Power of shell-rapping signals influences physiological costs and subsequent decisions during hermit crab fights

Mark Briffa* and Robert W. Elwood

School of Biology and Biochemistry, Queen's University Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast BT7 1AE, UK

Understanding the costs of signals used in fights is the key to understanding decisions made by contestants. Hermit crabs use shell rapping. This is a clearly defined agonistic signal, which can be quantified in temporal terms and in the power of the key shell-rapping signal component. We examine the relationship between the power expended by attacking hermit crabs and their consequent lactate levels. High power expenditure over the whole fight leads to high lactate, and attackers give up when lactate is high. Some defenders give up early in fights, particularly if the power of raps in early bouts they receive is high. These defenders and those not allowed to fight have low glucose, but those that successfully resist eviction have high glucose. Glucose is mobilized in an attempt to resist; nevertheless, some defenders that attempt resistance are still evicted by persistent attackers. Thus, early power of the signal is a major determinant of success for attackers, albeit at a cost. These data show the link between power, repetition of a signal, metabolic consequences and decisions of contestants in fights. The different activities, decisions and costs of the two roles are not adequately described by existing models of contests.

Keywords: hermit crab; aggression; signals; decisions; costs; physiology

1. INTRODUCTION

Activities used by animals to resolve aggressive encounters may affect the opponent in different ways. Some are signals that advertise the fighting ability and/or motivation of the sender and can be thought of as being 'pay-off irrelevant' in that the choice of behaviour is strategic (Maynard Smith & Parker 1976) and does not affect the cost to the receiver directly (e.g. Enquist & Leimar 1983; Payne & Pagel 1996). At the other extreme are those that impose direct costs on receivers (Enquist 1985; Grafen 1990), particularly in terms of wounds, as in the case of 'dangerous displays' (Payne 1998). Thus, in the case of 'pure signals', the only costs incurred are those of producing the signal, whereas 'dangerous displays' will also impose 'direct costs' on receivers. Various theoretical models have been produced to analyse these differences in the sources of costs (Enquist & Leimar 1983; Payne 1998) and methods for distinguishing between the models have been proposed (Taylor & Elwood 2002).

These analyses have typically been applied to 'symmetrical' contests in which both opponents use similar activities, i.e. they fight in the same way. There are numerous examples of this across the animal kingdom, including roaring contests in red deer, *Cervus elephas* (Clutton-Brock *et al.* 1979), mouth wrestling in the cichlid fish *Tilapia zillii* (Neat *et al.* 1998) and the 'perch-coo' of male collared doves, *Streptopelia decaocto* (Ballintijn & ten Cate 1999). Equally prevalent, however, are 'asymmetrical' contests, which occur between opponents that assume, or are in, different positions, such as mate guarding in dungflies (Parker 1970), newts (Verrell 1986) and amphi-

pods (Dick & Elwood 1996). In these cases one male holds the female and the other tries to prise the female away. Because the opponents fight in different ways, the costs and the manner of incurring the costs may also differ.

Such is the case with 'shell fighting' between hermit crabs over ownership of their gastropod shells. During these contests the two participants take on very different roles. Attackers initiate the fight and, after grasping the defender's shell, rap their own shell against it by bringing the shells rapidly and repeatedly into contact in a series of bouts. The defender, on the other hand, performs very little overt activity, withdrawing into its shell at the beginning of the encounter, when the attacker first grabs it, and gripping the columella of its shell with its abdomen. The defender may release its abdominal grip of its shell and allow the attacker to pull it out of the shell through the aperture. In this case, the attacker is victorious and is free to choose between the two shells. Alternatively, the attacker may 'give up' without first evicting the defender. For a full description of shell fighting see Elwood & Briffa (2001).

Successful attackers rap with a higher temporal rate than do those that give up (Briffa *et al.* 1998) and the rate of rapping appears to be influenced by the attacker's physiological state. Low oxygen prior to a fight reduces the rate of rapping and the chance of success in attackers but does not affect the success of defenders (Briffa & Elwood 2000a). Rapping increases lactic acid in the blood of attackers and they tend to give up if lactate is particularly high (Briffa & Elwood 2001).

