



The costs of bearing arms and armour in the hermit crab *Pagurus bernhardus*

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Hermit crabs use empty gastropod shells as protective armour and enlarged chelipeds as signals and weapons. However, carrying armour and arms may impose energy costs that result in increased lactate and hence potential fatigue and there may be consequent effects on general activity. We investigated whether variation in shell and cheliped size influences lactate levels in hermit crabs. Lactate was positively related to residual cheliped size for both sexes and was higher in males than females; when we controlled for body size, the former had larger chelipeds. Shell weight unexpectedly had no effect on lactate but crabs in small shells had high lactate, possibly because of reduced ability to maintain a respiratory current. The size of natural shells had no effect on activity but the addition of food odour increased locomotion. However, activity was not related to lactate. We conclude that possession of larger chelipeds than expected for body size imposes significant costs and may limit development of sexual dimorphism.

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In the history of human conflict the use of both arms and armour had limitations. For example, the body armour that offered the most protection was typically the heaviest and induced fatigue during movement. Similarly, large two-handed, broad swords could only be used by the largest and strongest men as even brief swinging and hitting using these weapons induced fatigue (Melville 2000). Therefore for arms and armour there were trade-offs between their effectiveness in certain situations and the costs in terms of fatigue when bearing them. Here we examined an analogous situation in hermit crabs.

As well as using shells for armour, hermit crabs possess two chelae (claws), used in feeding and fighting. One is much enlarged and plays an important role in preflight displays (Elwood et al. 2006; Laidre & Elwood 2008) and as an operculum, protecting the crab when it is withdrawn into the shell (Dowds & Elwood 1983). There is considerable variation in cheliped size, even after taking body size into account (Arnott & Elwood 2010), and cheliped displays influence which individual becomes the attacker and which the defender and hence the outcome of encounters (Neil & Elwood 1986; Elwood et al. 2006). Cheliped size appears to be a signal of individual quality to opponents (Neil & Elwood 1986; Arnott & Elwood 2007).

Theory suggests that signals of individual quality during contests and courtship should typically be honest (Evans 1993; Johnstone & Grafen 1993), because the production cost of an inaccurately high level of the signal should outweigh the potential benefits of an exaggerated advertisement (Briffa 2006). These costs have been viewed as handicaps, where individuals that possess exaggerated characters to enhance fighting performance or attractiveness incur a cost that weaker individuals cannot afford (Zahavi 1975; Grafen 1990). However, when signals are cheap to produce there may be some deception, as in the case of the snapping shrimp, *Alpheus heterochaelis* (Hughes 2000) where increased use of the open chela display by males exaggerates body size. These costs may be apparent not only during courtship or aggressive behaviour but also during normal routine activities as seems to occur in other taxa such as male swordtails, *Xiphophorus montezumae* (Basolo & Alcaraz 2003), red-collared widowbirds, *Euplectes ardens* (Pryke & Andersson 2005), moose, *Alces alces* (Solberg & Sæther 1993) and fiddler crabs, *Uca pugilator* (Allen & Levinton 2007). In the latter study individuals with intact claws had greater stamina and higher respiration rates than those that were experimentally induced to autotomize (Allen & Levinton 2007). In this study, we examined the possibility that hermit crabs with natural chelipeds that are larger than expected for their body size pay an energetic cost. Crabs of both genders display their claws in contests over food (Laidre & Elwood 2008) and shells and those with large claws use them more than crabs with small claws (Arnott & Elwood 2010). But because the displays are brief it was assumed that they are cheap to use (Elwood et al. 2006).

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The important cost, however, may be in carrying the chelipeds at times other than while briefly interacting with other individuals. Thus, while large weapons may offer benefits in specific circumstances there may be physiological costs that limit the degree of development.

Hermit crabs lack calcification of their abdomens and rely on empty snail shells for their protection. However, the size and mass of this armour have important implications for fitness. Carrying shells increases oxygen consumption in terrestrial hermit crabs, *Coenobita compressus* (Herreid & Full 1986) and additional weight, or possibly hydrodynamic drag caused by epibionts, elevates haemolymph lactate levels for aquatic hermit crabs (Briffa & Elwood 2005a). Hermit crabs thus select shells that are sufficiently large but not too heavy (Elwood & Neil 1992; Osorno et al. 1998; Contreras-Garduño et al. 2009). On the other hand, the possession of an unsuitably small shell can reduce growth (Markham 1968; Fotheringham 1976), and males in inferior species or sizes of gastropod shell may fail to achieve copulations (Hazlett & Baron 1989) whereas females in such shells produce smaller and fewer broods (Elwood et al. 1995). Hermit crabs readily investigate empty shells (Elwood & Stewart 1985) or fight to take more suitable shells from other crabs (Dowds & Elwood 1983) and trade off the benefits of possessing a shell with the costs of carrying it. A decrease in ambient oxygen shifts their preference to shells of lower mass (Côté et al. 1998).

