



## Aerobic capacity influences giving-up decisions in fighting hermit crabs: does stamina constrain contests?

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Strategic decisions in animal contests have been increasingly understood in terms of the physiological consequences of fighting, in particular by investigating energetic costs. In addition to these costs, the scope for vigorous agonistic activity may be modified by the aerobic capacity of individuals, engaged in a fight, which can be linked to circulating levels of respiratory pigment. Greater concentrations of respiratory pigment should increase aerobic capacity, thus enhancing aerobic respiration, postponing the onset of anaerobiosis, and reducing the amount of metabolic acidosis incurred. We examined postfight levels of the respiratory pigment haemocyanin in the hermit crab *Pagurus bernhardus*. The concentration of haemocyanin was higher in winners than losers, but was also positively correlated with body size. Residuals calculated for how much each individual deviated from this relationship revealed that individuals that had more positive residuals were more likely to win aggressive encounters. Thus, greater levels of respiratory pigment appear to enhance agonistic performance via their influence on endurance and aerobic capacity.

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Game theory predicts that natural selection should favour the use of nondangerous tactics during aggressive encounters. Indeed, 'fighting' often involves the use of signals that are assumed to advertise the 'resource-holding potential' (RHP, Parker 1974) of the sender. In many cases these signals may be energetically demanding to perform and the vigour of performance may be linked to the stamina of the sender (Payne & Pagel 1996, 1997). In such contests the 'stamina' of the sender is assumed to be equivalent to the maximum amount of energy it can allocate to the contest, such that giving-up decisions are related to a maximum 'cost threshold', which acts as a switching line for withdrawal. In some examples the decision to withdraw is based on the loser comparing its own cost threshold to that of the opponent, if such information is available. Here, the opponent's RHP is assessed and the loser gives up as soon as it has determined that it is the weaker of the two opponents. Such 'mutual assessment' (e.g. Taylor & Elwood 2003; Briffa & Elwood 2009) is a key feature of the sequential assessment model, SAM (Enquist & Leimar 1983), although there may be situations when information about the opponent is unavailable, and the decision to withdraw may be entirely based on 'self-assessment' (e.g. Taylor & Elwood 2003; Briffa & Elwood 2009). Here, the loser makes

a decision to withdraw on the basis of its own condition. Self-assessment is a central feature of models such as the energetic war of attrition, EWOA (Payne & Pagel 1996) and the cumulative assessment model, CAM (Payne 1998). In some contests the opponents may adopt different roles, such as owner and intruder or attacker and defender, and in such cases there may be asymmetries not only in RHP and perceived resource value but also in the available information about the opponent's RHP. This means that individuals may use different rules as the basis of their giving-up decisions depending on their role in the contest. Indeed, none of the current models of contest behaviour assume that both opponents should play by the same rules, and during fights in hermit crabs it appears that different decision rules are used by each role (Briffa & Elwood 2001). However, both roles engaging in a noninjurious contest can potentially make a giving-up decision and in each case this decision may be related to the loser's stamina. Our aim in this study was therefore to determine whether aerobic capacity, an aspect of stamina, influenced strategic decisions, using hermit crab shell fights as a model system.

Fights between hermit crabs commonly occur over the ownership of gastropod shells and involve two distinct modes of fighting. The initiating crab or 'attacker' attempts to take the shell of the non-initiator or 'defender' following an assessment period comprising bouts of 'shell rapping', during which the defender remains tightly withdrawn inside its shell. The attacker grasps the defender, gripping

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the contested shell with its walking legs, and proceeds to bring its own shell rapidly and repeatedly into contact with that of the defender. The shell fight consists of a series of such bouts of rapping, separated by distinct pauses. Shell fights can end in one of two ways: either the defender decides to give up, allowing itself to be evicted by the attacker, which removes the defender through the aperture of the shell, or the attacker may decide to give up without having evicted the defender. During these encounters there is the clear possibility for information asymmetries as the defender remains withdrawn inside the contested shell while the attacker performs vigorous bouts of shell rapping. The attacker has a greater opportunity to gather information about the contested resource value (the subjective difference in quality between the two shells in the contest) whereas the defender has the potential to gather information about the attacker's RHP by monitoring the vigour of shell rapping. Indeed, the vigour of shell rapping is a key determinant of the outcome of shell fights, and it has been consistently shown that successful attackers perform more raps per bout, leave shorter pauses between bouts of rapping (Briffa et al. 1998), and perform more powerful raps (Briffa & Elwood 2002). This suggests that the pattern of rapping is linked to the fighting ability of the attacker, and the presence of both escalation and de-escalation in the vigour of rapping as the fight progresses (Briffa et al. 1998; Briffa & Elwood 2000a, b) is consistent with the idea that shell rapping demonstrates the attacker's 'stamina' as predicted by the EWOA and CAM.

