ENERGETICS OF HERMIT CRABS DURING LOCOMOTION: THE COST OF CARRYING A SHELL

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SUMMARY

Oxygen consumption ($\dot{V}_{O_2}$) was measured as hermit crabs (*Coenobita compressus*) walked at controlled velocities on a motor-driven treadmill inside a small respirometer. The crabs displayed an aerobic response to exercise with a rapid increase in $\dot{V}_{O_2}$ reaching a steady state in about 5–6 min followed by a rapid recovery. The highest $\dot{V}_{O_2}$ was four times the resting rate. $\dot{V}_{O_2}$ was directly dependent on the velocity of travel (V): $\dot{V}_{O_2} = 0.29 + 1.98V$. Metabolic rate was increased significantly in crabs with bilateral leg ablation.

The cost of shell carrying was evaluated by comparing $\dot{V}_{O_2}$ of crabs with and without their protective snail shells at different velocities; the absolute difference was constant ($0.17 \, \text{ml} \, O_2 \, g^{-1} \, h^{-1}$), suggesting that the cost of shell support was constant per unit of time regardless of speed.

The cost of transport dropped dramatically with speed for crabs both with and without snail shells. Crabs carrying shells used twice as much O_2 per gram per kilometre as did 'nude' crabs walking slowly at $0.02 \, \text{km} \, h^{-1}$, but the difference decreased to 1·3 times when velocity was increased 10-fold. Hermit crabs did not increase their $\dot{V}_{O_2}$ proportionately with load: the $\dot{V}_{O_2}$ loaded/unloaded ratio was consistently less than the mass loaded/unloaded ratio. This apparent increase in efficiency may be due to the fact that crabs carrying heavy shells alter their leg position and tend to drag their shell.

Crabs with and without shells have the same minimum cost of transport C_M, so travel at the highest velocity is theoretically the most economical way to cover a given distance. Appropriately, crabs on the beach average a fast $0.23 \, \text{km} \, h^{-1}$ which produces a low cost of transport only 1·3 times higher than C_M. The C_M of six-legged hermit crabs is comparable to that of mammals, birds, crabs and insects of similar size and indicates that leg number does not affect fuel economy.

INTRODUCTION

The first studies on the energetics of pedestrian locomotion in invertebrates were on the eight-legged, lateral walking of land crabs (Herreid, Lee & Shah, 1979; Herreid, O'Mahoney & Full, 1983; Full & Herreid, 1983, 1984). Soon afterwards, results began to accumulate on the energetics of forward locomotion of six-legged

insects (Jensen & Holm-Jensen, 1980; Herreid, Full & Prawel, 1981a; Herreid, Prawel & Full, 1981b).

Although certain general principles have begun to emerge (Herreid, 1981), the enormous number of arthropod species and their diverse forms of locomotion have hardly been explored. In this paper we examine the energetics of locomotion of terrestrial hermit crabs, animals that are extraordinarily interesting subjects for studies on comparative locomotion.

Hermit crabs are novel because they walk differently from the other crustaceans studied energetically on a treadmill. As noted in the previous paper (Herreid & Full, 1986), they walk forward with hexapodal locomotion and they have an asymmetrical body morphology. But their most distinctive characteristic is that most hermit crabs carry snail shells for protection against environmental stress and predators (e g. Reese, 1969; Vance, 1972; Bertness, 1980). These shells are periodically exchanged for ones of different size; moreover, because of the intense competition for mollusc shells in short supply, crabs of the same size can carry shells of greatly different masses. Therefore, we have a natural situation where an animal carries a load which may seriously influence the energetic costs of locomotion. Load carrying has been considered in humans, domestic and laboratory mammals (e g. Taylor, Heglund, McMahon & Looney, 1980), but little information is available on other species or on wild animals that normally carry loads during their life, e.g. animals carrying offspring. Consequently, the current study of hermit crabs with and without shells provides useful comparative data on the effects of load carrying.

MATERIALS AND METHODS

The tropical hermit crab *Coenobita compressus* lives in the rocks and grass above high tide. It forages on the natural debris washed up in the intertidal area. We observed and collected animals along Boyscout Beach just off Naos Island, Panama City, Panama. Crabs were transported a few hundred metres away to the Smithsonian Tropical Research Institute where they were held in small jars with moist sand for a few days while metabolic experiments were conducted.

