How resource quality differentially affects motivation and ability to fight in hermit crabs

S. Doake* and R. W. Elwood

School of Biological Sciences, Queen's University, Belfast, Belfast BT9 7BL, UK

Contesting animals typically gather information about the resource value and that information affects fight motivation. However, it is possible that particular resource characteristics alter the ability to fight independently of the motivation. Using hermit crabs, we investigate how the resource in terms of shell quality affects both motivation and ability to fight. These crabs fight for shells, but those shells have to be carried and may impose physiological costs that impede fight vigour. We find that the shell has different effects on motivation and ability. Potential attackers in very small shells were highly motivated to attack but, rather than having enhanced ability, unexpectedly quickly fatigued and subsequently were not more successful in the fights than were crabs in larger shells. We also examined whether defending crabs could gather information about the attacker's shell from the vigour of the attack. Defending crabs gave up quickly when a potential gain had been assessed, indicating that such information had been gathered. However, there was no indication that this could be owing to the activity of the attacker and the information is probably gathered via visual assessment of the shell.

Keywords: contests; motivation; resource-correlated resource-holding potential; hermit crab; negotiation hypothesis

1. INTRODUCTION

Fight outcomes are typically determined by two main factors. One is the resource-holding potential (RHP) [1] or the ability to fight and is typically correlated with body size and/or condition [2]. The other is the resource, the value of which is commonly assessed by both contestants [3], but sometimes by just one [4], and is positively related to fight motivation in terms of willingness to initiate and remain in the fight [5]. Ownership also affects outcome, often because it directly affects RHP, in which case the effect is termed resource-correlated RHP [6,7]. For example, in speckled wood butterflies, sun spot territory holders are more likely than intruders to win because sunspots increase the body temperature and hot males are more likely to win ([8], but see [9]). Further, male amphipods holding females in amplexus are considerably more likely to win against intruders because of a positional advantage that enhances RHP [10]. In these cases, holding any sunspot territory or female amphipod seems to enhance RHP, but it is possible that variation in these could cause variation in resource-correlated RHP. That is, sun spots may vary in thermal quality and thus vary body temperature and hence resource-correlated RHP. With amphipods, a male that carries a large female faces an increased energetic cost in terms of depleted glycogen and lipids [11] and the poorer condition might negatively affect the male's resource-correlated RHP. Another example, not involving physiological change, concerns contests over burrows, the width of which might affect how easily an intruder is excluded [12]. Thus, variation in resource quality might commonly

influence resource-correlated RHP. Here, with hermit crabs, we examine the effects of carrying shells of different sizes/weights on the ability to fight for alternative shells.

Hermit crabs carry empty snail shells for protection, but excessive shell weight decreases mobility [13] and growth [14] and increases haemolymph lactate levels [15]. To reduce weight, crabs might take a small shell, but protection is reduced because the crab cannot withdraw fully [16,17] and lactate is also elevated, probably because of restricted flow of oxygenated water to the gills [18]. Therefore, a hermit crab requires a shell that is not too heavy and not too small for its body size and crabs in poor shells are highly motivated to acquire shells that are nearer to their optimum [19]. They are more likely to initiate fights by which they take shells from other crabs [20–24]. In these shell fights, hermit crabs assume different roles, where the initiator attacks and the other defends. The attacker, usually the larger, grasps the opponent's shell and then engages in shell rapping, by pulling the two shells towards each other such that they repeatedly impact with high energy [25,26]. If the defender is evicted from the shell, the attacker can take the defender's shell and hence win the contested resource. The defender then takes the abandoned shell of the attacker [20]. Alternatively, the attacker may give up prior to evicting the defender.