In addition to variations in the rate of performance, contest activities can also vary in terms of magnitude, and this should also affect contest outcomes. In the case of shell rapping, attackers that rap harder and show a relatively

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

slow decline in power are more likely to evict the defender (Briffa & Elwood 2000b; Briffa *et al.* 2002). For most species, measurement of variation in the magnitude of signals would be difficult to achieve without interfering with the interaction and therefore has not been attempted. Hermit crabs, however, are useful in this respect because the power of the raps is proportional to the sound energy produced, and this may be readily measured. Furthermore, it is possible to gain an index of the total effort used by attackers from the product of average sound intensity and number of raps. This 'energy expenditure index', gained from a behavioural estimate, may then be related to the key physiological measure of lactate level.

The decision of defenders, however, appears to be independent of their lactate, but might be influenced by glucose (Briffa & Elwood 2001). Haemolymph glucose concentration is low in those that are evicted, but does not appear to be influenced by the rate of the raps that they receive (Briffa & Elwood 2001).

The aim of the present study is to determine the key physiological costs of shell rapping for attackers and defenders in relation to the total effort with which the raps are performed, rather than in relation to just the temporal pattern, as has been achieved previously (Briffa & Elwood 2001). If the main physiological demands of performing raps are primarily determined by the power, then in attackers we would expect to see lactate concentration increase in direct proportion to this component, since high power would incur high energy demands.

The power of rapping by the attacker influences the decisions of the defender (Briffa & Elwood 2000b; Briffa *et al.* 2002) and thus should also influence the defender's key physiological variable, circulating glucose. Whether glucose is metabolized during the contest and a subsequent decline causes the defender to give up, or is simply not mobilized in losing defenders is not clear. We aim to analyse lactate levels in attackers and glucose levels in defenders, as analysis of both is not possible from the small amount of haemolymph obtained from a single animal (Briffa & Elwood 2001). We then aim, for the first time to the best of our knowledge, to relate these key physiological variables and behavioural decisions to the power used by fighting animals and to determine how these asymmetric contests are resolved.

2. MATERIAL AND METHODS

(a) *Staging fights and recording behaviour*

Littoral specimens of the common European hermit crab, *Pagurus bernhardus*, of sufficient size for collection of adequate haemolymph samples (0.6–1.8 g), were collected weekly from Minerstown, County Down, Northern Ireland, between March and September 2001. They were held in groups of 40–50 animals in 60 cm × 30 cm plastic tanks, which were filled with aerated seawater 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, and only males were used in the experiments. Females were supplied with new shells and returned to the sea, thus avoiding the sex differences in fighting behaviour that have been noted in previous studies (Neil & Elwood 1985). Only male crabs that were free from obvious parasites, loss of appendages and recent moult

were used. Male crabs were grouped into pairs, such that each pair contained a small crab and a large crab.

The relative weight difference (RWD), calculated by

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

was varied between the pairs to provide a range of RWDs (0.05–0.60; mean RWD = $0.25 \pm \text{s.e.} = 0.017$). 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 small 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 choice experiments.

Encounters were staged in two groups. In the first, the encounter was stopped as soon as the attacker made contact with the shell of the defender, and a haemolymph sample was taken from each crab (see § 2b). This group therefore contained attackers that would have fought, but were prevented from doing so. In the second group, when fights were initiated they were allowed to continue until either the defender was evicted or the attacker gave up, and then haemolymph samples were taken. Removal of a crab from its shell, by means of the vice, and collection of the haemolymph sample (see § 2b) was completed in under 1 min. In all cases where the attacker failed to initiate a fight no sample was taken for analysis and the observation was discarded. Thus, three possible outcomes of staged encounters emerged for analysis: 'no fight', 'eviction' or 'no eviction'.

Fights were staged in a 120 mm crystallizing dish filled to a depth of 7 cm with aerated seawater 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.