We measured oxygen consumption ($\dot{V}_{O_2}$) of hermit crabs as they ran on a motor-driven treadmill enclosed within an airtight Plexiglas chamber. Details of the apparatus and procedure are described in Herreid (1981) and Herreid *et al.* (1981a). Room air was drawn through the treadmill respirometer and passed through a Drierite filter and *via* a flow meter into one channel of a dual channel Applied Electrochemistry S-3A Oxygen Analyzer. For comparison, room air was also passed *via* a Drierite filter and flow meter into the second channel of the O_2 analyser. The difference in O_2 concentration between the two channels multiplied by the rate of gas flow represents the O_2 consumption of the crab. The experiments were conducted at $22 \pm 1\,°C$ and all readings have been converted to STPD conditions.

The protocol for our metabolic experiments using the treadmill involved weighing the animal and placing it within the respirometer for at least 30 min before an exercise bout. This time was generally sufficient for the crab to recover from handling so that
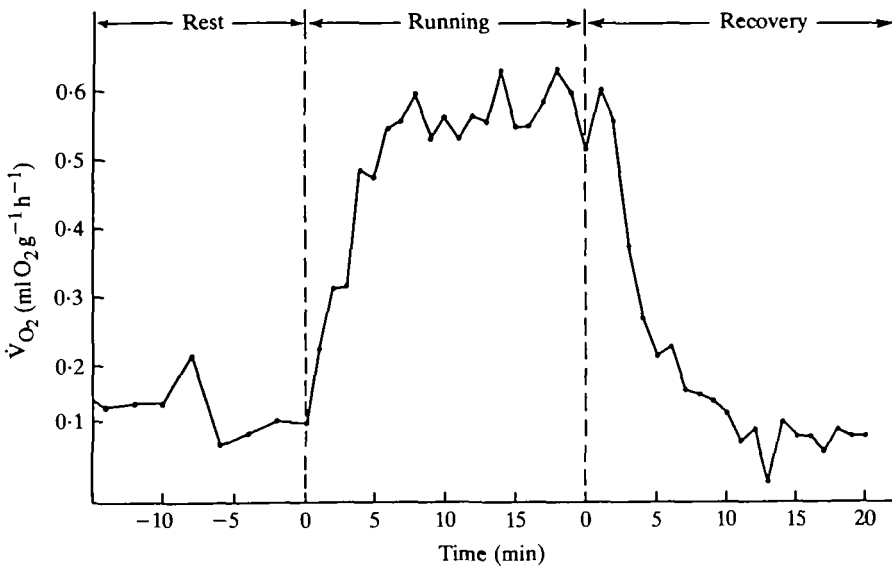
Fig. 1. Oxygen consumption of a single hermit crab during rest, a 20-min run at $0 \cdot 19 \, km \, h^{-1}$, and a recovery period.

we obtained constant resting $\dot{V}_{O_2}$ values. After rest, we turned the treadmill on to a specific velocity and the crab ran in place for 20 min. This was followed by a 30-min recovery period where we continued to monitor $\dot{V}_{O_2}$. Each crab was run at three different speeds on different days. The highest speed was the maximum velocity a crab could sustain for 20 min. The lowest speed was the minimum velocity at which a crab would walk at a relatively constant pace without wandering excessively in the chamber.

RESULTS

In order to determine the energetic cost of locomotion, hermit crabs were placed in a treadmill respirometer and run at specific velocities. Before the run, resting O_2 consumption was measured. Eighteen hermit crabs with an average animal mass of $3 \cdot 7 \pm 0 \cdot 7 \, g$ (S.D.) used $0 \cdot 16 \pm 0 \cdot 05 \, ml \, O_2 g^{-1} h^{-1}$; this value was measured on crabs within their snail shells, although the data are expressed in terms of animal mass without the shell. Resting $\dot{V}_{O_2}$ was also measured on 13 hermit crabs outside their shells and was, on average, $0 \cdot 13 \pm 0 \cdot 03 \, ml \, O_2 g^{-1} h^{-1}$. The average crab body mass was $3 \cdot 5 \pm 0 \cdot 7 \, g$. A t-test revealed no significant statistical difference ($P < 0 \cdot 05$) between resting $\dot{V}_{O_2}$ of crabs inside or outside their shells.

General pattern of $\dot{V}_{O_2}$ during locomotion

The general pattern of O_2 consumption for a hermit crab is shown in Fig. 1. Because of the excitable nature of most crabs, especially after the run, records of

recovery were rarely as regular as that shown. Keeping this in mind, the patterns of all hermit crabs showed a rapid rise in $\dot{V}_{O_2}$ after the run started with a half time ($t_{1/2}$on) of 1–3 min, a steady-state O_2 consumption ($\dot{V}_{O_2ss}$) of at least 15 min followed by a rapid decline in $\dot{V}_{O_2}$ once the run finished. In the few crabs that remained somewhat quiescent after the exercise, the half-time to recovery ($t_{1/2}$off) was 3 or 4 min, with complete recovery accomplished in 6–10 min. Because of the pre- and post-exercise excitement, it is not possible to be more precise.