Fights typically impose a physiological cost [27] and result in the depletion of energy reserves [10,28] and the accumulation of lactate in muscle tissues [29]. Lactate accumulates when demands for muscular action exceed the available oxygen for aerobic respiration and the animal uses anaerobic respiration. High lactate causes fatigue and reduces the ability to win [29]. This is particularly clear in hermit crab fights, where lactate rapidly

* Author for correspondence (sdoake01@qub.ac.uk).

accumulates in attackers [30]. It constrains the vigour of their rapping [22,24], and the number of raps per bout [22] and the power of raps decline as the fight progresses [24]. Attackers that maintain high vigour are more likely to evict the opponent and gain the shell [24,30]. Crabs with a high aerobic capacity owing to high levels of haemocyanin [31] or high levels of metal ions that enhance oxygen affinity of haemocyanin [32] show increased stamina in fights. Thus, physiological condition has marked effects on the ability of hermit crabs to fight. The current shell might influence the ability of the attacker to fight because of the shell's effects on physiological state.

Information about shells is critical to the decisions that crabs make during these contests. The attacker assesses the quality of the defender's shell by feeling it with its appendages and escalation to rapping is more likely and continues for longer if it offers a large improvement on its current shell [20,33], suggesting that they are more motivated to obtain the contested resource when the benefits are high [25]. Defenders also have information about their current shell. Those with private information that their shell is of poor quality, owing to sand being glued to the interior, readily evacuate those shells when attacked, indicating that defenders' motivation is also influenced by its resource value [34]. Thus, the resource value influences the motivation of each contestant and influences strategic decisions. However, these fights are unusual because both opponents start and finish with a resource and both could gain from the encounter, for example, if a large crab in a shell too small for it exchanged shells with a small crab in a shell too large for it. Hazlett [35] showed that evictions occur more quickly if the defender could gain from exchange [36,37] and suggested that crabs 'negotiate' rather than fight. For this, the defender, like the attacker, must have information about both shells. However, while it clearly has information about its current shell [34,38], there seems to be no way to assess the attacking crab's shell as the defender remains withdrawn into its own shell throughout the fight [33]. Here, we consider whether the attacker's ability to fight vigorously is affected by shell size and whether the vigour of rapping might convey information to the defender about the suitability of the attacker's shell for the defender.

In this study, we vary the quality of the attacker's current resource but keep the quality of the defender's shell the same. The primary aim is to disentangle effects of current resource quality on fight motivation and resource-correlated RHP or fight ability of the attacker. Motivation may be inferred by the willingness to initiate (i.e. assume the attacker role and the physiological cost the crab is prepared to pay). The latter was gauged by lactate levels at the end of the fight. Shell-induced variation in ability may be shown by the vigour of shell rapping, particularly during the early bouts of rapping. A second aim is to investigate whether rapping vigour provides information to the defender as to attacker's shell quality. If so, we predict swift evictions and more shell exchanges when the attacker's shell is suitable for the defender.

2. METHODS

Hermit crabs (*Pagurus bernhardus*) were collected from the shore at Minerstown, County Down, Northern Ireland

(54°15'1" N, 05°42'12" W), from July to November 2008, held in tanks (30 × 48 × 14 cm) filled with aerated, ultraviolet (UV)-filtered, sea water with a constant temperature of 12°C and a 12 L:12 D light cycle, and fed twice a week on snail meat (*Littorina littorea*). Crabs were removed from their shells using a bench vice, dried, by patting with paper towels, weighed and sexed. Each was assigned to a same sex pair so that one was approximately 20 per cent lower weight than the other (female pairs $n = 84$, male pairs $n = 46$). Both sexes were included in the study to increase the sample size as it was difficult match crabs by the required weights. The weight of the larger crab varied between 0.214 and 1.252 g ($\bar{x} = 0.492$, ± 0.177) and the weight of the smaller crab varied between 0.169 and 1.031 g ($\bar{x} = 0.389$, ± 0.142). These pairs were randomly allocated into three groups (by drawing lots) and each crab was given a specific shell according to their group. All smaller crabs of each pair were given a shell that was the optimal weight for the larger crab and thus too heavy for the smaller crab (optimal weights determined from preliminary choice experiments and regression analysis). In group A ($n = 44$), the large crab was given a shell 50 per cent too heavy for the small crab (i.e. 45% too heavy for the large crab), in group B ($n = 42$), the large crab was given a shell that was of optimal weight for the small crab (i.e. 10% too light for the large crab) and in group C ($n = 44$), the large crab was given a shell 50 per cent too light for the small crab (i.e. 55% too light for the large crab). Each crab was placed in individual, numbered pots (9 × 15 cm) containing UV-filtered sea water and aerated overnight. The shells were from *L. littorea*, collected from the same shore as the hermit crabs.