In order 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 an Apple Macintosh computer. Briffa *et al.* (2002) contains full details of the methods used for measuring sound intensity. Under ideal conditions sound intensity is related to the acoustic power (energy transferred/time) by the spherical spreading law,

$$P = 4\pi r^2 \times i,$$

where P is the power (W), r is the distance from the source (m) and i is the sound intensity (W m^{-2}). Power, in turn, will be proportional to the force of the impact received by defenders and to the effort supplied by attackers. The accuracy of sound-intensity measurements, in absolute terms, will have been compromised by deviations from the ideal conditions assumed by the above equation; for instance, sound intensity may have been altered by the reflection of sound waves from the wall of the crystallizing dish, by the acoustic properties of the dish, sand and shells, and by the plane of orientation of the shells towards the hydrophone. Within fights, however, these complicating variables would have been constant since the crabs did not change position once the fight had been initiated. Furthermore, a large sample size was used to ensure that these variables did not influence comparisons between fights. 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.

Figure 1. Metabolite levels in crabs that had not fought, had engaged in fights where the defender was evicted and had engaged in fights where there was no eviction; (a) lactate levels in attackers and (b) glucose levels in defenders. Error bars show s.e.

(b) Analysis of lactate concentration in attackers

After each observation, attackers were again removed from their shells by means of the vice. A 50 µl haemolymph sample was taken from each crab by piercing the arthroidal membrane at the base of the third pereopod with a 21 gauge hypodermic needle attached to a 1 ml disposable syringe. Each sample was immediately de-proteinized with perchloric acid and the neutralized supernatant was stored at -20°C until the assay for lactate was conducted, using the enzymatic technique of Gutmann & Wahlefeld (1974) as modified by Engel & Jones (1978).

(c) Analysis of glucose concentration in defenders

As in § 2b, defenders were again removed from their shells after each observation. Haemolymph samples were taken from defenders as in § 2b, and the concentration of glucose was assayed using a standard kit (Sigma Diagnostics Ltd., Poole, UK) for the enzymatic determination of glucose concentration (Raabo & Terkildsen 1960).

3. RESULTS

(a) Effects of outcomes of encounters on metabolite levels

In order to determine the effect of fighting and fight outcome on the haemolymph concentration of lactate in attackers and glucose in defenders, two one-factor ANOVAs were performed. The factor was the outcome of the staged encounter: 'no fight', 'eviction' or 'no eviction'. In attackers, the outcome had a significant effect on lactate concentration ($F_{2,70} = 13.6$, $p < 0.0001$) (figure 1a). The concentration in attackers that failed to evict the defender was greater than in those that were successful (Fisher's

Figure 2. The negative association between lactate concentration in attackers and the sound intensity with which they rapped. Lactate concentration appears to constrain the power with which attackers may rap. Regression line shown for illustration only.

PLSD; $p < 0.01$) and the concentrations in both groups that had fought were greater than in those that were prevented from fighting (Fisher's PLSD; eviction versus no fight $p < 0.005$, no eviction versus no fight $p < 0.0001$). The outcome also had a significant effect on glucose concentration in defenders ($F_{2,70} = 3.9$, $p < 0.05$) (figure 1b); the concentration in defenders that retained their shell was greater than in those that were evicted (Fisher's PLSD; $p < 0.05$) and than in those that were prevented from fighting (Fisher's PLSD; $p < 0.01$). There was no significant difference in glucose concentration between defenders that were evicted and those that had not fought.

(b) Relationships between vigour and metabolite levels

Stepwise regression was used to determine whether there were relationships between the measures of vigour and the two physiological variables, lactate in attackers and glucose in defenders. In the case of lactate, the total number of raps, mean duration of pauses and mean sound intensity were shown to be significantly related to lactate concentration, but the total number of bouts, mean raps per bout and mean gap duration were excluded from the model ($F_{3,48} = 7.0$, $p < 0.0005$). Subsequent correlation between each of the three included variables and lactate concentration showed that with increasing lactate the average sound intensity decreased ($r_{50} = -0.33$, $p < 0.01$) (figure 2), the total number of raps increased ($r_{50} = 0.33$, $p < 0.01$) (figure 3) and the mean duration of pauses increased ($r_{50} = 0.32$, $p < 0.05$) (figure 4).

In the case of glucose concentration in defenders, the only significant relationship was with sound intensity, all other variables being excluded ($F_{1,50} = -0.256$, $p < 0.05$). The sound intensity of rapping showed a negative relationship with glucose in the haemolymph of defenders ($r_{50} = -0.256$, $p < 0.02$) (figure 5). Furthermore, the sound intensity was greater in fights where the defender was evicted than in those where the attacker gave up ($t_{51} = 3.6$, $p < 0.001$) (figure 5).