The effect of velocity on $\dot{V}_{O_2}$ in hermit crabs may be seen in Fig. 2. Three points are apparent. (1) Crabs exercising with shells (average shell mass for 12 crabs is $4\cdot1 \pm 0\cdot9$g) have a $\dot{V}_{O_2ss}$ that is linearly dependent upon velocity. The best fit regression line is $\dot{V}_{O_2ss} = 0\cdot29 + 1\cdot98V$, where $\dot{V}_{O_2ss}$ is in units of $ml\,O_2\,g^{-1}\,h^{-1}$ and V is velocity in $km\,h^{-1}$. The correlation coefficient is $r = 0\cdot80$. The 95 % confidence limits for the y-intercept are $0\cdot21$ to $0\cdot37$ and for the slope are $1\cdot36$ to $2\cdot60$. Again $\dot{V}_{O_2ss}$ is represented in terms of animal mass only, exclusive of shell mass. (2) Hermit crabs without shells also show the same direct relationship and slope between $\dot{V}_{O_2ss}$ and velocity. This is represented by the regression line $\dot{V}_{O_2ss} = 0\cdot12 + 2\cdot00V$, $r = 0\cdot88$. The 95 % confidence limits for the y-intercept are $0\cdot07$ to $0\cdot18$ and for the slope are $1\cdot58$ to $2\cdot42$. Most importantly, the average metabolic rate of 'nude' hermit crabs at any given velocity value is about 67 % of that of a hermit crab with a shell. (3) The y-intercept of the regression line for hermit crabs with shells is $1\cdot9$ times higher
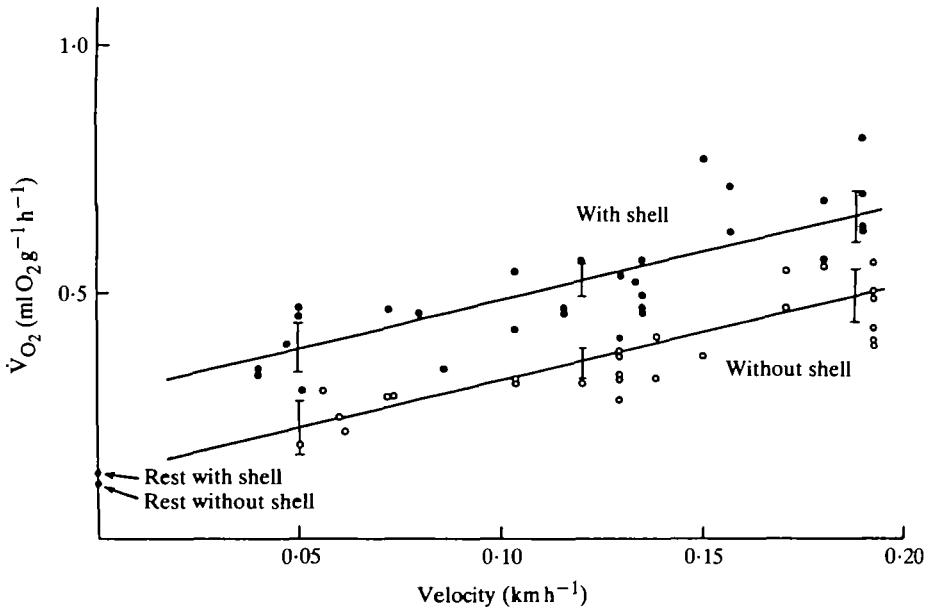

Fig. 2. Oxygen consumption ($\dot{V}_{O_2}$) of hermit crabs running at different velocities (V). The solid circles represent crabs carrying snail shells as they walked on the treadmill and the open circles are crabs without shells. In all cases $\dot{V}_{O_2}$ is presented in terms of a crab lacking a snail shell. The lines through the points are least-squares regression lines: with shell, $\dot{V}_{O_2} = 0\cdot29 + 1\cdot98V$; without shell, $\dot{V}_{O_2} = 0\cdot12 + 2\cdot00V$. The error bars are 95 % confidence intervals.

than the resting value. The y-intercept of the regression line for hermit crabs without shells is slightly, but not significantly, higher (1·2 times) than the value at rest.