The observation arena comprised a crystallizing dish (diameter 13.5 cm, height 7.5 cm) with a layer of coarse gravel as a substrate, filled with 800 ml of UV-filtered sea water and placed behind a one-way mirror. A microphone (Yoga dynamic DM-2100), with a waterproof latex cover, was hung into the centre of the arena at a height of 2.5 cm from the bottom. The microphone was connected to a solid-state, digital recorder (Marantz PM600 Prof.), and AVISOFT-SASLAB pro-software was used to calculate times between raps and bouts and numbers of raps and bouts from each fight, while AUDACITY 1.2.6 software was used to obtain the amplitude of each rap. A bout of rapping was defined as a series of individual raps separated by short gaps (less than 1 s). The crabs were placed at opposite sides of the arena at the same time and recording continued until either the defender was evicted or the attacker gave up, or if no fight occurred for 25 min. Each crab was immediately dropped into a canister of liquid nitrogen and then removed and defrosted for 45 min. Haemolymph samples were drawn from the base of the third and fourth walking legs using a syringe and analysed for lactate levels using a lactate meter (ARKRAY Lactate Pro).

(a) Statistical analysis

STATVIEW v. 15.0 and SPSS v. 17.0 were used for the analyses. The data were tested for normality using Kolmogorov–Smirnov tests and, if required, were log transformed before carrying out parametric analyses. χ^2 and G tests, when the former were not appropriate, were used in the initial exploration of contingency data, followed by analysis of variance and regression analysis for continuous measures. As the aim of the experiment was to investigate the effects of the larger crab's shell on the larger crab's motivation and

Figure 1. Cumulative plot showing the number of crabs giving up after each bout of rapping for all three groups. Black circles, A; grey circles, B; white circles, C.

ability, cases where the small crab initiated the fight were excluded in subsequent analyses on measures of fight vigour. There was no difference between male and female pairs on motivation to engage in a contest ($\chi^2_1 = 0.452$, $p = 0.501$). There were no gender effects on the probability of eviction ($\chi^2_1 = 0.470$, $p = 0.493$) and no significant difference between genders for the lactate of the attacker ($F_{1,67} = 0.505$, $p = 0.4799$) or defender ($F_{1,67} = 2.321$, $p = 0.1323$); therefore, gender was not considered in any further analyses.

3. RESULTS

Of the 130 interactions, 96 resulted in a fight (table 1), of which there were 70 evictions and 26 non-evictions (table 2). Fights were significantly more likely in group C, when the larger crab was in a shell much too small for it than in the other two groups ($\chi^2_2 = 10.06$, $p = 0.0066$; table 1). Overall, larger crabs were more likely than smaller crabs to initiate the fight (69 versus 27; $\chi^2_1 = 18.37$, $p < 0.001$) and, when they initiated a fight, were more likely to evict their opponent than were smaller crabs ($\chi^2_1 = 22.02$, $p < 0.0001$, large: 60/99, small: 10/27; table 2). A larger proportion of fights were initiated by the larger crab compared with the smaller crab in group C than in the other two groups ($\chi^2_2 = 11.44$, $p = 0.0033$; table 2). However, for fights initiated by the larger crab, there was no significant difference between groups in the probability of eviction ($G^2_2 = 0.855$, $p = 0.650$).

For fights initiated by the larger crab, the number of bouts of rapping prior to eviction was greatest in group A and fewest in group B ($F_{2,65} = 3.873$, $p = 0.0258$). A cumulative plot (figure 1) shows that the majority of group B defenders gave up within three bouts of rapping compared with over 10 bouts for group A.

