobilization of reserves occurs in attackers, as there is no significant difference in glucose, glycogen or the proportion of TEP in the form of glucose between those that fought and those that did not. An alternative explanation is that these relationships are caused by variation in resting levels of muscular glucose. Such variation could be a result of differences in time from last feeding or differences in condition. We can measure persistence only in those animals that give up and persistence may be determined by the availability of glucose. Indeed, it seems that these resting levels of glucose influence the total effort used by those attackers that give up. We have noted previously (Briffa & Elwood 2001, 2002) that attackers that give up have higher lactate levels than those that win but also that lactate levels positively correlate with the number of raps performed. It is possible that those attackers that give up after a low number of bouts do so because of insufficient glucose, whereas for the majority that give up after performing a greater number of bouts increased lactate concentration is the limiting factor.

The situation in other crustaceans, where fighting does not lead to decreased glycogen levels and there are no differences in glycogen concentration between winners and losers, is clearly different from the situation in hermit crabs, where, in defenders at least, the concentrations of glucose and glycogen differ significantly between the two outcomes. In swimming crabs, there is little difference in the behaviour of winners and losers in the final stages of the fight (Thorpe et al. 1995). Little is known about activity rates in defenders during hermit crab shell fights but they may be very different between the two outcomes. Certainly, activity rates in attackers differ between outcomes, particularly during the final bouts of the fight (Briffa et al. 1998), such that defenders may also be separated by outcome based on the vigour of rapping that they must attempt to resist. Two distinct roles, with different fight activities, is not an unusual situation in animal contests. Such a situation is often seen when the contest involves one individual attempting to prise away a resource in the possession of its opponent. Examples other than shell fighting in hermit crabs include contests over shelters in stomatopods (Shuster & Caldwell 1982) and over guarded females in amphipods (Dick & Elwood 1996), damselflies (Cordero 1999) and newts (Verrell 1986).

The trigger for the mobilization of glycogen reserves in defenders may be a strategic decision based on the likelihood of resisting the attacker. Thus, in addition to metabolite levels influencing the behaviour of and decisions made by fighting animals, some behavioural decisions, made on the basis of information about the opponent, might directly influence an individual's physiological state and hence their capability to engage in the contest.

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