Energetics of running with four legs

Five crabs which had two limbs removed by bilateral amputation (Herreid & Full, 1986) were successfully run in the treadmill respirometer. All were tested without shells. Two crabs were run lacking their second walking legs (L_3,R_3) at a velocity of $0·13\,km\,h^{-1}$. Crab no. 6, which used a combination of gaits (diagonal quadrupedal, sideways push-pull and rowing – see Herreid & Full, 1986), used $0·38\,ml\,O_2\,g^{-1}\,h^{-1}$ which is exactly that predicted for a six-legged hermit crab at that speed. However, this rate is probably low because the crab was a poor runner and tended to ride the treadmill. Crab no. 17, using the diagonal quadrupedal gait, consumed $0·49\,ml\,O_2$ $g^{-1}\,h^{-1}$ which is 1·3 times higher than normal.

Two crabs lacking the first walking legs (L_2,R_2) were successfully run; both used the diagonal quadrupedal gait. Crab no. 23, run at $0·13\,km\,h^{-1}$, used $0·63\,ml\,O_2$ $g^{-1}\,h^{-1}$, which is 1·7 times the normal average. Crab no. 22 could not be run except at a slower speed, $0·08\,km\,h^{-1}$, where it used $0·40\,ml\,O_2\,g^{-1}\,h^{-1}$ or 1·4 times the normal average. Only one crab lacking chelae (L_1,R_1) was successfully run for 13 min at a slow speed of $0·05\,km\,h^{-1}$. The crab used the diagonal quadrupedal gait and consumed $0·40\,ml\,O_2\,g^{-1}\,h^{-1}$ or 1·8 times the value predicted for a six-legged crab.

In none of the above cases did bilateral amputation alter resting $\dot{V}_{O_2}$. It did affect $\dot{V}_{O_2}$ during locomotion, however: in four out of five crabs tested, $\dot{V}_{O_2}$ fell above the 95 % confidence limits for normal six-legged crabs using tripod locomotion. In addition to any other debilitation caused by leg loss, there appears to be a modest but significant increase in energy consumption probably because of problems with balance and irregular locomotion. Whether such problems would diminish with practice over time is unknown.

Energetic cost of transport

One may calculate the cost of transport for a hermit crab by dividing the $\dot{V}_{O_2,ss}$ by the velocity of locomotion. This is a measure of the O_2 consumption required to move 1 g of crab over 1 km (i.e. $ml\,O_2\,g^{-1}\,km^{-1}$).

The total gross cost of transport (C_G), a value calculated by dividing weight-specific $\dot{V}_{O_2,ss}$ by velocity, decreases in a curvilinear fashion with velocity, approaching a lower asymptote at high velocities (Fig. 3). The asymptote is known as the minimum cost of transport (C_M); this value is also the slope of the line in Fig. 2 plotting $\dot{V}_{O_2,ss}$ against velocity. Since the slopes of the regression lines for hermit crabs running with and without shells are identical, it is plain that the C_M has not been altered by carrying a shell, although the gross cost of transport (C_G) is clearly influenced. Fig. 3 shows that the C_G escalates greatly at low velocities. The difference between the curves of cost with and without shell (known as the extra cost of transport, C_E) becomes greater at low velocities and vanishes altogether as the

curves approach the minimum cost of transport. Crabs travelling on the beach choose to run at high velocities, which minimizes both C_G and C_E.

Energetics of carrying a load

Oxygen consumption is directly related to the load carried. Fig. 4 shows that the crabs without shells generally increase their total O_2 consumption with size and with velocity. This trend continues as snail shells are carried: the greater the load and the higher the velocity, the higher the O_2 consumption.