To examine ability, the first three bouts of each fight were examined irrespective of fight outcome. The first three bouts were chosen as this avoids confounding effects

Figure 2. Mean $\pm$ s.e. mean amplitude of raps per bout for the three groups. Black bars, A; grey bars, B; white bars, C.

Table 1. Number of interactions that resulted in a fight for each group.

	A	B	C	total
fight	29	27	40	96
no fight	15	15	4	34
total	44	42	44	130

of fight duration and because few fights in group B exceeded three bouts. Amplitude decreased across the first three bouts of rapping ($F_{2,80} = 4.067$, $p = 0.021$), but there was no effect of group ($F_{2,80} = 0.4601$, $p = 0.4601$) and there was no interaction ($F_{4,80} = 0.446$, $p = 0.775$; figure 2). There was no change in the pause duration over the first three pauses ($F_{2,70} = 1.203$, $p = 0.307$) and no effect of group ($F_{2,70} = 1.536$, $p = 0.229$) and there was no interaction ($F_{4,70} = 1.784$, $p = 0.142$). Gaps between raps (within a bout) increased across the first three bouts ($F_{2,84} = 5.354$, $p = 0.006$), but there was no effect of group ($F_{2,84} = 0.516$, $p = 0.601$) and there was no interaction ($F_{4,84} = 1.809$, $p = 0.135$; figure 3). The number of raps per bout did not differ over the first three bouts of rapping ($F_{2,86} = 2.258$, $p = 0.111$) and there was no effect of group ($F_{2,86} = 0.212$, $p = 0.810$) but there was an interaction effect ($F_{5,86} = 2.686$, $p = 0.037$; figure 4). The number of raps per bout in group C declined more than did those of the other two groups, in fact, in groups A and B they seem to increase.

Lactate of attackers did not vary with fight outcome ($F_{1,63} = 0.001$, $p = 0.9714$) or group ($F_{2,63} = 0.832$, $p = 0.4401$); however, there was a significant interaction effect ($F_{2,63} = 4.043$, $p = 0.0223$). In groups A and B, attackers gaining eviction had higher lactate than attackers that gave up, whereas in group C the reverse was found (figure 5). Post hoc tests revealed no difference between fight outcomes for groups A and B, but a significant difference for group C ($t_{33} = 2.464$, $p = 0.0191$).

Figure 3. Mean $\pm$ s.e. time between raps (gaps) for the three groups over three bouts. Black bars, A; grey bars, B; white bars, C.

Figure 4. Mean $\pm$ s.e. $\log(n + 1)$ mean number of raps per bout for three groups. Black bars, A; grey bars, B; white bars, C.

Table 2. The number of evictions resulting from fights for each group.

attacker	A		B		C		total
	small	large	small	large	small	large	
eviction	4	15	4	14	2	31	70
no eviction	7	3	8	1	2	5	26
total	11	18	12	15	4	36	—
	29		27		40		96

Lactate of defenders did not vary with fight outcome ($F_{1,63} = 0.360$, $p = 0.5506$) or group ($F_{2,63} = 0.504$, $p = 0.6067$), and there was no interaction effect ($F_{2,63} = 0.503$, $p = 0.6072$).

4. DISCUSSION

We used the probability of taking the attacker role as a measure of fight motivation. Overall, the larger contestants took the attacker role more often than did the smaller, showing that size is a major determinant in fight decisions [2,39], but the larger crab was significantly more likely to take that role when its current shell was much too small. Small shells offer less protection from predators and may restrict respiration, and a high motivation was expected. However, we had expected that crabs in shells that were much too large would also be highly motivated [19], but this was not found.