(c) Relationships between energy expenditure and metabolite levels

In order to obtain an index of the total amount of energy expended by attackers during fights, we multiplied

Figure 3. The positive association between the number of raps that attackers performed and the concentration of lactate in their haemolymph at the end of fights. Lactate appears to accumulate according to the number of raps performed. Regression line shown for illustration only.

Figure 4. The positive association between lactate concentration in attackers and the mean duration of pauses. High lactate appears to lead to long pauses. Regression line shown for illustration only.

the total number of raps by the average sound intensity. The values of the energy-expenditure index were not normally distributed and the data were thus $\log_{10}$ -transformed prior to analysis. In attackers, there was a positive relationship between this measure and the concentration of lactate in their haemolymph ($r_{50} = 0.36$, $p < 0.01$) (figure 6), but there was no significant relationship between the energy-expenditure index and the concentration of glucose in the haemolymph of defenders. Furthermore, there was no difference in the energy-expenditure index between attackers that effected an eviction and those that did not.

The energy expenditure during early bouts of the encounter, however, might influence the number of bouts required to effect an eviction. The average number of bouts in a fight was 8.25 (s.e. = 0.64) and we thus examined the relationship between the average energy expenditure during the first four bouts and the total number of bouts performed by attackers that evicted the defender after performing four or more bouts of rapping, and found a negative relationship ($r_{26} = -0.48$, $p < 0.005$) (figure 7). Furthermore, for all fights the average energy-expenditure index of attackers that eventually evicted the defender was higher during these initial four bouts than for those that gave up (eviction, mean = 296.0 (s.e. = 9.1); no eviction, mean = 237.1 (s.e. = 11.3), unpaired t -test, $t_{42} = 3.9$,

Figure 5. The negative association between sound intensity and glucose concentration in defenders. Receiving powerful raps may lead to the depletion of circulating glucose reserves in defenders, particularly in the case of defenders that were evicted. The dotted line indicates the mean concentration of glucose in defenders that had not fought. Filled squares represent eviction, open squares, no eviction. Regression line shown for whole dataset and for illustration only.

Figure 6. The positive relationship between the energy-expenditure index, calculated by multiplying the total number of raps by the average sound intensity, and the concentration of lactate in the haemolymph of attackers. Regression line shown for illustration only.

Figure 7. The negative association between the average energy-expenditure index during the first four bouts of rapping and the number of bouts required before the attacker was able to evict the defender. Only attackers that effected an eviction after performing at least four bouts of rapping were included in the analysis. Regression line shown for illustration only.

$p < 0.0003$). There was, however, no significant correlation between the average energy expenditure over the first four bouts and the final concentration of either lactate in attackers or glucose in defenders.

4. DISCUSSION

This is the first report, to the best of our knowledge, that quantifies the magnitude of a repeated signal used in contests and relates it to physiological changes and behavioural decisions. Attackers with high lactate employed a large number of raps (figure 3), left longer pauses between bouts (figure 4) but supplied less power, on average, to their raps (figure 2). This is explained by attackers that used low power early in fights having longer fights (figure 7). The index of the total energy expenditure of attackers, however, which provides an estimate of the 'effort' employed by attackers over the course of the whole fight, exhibited a positive relationship with lactate concentration (figure 6). Thus, lactate appears to increase with the effort used by attackers and, as the fight progresses, constrains the rate (duration of pauses) and, possibly, power with which attackers may rap. Attackers give up the fight when the concentration of lactate in their haemolymph becomes high. Accumulation of lactate is a significant cost because it will restrict the behaviour of attackers, not only during the course of the encounter but for a recovery period after the fight. In decapod crustaceans the period required for recovery from demanding activity can be prolonged (e.g. Sneddon *et al.* 1999), with complete reconversion of lactic acid to pyruvate taking several hours.