Oxygen consumption does not increase proportionately with the load carried. This point is clearly seen in Fig. 5 which plots the $\dot{V}_{O_2,ss}$ of loaded/unloaded crabs against the mass of loaded/unloaded crabs. Thus if a crab doubled its shell mass and if the $\dot{V}_{O_2,ss}$ doubled as a result, the data point would fall on the line drawn on the figure. Obviously, all points fall to the right of the line and the difference between the data and the line becomes pronounced at high loads.
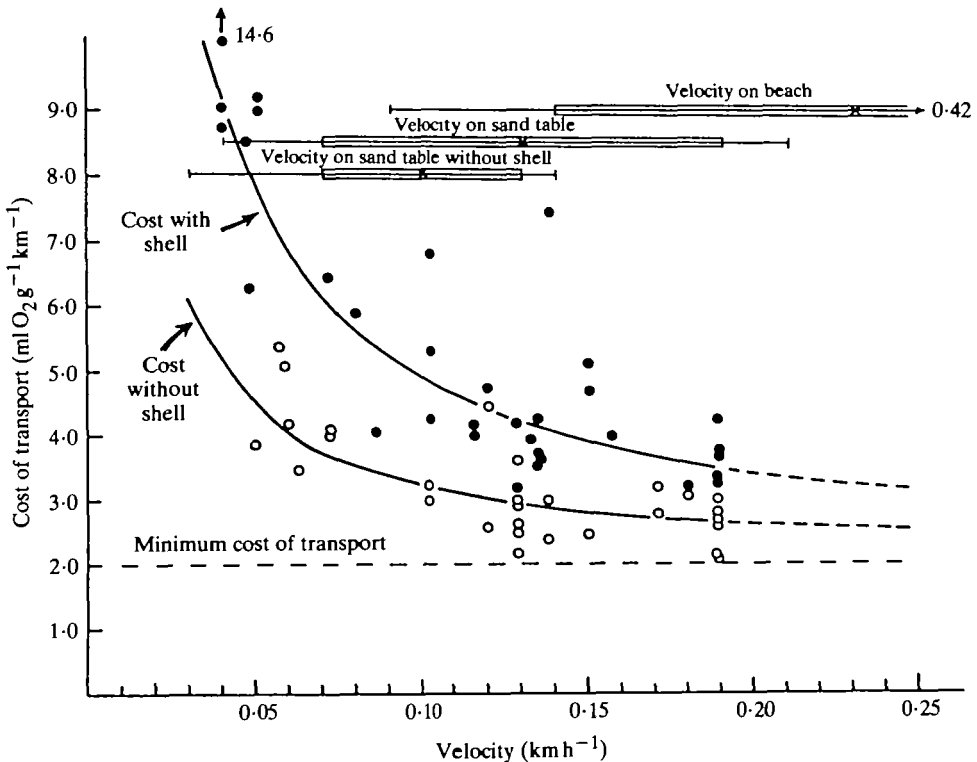

Fig. 3. Cost of transport (C_G) for hermit crabs travelling on a treadmill at different velocities (V). Solid circles represent individual crabs walking with a snail shell. The data are fitted to the equation: $C_G = (0.29 + 1.98V)/V$. Open circles represent individual crabs walking without snail shells. The data are fitted to the equation: $C_G = (0.12 + 2.00V)/V$. The difference between the two curves is the extra cost of transport (C_E). At the top of the diagram, the range of velocities, the mean velocity ($\times$), and standard deviation (open bar) on the beach and sand table are shown.

DISCUSSION

Coenobita compressus is basically an aerobic runner; consequently, it is similar to mammals, birds and insects as well as ghost crabs (e.g. Cerretelli, Pendergast, Paganelli & Rennie, 1979; Herreid & Full, 1984; Full & Herreid, 1983). Such animals have rapid increases in $\dot{V}_{O_2}$ (Fig. 1) when exercise begins [half-time $(t_{1/2}on)$ of the on-response was 1–3 min for hermit crabs]; they reach a clear steady-state $\dot{V}_{O_2}$ level which is sufficient to sustain locomotion over a range of speeds for 20 min or more; and they recover rapidly after endurance runs ($t_{1/2}off$ response was 3–4 min). Therefore, these hermit crabs are unlike the more anaerobic crustacean runners such as *Cardisoma guanhumi, Gecarcinus lateralis* and *Uca pugilator* which show slow $t_{1/2}on$ and $t_{1/2}off$ responses and lack a $\dot{V}_{O_2 ss}$ (Herreid *et al.* 1979, 1983; Full & Herreid, 1984). Reasons for such species differences are at present obscure.