A second measure of motivation was the physiological cost in terms of accumulation of lactate that the attacker was prepared to pay for the contested resource. There was a significant interaction between group and outcome; attackers in shells that were much too small that eventually gave up, revealing the cost they were prepared to pay [2], had particularly high lactate, and significantly higher than those that effected an eviction before revealing their cost threshold. Thus again, attackers in very small shells appear to have had a high motivation

compared with the other groups. The present data thus suggest that a shell that is too small is worse than one that is too large. However, this is consistent with the finding that while very small shells cause elevated lactate, large shells, similar to sizes used here, do not [18]. Resource quality clearly influences fight motivation in the present study and across a range of taxa [5].

To investigate variation in resource-correlated RHP, we examined the vigour of rapping because this appears to be an honest signal of ability [40]. Rapping is energetically demanding [24,30,41], and crabs that fight with high vigour, indicated by short pauses between bouts and powerful raps, gain evictions [21]. Thus, shell rapping advertises true ability, and crabs that are in poor condition because they occupy unfavourable shells were predicted not to be able to rap as well as stronger individuals. Further, this effect should be apparent early in the contest as the physiological effects of unfavourable shells should be established prior to the contest. However, we found no difference in the vigour of rapping that was dependent upon an immediate effect of the current resource. The amplitude of raps decreased over the first three bouts, whereas gap duration within bouts increased, consistent with the idea of fatigue inhibiting the ability to fight [25]. Crabs with small, light shells should be able to move them with less energy demand during a fight, and therefore be able to rap more easily. However, rather than showing greater vigour, crabs with very small shells

Figure 5. Mean $\pm$ s.e. log ($n + 1$) lactate of attackers between fight outcomes and groups. Black bars, eviction; white bars, no eviction.

seemed to become fatigued more quickly because the number of raps per bout seemed to decline in this group. A recent study indicated that non-fighting crabs in very small shells surprisingly had elevated lactate levels possibly because of reduced respiratory flow through the small shell aperture [18]. At the start of the fight, this elevated lactate does not immediately affect vigour, but apparently results in a more rapid fatigue in terms of raps per bout. Further, we note the higher lactate in this group for attackers that eventually gave up despite the duration of contests not being greater for attackers in very small shells compared with those in very large shells; indeed the trend was for the opposite. This is consistent with the idea that very small shells impose a physiological cost that affects resource-correlated RHP. We note that despite the very high motivation of attackers in small shells, there was no increase in their ability to evict the opponent. It seems that the high motivation was offset by a decreased ability of this group.

There are similarities between our findings and those of other studies, such as those investigating the differing thermal effects of sun spots on fighting ability for territorial butterflies [8] and the physiological effects of carrying females in male amphipods [11]. Thus, rather than resources having the same resource-correlated effect, the size of the effect is determined by some aspect of resource quality. We argue that although rarely studied, this effect is likely to be widespread. For example, it should occur in any system in which the resource can vary in size and has to be carried by the owner, such as scorpionflies carrying prey items that serve as nuptial gifts [42], males carrying females and a wide range of animals that carry shelters, all of which will affect the physiological state of the owner. There might be mechanical constraints for males holding females, and the male's grip may be more easily maintained for a particular female size irrespective of physiological cost, and mechanical constraints of a wide range of animals defending shelters of different sizes [12]. Thermal effects might be widespread among ectotherms [8].

According to the negotiation model [35,36], there should have been significantly more evictions in group B, when the attacker was in a shell that was of optimal size for the defender. However, this was not found. Nevertheless, defenders in group B gave up more quickly than those in other groups. This agrees with another prediction of the negotiation hypothesis. The value of the defender's shell influences how long it persists in defence [34], but here groups did not differ in terms of defender's shell. Crucially, this indicates that the defender must be gaining some information on the quality of the attacker's shell [36]. However, there is no indication here that this is owing to the ability of attackers to rap when in particular shells as attackers in this group did not rap with greater vigour. It is not clear how the defender may gain information on the attacker's shell. Hazlett [36,37] suggested that shell rapping may provide the defender with information on the quality of the attacker's shell by the harmonics of the sounds produced [43]. However, no evidence to support this idea has yet been found. Second, Hazlett [37] suggested that hermit crabs can gain information on shell size using visual cues, and it may be possible for defending crabs to assess the quality of the attacker's shell during the pre-fight approach. However, it is thought that this visual assessment from a distance is limited and further information on shell quality must be gained from direct contact with the shell [44]. The original negotiation hypothesis [35] arose from a study of large/old hermit crabs of the same species used here. The studies that failed to support negotiation used smaller (young) crabs [17,33]. Those used here were larger and hence older, and it is possible that hermit crabs develop the ability to assess shells from a distance. Although the evidence of the present study supports the idea that defenders are able to gather information about the attacker's shell, it does not support the idea of negotiation *per se*. Each contestant simply uses the information that it can access to make optimal decisions during agonistic encounters [5].