We therefore speculated that the nature of the shell and the size of the chelipeds will have direct effects on energetic costs in hermit crabs. We examined these costs in terms of lactate levels. High lactate indicates recent use of anaerobic respiration when the requirement for energy exceeded aerobic ability. For example, lactate levels increase rapidly in attackers during attempts to obtain a better shell in shell fights (Briffa & Elwood 2005b), and are higher for long than short fights (Briffa & Elwood 2002). Attackers fight by rapping their shells and those of defenders together and this is energetically costly (Briffa & Elwood 2000a); attackers with high lactate cannot rap with sufficient power to evict the opponent (Briffa & Elwood 2000b, 2004) and tend to give up the contest at an early stage. Furthermore, increased aerobic capacity enhances stamina in hermit crabs (Mowles et al. 2008, 2009). Thus lactate is a major indicator of condition in these animals.

The main objective of this study was to investigate how particular adaptations such as living in shells or bearing large weapons impose physiological costs. Specifically, we sought to determine whether variation in the shell and in cheliped size influences lactate levels in hermit crabs. With natural shells, size and mass covary; however, here we attempted to separate internal size effects from those of mass by artificial manipulation of shells. We predicted that crabs in heavy shells would have high lactate but we made no prediction about effects of internal size per se. We investigated whether cheliped size is sexually dimorphic and predicted that crabs with a larger than expected major cheliped would have high lactate. A second experiment examined whether natural shells of different sizes and weights influence activity levels, whether food odour increases activity and whether activity is related to lactate.

METHODS

Experiment 1: Lactate Levels

Hermit crabs were collected from February to April 2008 from rock pools on the shore at Minerstown, Co. Down, Northern Ireland, U.K. (54°15'1"N, 05°42'12"W). They were placed in holding tanks (52 × 30 cm and 12.5 cm high; <200 individuals per tank) containing 7.8 litres of constantly aerated, ultraviolet-filtered sea water. The crabs were maintained at 13 °C and a 12:12 h light cycle and were fed every 3–4 days on snail meat (*Littorina littorea*). They

were allowed 24 h to acclimate before the experimental trials. Only crabs free of parasites and with no missing appendages were used in the trials. Any crab not used was given a new shell and returned to the shore as soon as possible.

We first conducted a shell choice experiment to determine the optimum natural shells for a particular size of crab. All shells were obtained from live specimens of *L. littorea* from Minerstown that were boiled before removing the snail. Hermit crabs were placed in a tank containing *L. littorea* shells, with each crab having the choice of 80 available shells of various sizes and weights. The shell occupied after 24 h was noted and the shell mass regressed against crab mass (shell weight = 1.394 + 1.655 × crab weight; $N = 98$).

For the main experiment, crabs were picked randomly from the holding tanks and cracked out of their shells by means of a bench vice. Each crab was carefully dried with a paper towel, weighed and sexed. 'Naked' crabs were then put into individual pots, 13.5 cm in diameter and 9.5 cm in depth containing 500 ml of aerated ultraviolet-filtered sea water. The crabs were left for 4–6 h in these pots while new shells were prepared. Each crab was then randomly allocated to one of six groups. The groups are each defined by two letters. The first refers to the mass of the shell (L, O and H = light, optimal and heavy); the second refers to the internal size of the shell (S, O and L = small, optimal and large). The six groups are: LS = natural shells 50% lighter and hence smaller than optimal; group OO = natural shells of optimal mass and hence optimal size; group HL = natural shells originally 50% heavier and hence larger than optimal; group OS = modified shells originally 50% lighter than optimal (and hence too small) but adjusted to be the same mass as the optimal; group HO = modified shells originally of optimal mass and size but adjusted to be 50% heavier; group HS = modified shells originally 50% lighter (and hence too small) than optimal but adjusted to be 50% heavier than the optimal. All shell masses were within ±0.05 g of the mass required.

In groups OS, HO and HS the shells were adjusted to make them heavier using an aquarium epoxy (Aquascape), which is inert and was moulded around the exterior of the shell to follow the natural contours, and placed into an oven for around 2–3 h at 40 °C to harden.

Once the crabs were in their new shells they were transferred to larger, individual tanks (32 × 17.5 cm and 18.5 cm high) containing 2600 ml of aerated sea water. There was no substrate added and the crabs moved around on the plastic bottom of the tank. After 24 h each crab was humanely killed by placing it in liquid nitrogen before being defrosted at room temperature for 45 min. To measure lactate, a haemolymph sample was drawn from the base of the third and fourth walking legs by a small insulin syringe (BD micro-fine 0.30 mm, 30G, × 8 mm) and analysed with a lactate meter (ARKRAY Lactate Pro, Kyoto, Japan) which measures lactate concentrations between 0.8 and 25 mmol. The mass of the major cheliped was measured after removing the appendage from the joint at the thorax. This mass was subtracted from the total mass to give the body mass used in regression analyses. A total of 167 crabs were used, with 27–28 individuals per experimental group. There was no difference in crab mass between the groups ($F_{1,161} = 0.464$, $P = 0.803$) and males and females were distributed equally between the groups ($\chi^2 = 1.481$, $P = 0.915$).

Experiment 2: Activity Rate

Hermit crabs were collected from Minerstown during April 2009 and maintained in conditions as above. Each crab was starved for 3 days prior to observations to increase hunger levels and hence increase their motivation to search for food. They were removed from their original shell using a bench vice and the mass and sex of each naked individual were recorded. They were randomly allocated to experimental groups. The factors were either odour of food

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