Hermit crabs, like virtually all other pedestrian travellers at moderate speeds (Herreid, 1981) increase O_2 consumption directly with velocity. This relationship is apparent with or without a load (shell). When the regression line is extrapolated back to zero velocity, the y-intercept of the crabs with shells falls substantially higher
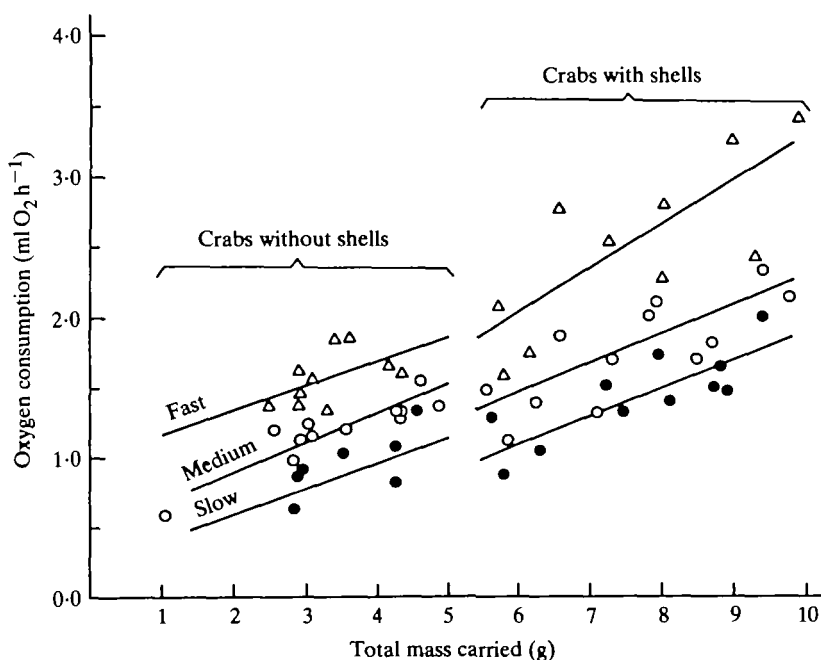

Fig. 4. Oxygen consumption $(ml\,O_2\,h^{-1})$ of hermit crabs compared to the total mass of the animal and snail shell carried at three speeds: low $(0.06 \pm 0.02\,km\,h^{-1})$, medium $(0.12 \pm 0.01\,km\,h^{-1})$, high $(0.18 \pm 0.02\,km\,h^{-1})$. Least-squares regression lines are drawn for crabs without shells: low speed, $\dot{V}_{O_2} = 0.48 \pm 0.21M$ $(r = 0.69)$; medium speed, $\dot{V}_{O_2} = 0.48 \pm 0.21M$ $(r = 0.91)$; high speed, $\dot{V}_{O_2} = 1.02 \pm 0.17M$ $(r = 0.48)$ where M is animal mass without shell. The regression equations for crabs with shells are as follows: slow speed, $\dot{V}_{O_2} = -0.10 \pm 0.20T$ $(r = 0.80)$; medium speed, $\dot{V}_{O_2} = 0.15 \pm 0.22T$ $(r = 0.77)$; high speed, $\dot{V}_{O_2} = 0.22 \pm 0.30T$ $(r = 0.77)$ where T is animal mass plus shell.
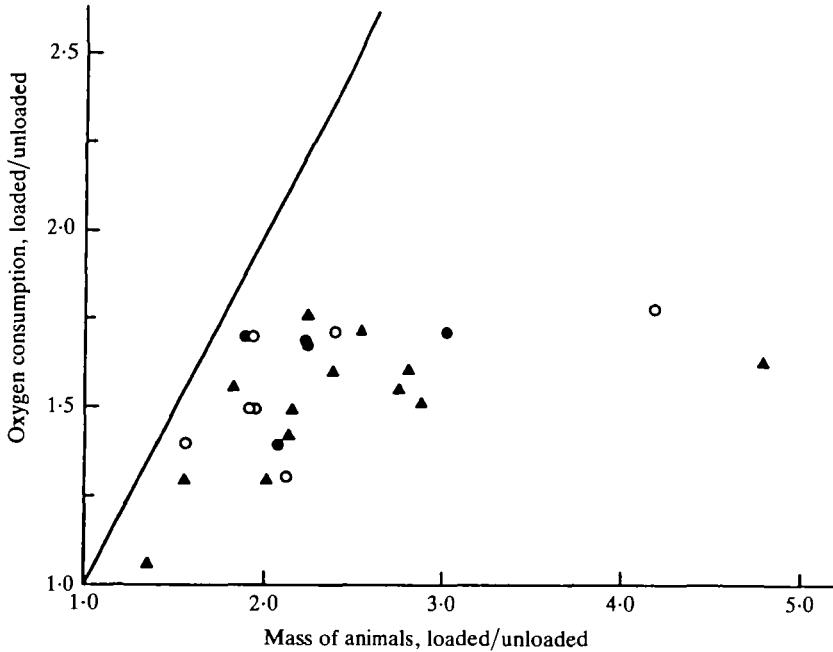
Fig. 5. Oxygen consumption (loaded/unloaded ratio) of hermit crabs compared to mass (loaded/unloaded ratio). Crabs without snail shells would fall at 1·0. The identity line represents the way in which $\dot{V}_{O_2}$ would change if $\dot{V}_{O_2}$ increased in direct proportion to an increase in load. Each point represents a different crab walking at low speed ($0.06 \pm 0.02 \,\mathrm{km\,h^{-1}}$; solid circles), medium speed ($0.12 \pm 0.01 \,\mathrm{km\,h^{-1}}$; triangles), and high speed ($0.18 \pm 0.02 \,\mathrm{km\,h^{-1}}$; open circles).