To conclude, shell quality has different effects on the motivation and ability of attackers to fight. Defenders give up quickly when they can gain an optimum shell, indicating that they gather information about attacker's shell quality. These data indicate the complexity of these fights and the interplay between information affecting motivation of each competitor and physical characteristics of resources affecting their fight ability. In particular, we note that variation in resource-correlated RHP found here is likely to be widespread among taxa.

We thank the Department of Education and Learning for Northern Ireland for funding, two anonymous referees for some excellent suggestions for improvement and Gillian Riddell for technical support.

REFERENCES

- 1 Parker, G. A. 1974 Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* **47**, 223–243. (doi:10.1016/0022-5193(74)90111-8)
- 2 Arnott, G. & Elwood, R. W. 2009 Assessment of fighting ability in animal contests. *Anim. Behav.* **77**, 991–1004. (doi:10.1016/anbehav.2009.02.010)
- 3 Dick, J. T. A. & Elwood, R. W. 1990 Symmetrical assessments of female quality by male *Gammarus pulex* (Amphipoda) during struggles over precopula. *Anim.*

- Behav.* **40**, 877–883. (doi:10.1016/S0003-3472(05)80989-3)
- 4 Bridge, A. P., Elwood, R. W. & Dick, J. T. A. 2000 Imperfect assessment and limited information preclude optimal strategies in male–male fights in the orb-weaving spider *Metellina menzei*. *Proc. R. Soc. Lond. B* **267**, 273–279. (doi:10.1098/rspb.2000.0997)
 - 5 Arnott, G. & Elwood, R. W. 2008 Information gathering and decision making about resource value in animal contests. *Anim. Behav.* **76**, 529–542. (doi:10.1016/j.anbehav.2008.04.019)
 - 6 Kemp, D. J. & Wiklund, C. 2001 Fighting without weaponry: a review of male–male contest competition in butterflies. *Behav. Ecol. Sociobiol.* **49**, 429–442. (doi:10.1007/s002650100318)
 - 7 Humphries, E. L., Hebblethwaite, A. J., Batchelor, T. P. & Hardy, I. C. 2006 The importance of valuing resources: host weight and contender age as determinants of parasitoid wasp contest outcomes. *Anim. Behav.* **72**, 891–898. (doi:10.1016/j.anbehav.2006.02.015)
 - 8 Stutt, A. D. & Willmer, P. 1998 Territorial defence in speckled wood butterflies: do the hottest males always win? *Anim. Behav.* **55**, 1341–1347. (doi:10.1006/anbe.1998.0728)
 - 9 Kemp, D. J. & Wiklund, C. 2004 Residency effects in animal contests. *Proc. R. Soc. Lond. B* **271**, 1707–1711. (doi:10.1098/rspb.2004.2775)
 - 10 Prenter, J., Elwood, R. W. & Taylor, P. W. 2006 Self assessment by males during energetically costly contests over precopula females in amphipods. *Anim. Behav.* **72**, 861–868. (doi:10.1016/j.anbehav.2006.01.023)
 - 11 Plaistow, S. J., Bollache, L. & Cézilly, F. 2003 Energetically costly precopulatory mate guarding in the amphipod *Gammarus pulex*: causes and consequences. *Anim. Behav.* **65**, 683–691. (doi:10.1006/anbe.2003.2116)
 - 12 Morrell, L. J., Backwell, P. R. Y. & Metcalfe, N. B. 2005 Fighting in fiddler crabs *Uca mjoebergi*: what determines duration? *Anim. Behav.* **70**, 653–662. (doi:10.1016/j.anbehav.2004.11.014)
 - 13 Fotheringham, N. 1976 Population consequences of shell utilization by hermit crabs. *Ecology* **57**, 570–578. (doi:10.2307/1936441)
 - 14 Osorno, J. L., Contreras-Garduño, J. & Macías-García, C. 2005 Long-term costs of using heavy shells in terrestrial hermit crabs (*Coenobita compressus*) and the limits of shell preference: an experimental study. *J. Zool.* **266**, 377–383. (doi:10.1017/S0952836905007028)
 - 15 Briffa, M. & Elwood, R. W. 2005 Metabolic consequences of shell choice in *Pagurus bernhardus*: do hermit crabs prefer cryptic or portable shells? *Behav. Ecol. Sociobiol.* **59**, 143–148. (doi:10.1007/s00265-005-0020-0)
 - 16 Angel, J. E. 2000 Effects of shell fit on the biology of the hermit crab *Pagurus longicarpus* (Say). *J. Exp. Mar. Biol. Ecol.* **243**, 169–184. (doi:10.1016/S0022-0981(99)00119-7)