In contrast to the attackers, for defenders the main costs of fighting appear not to be associated with anaerobic respiration, but with the level of glucose (Briffa & Elwood 2001). Defenders that successfully resist eviction have a higher glucose concentration than evicted crabs, and the lowest levels were seen in crabs that were not allowed to fight. Thus, in defenders, glucose is elevated during fights and success is dependent upon this elevation. Defenders, therefore, may make a decision of whether or not to resist, with elevated glucose being seen only if they decide to do so. Such a decision should be based on information about the attacker's quality, as perceived early in the fight. This possibility is supported by the negative relationship between the energy-expenditure index of attackers early in the fight and the number of bouts of rapping that they must perform in order to gain an eviction (figure 7). When attackers rap with high power during the first four bouts, defenders give up. Thus, the power used by the attacker early in the fight seems to be of key importance in determining the outcome. The estimate made by defenders of attacker fighting ability, however, appears not to be completely accurate. Some defenders subsequently gave up even though they had moderately high glucose and were receiving raps of little power (figure 5). Thus, deciding to resist, and mobilizing glucose, does not guarantee success. This is because some attackers, although not able to rap with high power, are, nevertheless, persistent and eventually win.

The present data suggest that early in the fight defenders assess a composite measure of various parameters of power and temporal repetition of shell rapping performed by attackers, and make a key decision on

whether to resist or give up early. But why should the defender give up? Perhaps early power is a pure signal of high stamina and/or high motivation and has no direct effect on the defender. In the absence of direct effects, however, there is little reason for the defender to give up other than time costs. Indeed, as lactate incurred by attackers increases with power and as attackers give up when lactate is high, consistent high power should cause rapid fatigue in the attacker and the attacker should give up early. It is probable, therefore, that there is a direct cost to defenders in receiving powerful raps. The vibration effects caused by the impact of raps may directly affect the ability of defenders to maintain a grip on their shells. Indeed, *in vitro* studies of abdominal-muscle preparations indicate that mechanical vibration can interfere with the regulation of muscle stiffness necessary to support the shell (Chapple 1993). If the defender is able and decides to resist, then glucose is mobilized, but this is a physiological cost in that valuable energy reserves are depleted. Some defenders, however, give up much later in the contest, having resisted and elevated their glucose. These individuals may give up either because of the increasing cost of continued mobilization of energy reserves or owing to depletion of these reserves below a threshold level. Thus, evicted defenders might fall into two groups: early evictions resulting from the defenders being quickly incapacitated by the vibrational effects of rapping, and late evictions where defenders have resisted these effects but make a subsequent behavioural decision to give up because of costs exceeding the benefit of retaining the shell.

Shell rapping is, thus, a complex situation, involving two very different roles and not easily described by models of 'symmetrical' fights. The physiological costs to the attacker are determined by its own actions and it gives up when these costs are high. The decision of attackers is, therefore, similar to that predicted by the energetic war of attrition model (Payne & Pagel 1996). However, whereas this model assumes that the activity should not directly affect the opponent, we have suggested potential direct effects for shell rapping. The 'signal' of rapping appears to have rapid direct effects on the defender, if produced with sufficient power, otherwise the defender will resist but at a physiological cost. This is similar to predictions of the cumulative assessment model of Payne (1998), where decisions are based on the opponent's actions, which will impose costs on receivers. This model and others (e.g. sequential assessment model; Enquist & Leimar (1983)) assume that animals fight in the same way. In the case of these hermit crabs, however, the two contestants fight in very different ways. Such 'asymmetrical' contests with different roles are common in nature (e.g. Parker 1970; Verrell 1986; Dick & Elwood 1996), hermit crab shell fights representing an extreme and obvious case. During such fights, the contestants perform different activities and incur different costs in different ways, and the current data suggest that this is not adequately described by current models of symmetric contests, which do not take this possibility into account.

The authors thank the UK BBSRC for funding this work, and two anonymous referees for their comments on the manuscript.