(1·9 times) than the actual resting value, whereas the y-intercept for 'nude' crabs is not statistically different from the resting value. Most species also show an elevated y-intercept, and there may be several reasons for such an elevation (Herreid, 1981). There is little evidence for any hypothesis. But in this case, the hermit crab data provide unique insight into the problem. Since the y-intercept is clearly elevated when the crab walks with the shell and is not elevated when a shell is absent (Fig. 2), this strongly suggests that the elevation in this species is due to the cost of lifting the shell and holding it in position for locomotion. (This is not a postural cost of loco-motion, for crabs without shells do not show the elevation; it is a cost of supporting the shell.) The fact that the regression lines are parallel in Fig. 2 indicates that the extra cost for carrying the shell (C_E) remains similar over a range of velocities: the difference between the lines remains about $0.17 \,\mathrm{ml\,O_2\,g^{-1}\,h^{-1}}$ ($3.41 \,\mathrm{J\,g^{-1}\,h^{-1}}$) or 3 cal for an average 3·7-g crab carrying an average shell (4·1 g) for 1 h.

The energetic cost of transport (C_G) is a measure of the total O_2 or energy required per gram of an animal over 1 km. This value clearly drops as the velocity of travel increases until a minimum cost is approached (Fig. 3). Thus fast travel is more economical per kilometre than slow; a crab travelling at $0.06 \,\mathrm{km^{-1}\,h^{-1}}$ uses twice as much energy to travel 1 km than one moving at $0.19 \,\mathrm{km^{-1}\,h^{-1}}$. Consequently, it is not surprising to see that crabs travel along the beach at speeds near the high end of

their velocity spectrum (see Herreid & Full, 1986). At an average beach speed (0.23 km h^{-1}), the cost of transport for crabs with shells is still 1.6 times higher than the minimum, however. Even at double this speed ($0.46 \text{ km}^{-1} \text{h}^{-1}$), which was approached by one crab on the beach, the cost of transport is 1.3 times the minimum. Obviously, the crabs without the load (shell) are much closer to the minimum cost than those with the load. We should caution that the energetic cost values measured in the laboratory respirometer may be lower than those in the field due to differences in the terrain. Strydon *et al.* (1966) observed an 80% increase in energy cost for humans walking on soft sand compared to a firm surface. The effect would be diminished for light crabs, but our observations that crabs walk slower on soft than moist sand (Herreid & Full, 1986) suggest that some energetic differences probably exist.

The difference between the cost of transport of loaded and unloaded crabs has been called the extra cost of transport, C_E (Nielsen, Jensen & Holm-Jensen, 1982). This value declines as velocity increases (Fig. 3). At low velocities, the C_E due to the shell becomes grossly exaggerated whereas at high velocities, as the cost approaches the minimum cost of transport, the difference disappears. How does the cost of carrying a load compare with the cost of carrying 1 g of body mass? The values are identical according to studies on humans, dogs, horses and rats carrying light loads, and ants (e.g. Goldman & Iampietro, 1962; Taylor *et al.* 1980; Nielsen *et al.* 1982). This is not the case for hermit crabs. In all cases, the carrying of a shell requires less O_2 than carrying an equivalent body mass. For a crab carrying a shell that matches its body mass, C_E is only 25% of the gross cost of transport (C_G) at high velocities (e.g. 0.2 km h^{-1}). Only at low velocities does C_E approach 50% of the C_G, i.e. the point at which carrying 1 g of shell is similar to carrying 1 g of body mass.