 - 17 Elwood, R. W. & Neil, S. J. 1992 *Assessments and decisions: a study of information gathering by hermit crabs*. London, UK: Chapman & Hall.
 - 18 Doake, S., Scantlebury, M. & Elwood, R. W. In press. The costs of bearing arms and armour in the hermit crab, *Pagurus bernhardus*. *Anim. Behav.* (doi:10.1016/j.anbehav.2010.06.023)
 - 19 Elwood, R. W. & Stewart, A. 1985 The timing of decisions during shell investigation by the hermit crab, *Pagurus bernhardus*. *Anim. Behav.* **33**, 620–627. (doi:10.1016/S0003-3472(85)80086-5)
 - 20 Dowds, B. M. & Elwood, R. W. 1983 Shell wars: assessment strategies and the timing of decisions in hermit crab shell fights. *Behaviour* **85**, 1–24. (doi:10.1163/156853983X00011)
 - 21 Briffa, M. & Elwood, R. W. 2000 The power of shell rapping influences rates of eviction in hermit crabs. *Behav. Ecol.* **11**, 288–293. (doi:10.1093/beheco/11.3.288)
 - 22 Briffa, M. & Elwood, R. W. 2001 Decision rules, energy metabolism and vigour of hermit crab fights. *Proc. R. Soc. Lond. B* **268**, 1841–1848. (doi:10.1098/rspb.2001.1752)
 - 23 Briffa, M. & Elwood, R. W. 2001 Motivational change during shell fights in the hermit crab *Pagurus bernhardus*. *Anim. Behav.* **62**, 505–510. (doi:10.1098/rspb.2002.2158)
 - 24 Briffa, M. & Elwood, R. W. 2002 Power of shell-rapping signals influences physiological costs and subsequent decisions during hermit crab shell fights. *Proc. R. Soc. Lond. B* **269**, 2331–2336. (doi:10.1098/rspb.2002.2158)
 - 25 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)
 - 26 Elwood, R. W. & Briffa, M. 2001 Information gathering during agonistic and non agonistic shell acquisition by hermit crabs. *Adv. Study Behav.* **30**, 53–97. (doi:10.1016/S0065-3454(01)80005-X)
 - 27 Thorpe, K. E., Taylor, A. C. & Huntingford, F. A. 1995 How costly is fighting? Physiological effects of sustained exercise and fighting in swimming crabs *Necora puber* (L.) (Brachyura, Portunidae). *Anim. Behav.* **50**, 1657–1666. (doi:10.1016/0003-3472(95)80019-0)
 - 28 Plaistow, S. & Siva-Jothy, M. T. 1996 Energetic constraints and male-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). *Proc. R. Soc. Lond. B* **263**, 1233–1238. (doi:10.1098/rspb.1996.0181)
 - 29 Neat, F. C., Taylor, A. C. & Huntingford, F. A. 1998 Proximate costs of fighting in male cichlid fish: the role of injury and energy metabolism. *Anim. Behav.* **55**, 875–882. (doi:10.1006/anbe.1997.0668)
 - 30 Briffa, M. & Elwood, R. W. 2005 Rapid change in energy status in fighting animals: causes and effects of strategic decisions. *Anim. Behav.* **70**, 119–124. (doi:10.1016/j.anbehav.2004.10.013)
 - 31 Mowles, S. L., Cotton, P. A. & Briffa, M. 2009 Aerobic capacity influences giving-up decisions in fighting hermit crabs: does stamina constrain contests? *Anim. Behav.* **78**, 735–740. (doi:10.1016/j.anbehav.2009.07.003)
 - 32 Mowles, S. L., Briffa, M., Cotton, P. A. & Spicer, J. I. 2008 The role of circulating metal ions during shell fights in the hermit crab *Pagurus bernhardus*. *Ethology* **114**, 1014–1022. (doi:10.1111/j.1439-0310.2008.01542)
 - 33 Elwood, R. W. & Glass, C. W. 1981 Negotiation or aggression during shell fights of the hermit crab *Pagurus bernhardus*? *Anim. Behav.* **29**, 1239–1244. (doi:10.1016/S0003-3472(81)80075-9)
 - 34 Arnott, G. & Elwood, R. W. 2007 Fighting for shells: how private information about resource value changes hermit crab pre-fight displays and escalated fight behaviour. *Proc. R. Soc. B* **274**, 3011–3017. (doi:10.1098/rspb.2007.1196)
 - 35 Hazlett, B. A. 1978 Shell exchanges in hermit crabs: aggression, negotiation or both? *Anim. Behav.* **26**, 1278–1279. (doi:10.1016/0003-3472(78)90123-9)
 - 36 Hazlett, B. A. 1987 Information transfer during shell exchange in the hermit crab *Clibanarius antillensis*. *Anim. Behav.* **35**, 218–226. (doi:10.1016/S0003-3472(87)80227-0)
 - 37 Hazlett, B. A. 1996 Assessments during shell exchanges by the hermit crab *Clibanarius vittatus*: the complete negotiator. *Anim. Behav.* **51**, 567–573. (doi:10.1006/anbe.1996.0060)