Studies of repeated signals in a wide range of taxa, including toads (Sullivan & Walsberg 1985), birds (Weary et al. 1991; Horn et al. 1995) and red deer, *Cervus elaphus* (Clutton-Brock et al. 1979) have demonstrated a link between the pattern of performance and agonistic success, and indicate that performance may be constrained by the ability to meet the energetic demands associated with agonistic behaviour. In hermit crabs, fighting involves anaerobic respiration as evidenced by elevated postfight *L*-lactate levels in comparison to crabs that have not fought. Attackers that give up have greater lactate levels than the successful defenders that they failed to evict, but the same difference is not seen between successful attackers and defenders that give up (Briffa & Elwood 2001, 2002). Thus, the giving-up decision in one role, the attacker, appears to be based on a cost of high lactate, a potential correlate of stamina and threshold used in self-assessment. On the other hand, defenders that give up have low levels of circulating glucose, but rather than an effect of low energy reserves, this appears to be caused by a decision to offer a low level of resistance if high attacker vigour is perceived (Briffa & Elwood 2004, 2005). Thus, previous studies of both postfight energetic status and fight dynamics indicate the use of different decision rules by attackers and defenders; attackers use a self-assessment rule whereas defenders appear to assess the attacker's performance.

'Stamina' was first proposed as a key mechanism in contest behaviour under the EWOA and CAM (see Payne & Pagel 1997; Payne 1998). 'Stamina' in these threshold assessment models is assumed to be equivalent to endurance capacity although in other contexts maximum performance capacity may also be considered an aspect of stamina. In the context of contest behaviour 'stamina' can therefore be more formally described as 'the capacity for sustained performance while incurring cumulative energetic costs'. Since the main sources of energetic costs are depletion of energy reserves and accumulation of harmful metabolic by-products that result from any anaerobic metabolism of those energy reserves, two key physiological mechanisms contributing to stamina are therefore (1) the available energy reserves and (2) aerobic capacity. Anaerobic respiration is less efficient than aerobic respiration, producing less ATP per molecule of glucose (Sadava et al. 2008) and results in the accumulation of *L*-lactate (reviewed in Bridges 2001; Briffa & Sneddon 2007), a major cause of fatigue. Therefore the ability to

avoid anaerobic respiration while maintaining demanding activity is an important component of stamina that would confer an advantage to an individual in a noninjurious fight. Thus, physiological endurance capacity may dictate the duration of demanding activity an individual can perform before exhaustion or 'maximum exertion' (Lailvaux et al. 2005) and in hermit crabs this may be linked to the giving-up decision of attackers. Although high *L*-lactate does not appear to influence the giving-up decision in defenders directly, crabs adopting this role are also subject to elevated *L*-lactate and avoiding anaerobic respiration may also be of benefit.

In arthropods the key determinant of aerobic capacity is the concentration of circulating oxygen-transporting respiratory proteins in the haemolymph (Kobayashi & Gonoï 1985), which in most cases is haemocyanin (Truchot & Lallier 1992). This is freely circulating and accounts for up to 97% of oxygen transport (Redfield 1934; Redmond 1955; Terwilliger 1998). The ability of haemocyanin to transport oxygen may be modulated by several allosteric factors present in the haemolymph (see Mowles et al. 2008). However, a more direct process by which to increase aerobic capacity would be the synthesis of greater quantities of haemocyanin (Terwilliger 1998). Haemocyanin levels in crustaceans can increase significantly over approximately 24 h (Spicer & Baden 2001), but in the relatively short timescale of an agonistic encounter (typically lasting from a few seconds up to an hour in very protracted encounters) haemocyanin concentration is not expected to change significantly. Levels may therefore vary between opponents causing differences in stamina and hence RHP. Although high haemocyanin is expected to confer an advantage on crabs adopting the attacker role, there may also be advantages for defenders with high haemocyanin as they are also subject to elevated *L*-lactate while receiving raps when tightly withdrawn into their shells (Briffa & Elwood 2001). Our aim was therefore to determine how circulating concentrations of respiratory pigment influence contest behaviour in terms of strategic decisions, which are predicted to be strongly influenced by stamina and fight vigour, during hermit crab shell fights where there are two clear roles which fight in different ways.

## METHODS

### *Study Organisms and Staging Fights*

Hermit crabs, *Pagurus bernhardus*, were collected between December 2006 and March 2007 from rock pools at Hannaford Point, U.K. (50°20' N, 4°27' W). The hermit crabs were kept in groups of 80–150 in plastic aquaria (ca. 50 litres, dimensions 65 × 50 cm and 30 cm deep), filled with aerated sea water to a depth of 15 cm. These were maintained at 15°C in a temperature-controlled environment on a 12:12 h light:dark cycle. The crabs were fed ad libitum on a diet of catfish pellets and were returned to the shore within a month of collection.

We removed hermit crabs from their gastropod shells by carefully cracking the shells open in a bench vice. They were then sexed and examined for physical damage. Only intermoult male crabs, free from obvious parasites and physical damage, were used in the experiment to avoid sex-related behavioural differences found in previous studies (Neil & Elwood 1985). Unused crabs were provided with new shells and were returned to the shore within a month of collection.

The study crabs were assigned to pairs consisting of a small crab and a large crab (mean weights ± SE: small: 0.797 ± 0.013 g; large: 1.064 ± 0.021 g). The larger crab of the pair (potential attacker) was provided with a *Littorina littorea* shell that was only 50% of its preferred shell weight, while the smaller crab (potential defender) was provided with a *L. littorea* shell that would be 100% adequate for the larger crab of the pair. We determined the preferred shell size

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