Another way of evaluating the economy of travel is to calculate the net cost of transport (C_N) which is to subtract the resting rate from the $\dot{V}_{O_2ss}$. However, the resting rate of $0.16 \text{ ml} O_2 \text{g}^{-1} \text{h}^{-1}$ is modest and its removal does not seriously affect our conclusions. As with C_G, C_N also declines with velocity (e.g. at slow speed of 0.05 km h^{-1}, it is $4.6 \text{ ml} O_2 \text{g}^{-1} \text{km}^{-1}$; at a high speed of 0.23 km h^{-1} it is $2.5 \text{ ml} O_2 \text{g}^{-1} \text{km}^{-1}$) for crabs with shells. For crabs without shells, the net cost remains similar across velocities (at 0.05 km h^{-1} it was $1.9 \text{ ml} O_2 \text{g}^{-1} \text{km}^{-1}$; at 0.23 km h^{-1} it was $2 \text{ ml} O_2 \text{g}^{-1} \text{km}^{-1}$). Consequently, once again the difference with and without shells is large at low velocities and it disappears at high velocities. When the constant C_N without shells is compared to C_E, which decreases with velocity, it is seen that at velocities above 0.08 km h^{-1} the net cost of transport for 1 g of body still exceeds that for the shell. Below this speed, the shell becomes more costly to transport.

A final method for considering cost may be seen in Fig. 5. Increasing the load does not cause a corresponding proportional increase in oxygen consumption. Instead, the $\dot{V}_{O_2ss}$ loaded/unloaded ratio rises much less than the loaded/unloaded mass ratio. This is in contrast to the data collected by Taylor *et al.* (1980), who showed a directly proportional increase when humans, rats, dogs and horses carried light loads (7–27% of their body weight). However, both sets of data are quite different from

those reported for humans carrying heavy loads (1·5–1·9 times body mass); our calculations from Soule, Pandolf, & Goldman's (1978) data indicate a proportionately higher $\dot{V}_{O_2}$ loaded/unloaded ratio than mass loaded/unloaded ratio. That is, the data points lie above the identity line, suggesting a decreased energetic efficiency in humans carrying heavy loads. Following this line of argument, it would appear that the hermit crab is especially efficient carrying loads (shell). All the hermit crab measurements fall below the identity line. This unique pattern becomes especially pronounced at heavier loads, i.e. when the shell mass exceeds that of the 'nude' crab, a loaded/unloaded mass ratio of 2. In fact, $\dot{V}_{O_2ss}$ did not increase even when shells weighing four times the mass of the nude crab were carried.

How can we explain the unexpected low cost of shell transport? Three possibilities come to mind.

(1) The mechanical efficiency (work output/work input) may increase with larger loads. Hermit crabs with shells have the same stride frequency and stride length as crabs without shells across a range of velocities (Herreid & Full, 1986). Nevertheless, we observed crabs that carry large shells do shift their leg position, and tend to drag their shells (see also Chapple, 1973). Such adjustments might contribute to improvements in mechanical efficiency.

(2) Anaerobic ATP contribution might increase disproportionately with increasing loads to supplement ATP production from $\dot{V}_{O_2}$. If so, the $\dot{V}_{O_2}$ would not be an adequate measure of the total energy cost of shell transport. This explanation does not seem likely for two reasons: first, we did not witness increased O_2 debts at higher loads which one might expect with greater anaerobic metabolism. Second, the $\dot{V}_{O_2}$ maximum level (where lactate production is pronounced in aerobic runners) was not approached, at least in the low and middle velocity runs. This was obvious because $\dot{V}_{O_2}$ clearly increased when the crab was tested at high velocity. Yet at all velocities the loaded/unloaded $\dot{V}_{O_2ss}$ showed the same trend (Fig. 5); increased loads did not increase $\dot{V}_{O_2ss}$.

(3) Muscle efficiency might change at different loads. No direct evidence exists on this point, yet muscle fibre recruitment in organisms can vary under different conditions (e g. Armstrong et al. 1977). Perhaps heavier loads carried by hermit crabs may bring different muscle fibres into play with increased efficiency. Regardless of the mechanism, the hermit crab Coenobita compressus appears to be unusually efficient in the carrying of its shell.

Earlier we made the point that the minimum cost of transport does not change when six-legged hermit crabs carry a load (shell); in both cases C_M is about $2·00 \, \text{ml} \, O_2 \, \text{g}^{-1} \, \text{km}^{-1}$. When we compare this value with that expected for a four-legged mammal or two-legged bird of a comparable size (3·7 g), we note it is quite similar to the vertebrate data (Taylor, Heglund & Maloiy, 1982) and to six-legged cockroaches (Herreid & Full, 1984). It is also practically identical to the value we have recently calculated for the eight-legged locomotion of a fiddler crab, Uca pugilator (Full & Herreid, 1984). Thus, once again we have confirmed the basic principle (Fedak & Seeherman, 1979; Herreid, 1981) that the number of legs

involved in locomotion does not appear to have a major influence in determining the cost of transport.

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