REFERENCES

- Ballintijn, M. R. & ten Cate, C. 1999 Variation in number of elements in the perch-coo vocalization of the collared dove (*Streptopelia decaocto*) and what it may tell about the sender. *Behaviour* **136**, 847–864.
- Briffa, M. & Elwood, R. W. 2000a Cumulative or sequential assessment during hermit crab shell fights: effects of oxygen on decision rules. *Proc. R. Soc. Lond. B* **267**, 2445–2452. (DOI 10.1098/rspb.2000.1304.)
- Briffa, M. & Elwood, R. W. 2000b The power of shell rapping influences rates of eviction in hermit crabs. *Behav. Ecol.* **11**, 288–293.
- Briffa, M. & Elwood, R. W. 2001 Decision rules, energy metabolism and vigor of hermit crab fights. *Proc. R. Soc. Lond. B* **268**, 1841–1848. (DOI 10.1098/rspb.2001.1752.)
- Briffa, M., Elwood, R. W. & Dick, J. T. A. 1998 Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. *Proc. R. Soc. Lond. B* **265**, 1467–1474. (DOI 10.1098/rspb.1998.0459.)
- Briffa, M., Elwood, R. W. & Russ, J. M. 2002 Analysis of multiple aspects of a repeated signal: power and rate of rapping during shell fights in hermit crabs. *Behav. Ecol.* (In the press.)
- Chapple, W. D. 1993 Dynamics of reflex cocontraction in hermit-crab abdomen—experiments and a systems model. *J. Neurophysiol.* **69**, 1904–1917.
- Charif, R. A., Mitchell, S. & Clark, C. W. 1995 *Canary 1.2 user's manual*. Ithaca, NY: Cornell Laboratory of Ornithology.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979 The logical stag: adaptive aspects of fighting in red deer (*Cervus elephas* L.). *Anim. Behav.* **27**, 211–225.
- Dick, J. T. A. & Elwood, R. W. 1996 Effects of natural variation in sex ratio and habitat structure on mate guarding decisions in amphipods (Crustacea). *Behaviour* **133**, 985–996.
- Elwood, R. W. & Briffa, M. 2001 Information gathering and communication during agonistic encounters: a case study of hermit crabs. *Adv. Stud. Behav.* **30**, 53–97.
- Engel, P. C. & Jones, J. B. 1978 Causes and elimination of erratic blanks in enzymatic metabolite assays during use of NAD⁺ in alkaline hydrazine buffers: improved conditions for the assay of L-glutamate, L-lactate and other metabolites. *Anal. Biochem.* **88**, 475–484.
- Enquist, M. 1985 Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Anim. Behav.* **33**, 1152–1161.
- Enquist, M. & Leimar, O. 1983 Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. Theor. Biol.* **102**, 387–410.
- Grafen, A. 1990 Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546.
- Gutmann, I. & Wahlefeld, A. W. 1974 L-(+)-lactate determination with lactate dehydrogenase and NAD⁺. In *Methods of enzymatic analysis*, 2nd edn (ed. H. U. Bergmeyer), pp. 1464–1468. New York: Academic Press.
- Maynard Smith, J. & Parker, G. A. 1976 The logic of asymmetric contests. *Anim. Behav.* **24**, 159–175.
- Neat, F. C., Huntingford, F. A. & Beveridge, M. M. C. 1998 Fighting and assessment in male cichlid fish: the effects of asymmetries in gonadal state and body size. *Anim. Behav.* **55**, 883–891.
- Neil, S. J. & Elwood, R. W. 1985 Behavioural modifications during egg-brooding in the hermit crab *Pagurus bernhardus* L. *J. Exp. Mar. Biol. Ecol.* **110**, 275–297.
- Parker, G. A. 1970 The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *J. Theor. Biol.* **47**, 233–243.
- Payne, R. J. H. 1998 Gradually escalating fights and displays: the cumulative assessment model. *Anim. Behav.* **56**, 651–662.
- Payne, R. J. H. & Pagel, M. 1996 Escalation and time costs in displays of endurance. *J. Theor. Biol.* **183**, 185–193.
- Raabo, E. & Terkildsen, T. C. 1960 On the enzymatic determination of blood glucose. *Scand. J. Clin. Lab. Invest.* **12**, 402–408.
- Sneddon, L. U., Taylor, A. C. & Huntingford, F. A. 1999 Metabolic consequences of agonistic behaviour: crab fights in declining oxygen tensions. *Anim. Behav.* **57**, 353–363.
- Taylor, P. W. & Elwood, R. W. 2002 The mis-measure of animal contests. *Anim. Behav.* (In the press.)
- Verrell, P. A. 1986 Wrestling in the red spotted newt (*Notophthalmus viridescens*): resource value and contest asymmetry determine contest duration and outcome. *Anim. Behav.* **34**, 398–402.