- 38 Jackson, N. W. & Elwood, R. W. 1989 How animals make assessments: information gathering by the hermit crab *Pagurus bernhardus*. *Anim. Behav.* **38**, 951–957. (doi:10.1016/S0003-3472(89)80136-8)
- 39 Dowds, B. M. & Elwood, R. W. 1985 Shell wars 2: the influence of relative size on decisions made during hermit crab shell fights. *Anim. Behav.* **33**, 649–656. (doi:10.1016/S0003-3472(85)80088-9)
- 40 Briffa, M. 2006 Signal residuals during shell fighting in hermit crabs: can costly signals be used deceptively? *Behav. Ecol.* **17**, 510–514. (doi:10.1093/beheco/arj059)
- 41 Briffa, M. & Elwood, R. W. 2003 Use of energy reserves in fighting hermit crabs. *Proc. R. Soc. Lond. B* **271**, 373–379. (doi:10.1098/rspb.2003.2633)
- 42 Thornhill, R. 1984 Fighting and assessment in *Harpobittacus* scorpionflies. *Evolution* **38**, 204–214. (doi:10.2307/2408558)
- 43 Morse, P. M. 1948 *Vibration and sound*. New York, NY: McGraw-Hill.
- 44 Elwood, R. W. 1995 Motivational change during resource assessment by hermit crabs. *J. Exp. Mar. Biol. Ecol.* **193**, 41–55. (doi:10.1016/0022-098(95)00109-3)