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LOCOMOTION IN LAND CRABS: RESPIRATORY AND CARDIAC RESPONSE OF *GECARCINUS LATERALIS*

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Abstract—1. Land crabs with a respiratory mask were run on a miniature treadmill at controlled speeds. O_2 consumption ($\dot{V}_{O_2}$) and CO_2 production measurements showed that the aerobic response to exercise was slow.

2. Steady-state O_2 consumption was not attained during 10 min runs nor when they ran freely for 20 min in a treadmill respirometer. Recovery from exercise was prolonged in both cases.

3. This indicates that this species, like another land crab, *Cardisoma guanhumi*, relies heavily upon anaerobic fermentation, phosphagen and O_2 stores to support its energetic demands during running.

4. Aerobic compensatory devices were evident also. Peak O_2 consumption values did tend to rise with increased velocity of running as did the area under the $\dot{V}_{O_2}$ curve during running and recovery.

5. Both ventilation volume and O_2 extraction also rose during running; the latter seemed to be the most important of the two respiratory compensatory mechanisms.

6. Circulatory adjustments were evident. Heart rate showed a rapid rise with exercise and the O_2 pulse (the amount of O_2 delivered per heart beat) increased directly with O_2 consumption as well.

7. Energetic considerations suggest that running with a mask may be slightly more demanding than free running.

8. Estimation of an energetic cost of transport for this 53 g crab suggests it is comparable to that of quadrupedal and bipedal vertebrates of a similar size.

INTRODUCTION

Arthropod locomotion has received considerable attention from people interested in the mechanisms of locomotion or neuromuscular control (e.g., Manton, 1977; Herman *et al.*, 1976). Unfortunately, little information is available on the energetics or the physiologic adjustments involved with locomotion, aside from the important work on flying insects (e.g., Chadwick & Gilmour, 1940; Krogh & Weis-Fogh, 1951; Weis-Fogh, 1964, 1967; Vogel, 1966). Moreover, most of the evidence that has accumulated on arthropods has been collected somewhat incidently as investigators focused on other problems. Information has been largely gathered on animals without regard to either the duration or intensity of exercise. In spite of this situation, some interesting clues are available about exercise and locomotion in terrestrial and aquatic arthropods, especially crabs, the largest members of the phylum.

The first detailed information on crustacean locomotion under carefully controlled conditions were published on the land crab, *Cardisoma guanhumi*, running on a treadmill (Herreid *et al.*, 1979). O_2 consumption ($\dot{V}_{O_2}$) and CO_2 production ($\dot{V}_{CO_2}$) were found to increase slowly with the onset of exercise. The respiratory exchange ratio increased as well. The crabs exhausted rapidly and displayed a pronounced and prolonged elevation of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ after exercise. An increased ventilation volume ($\dot{V}_G$) was the primary respiratory response to exercise. Oxygen extraction ($Extr_a$) showed only a modest increase. Most surprisingly, a bradycardia occurred during fast running. Finally, since $\dot{V}_{O_2}$ increased directly as a function of the velocity of running, the energetic cost of transport was estimated for the crabs and found to be similar to a mammal of comparable size (Taylor *et al.*, 1970).

Several other investigators have experimental evidence which supports many of the above observations: namely, the increased metabolism with activity, increased ventilation and prolonged recovery period (Wallace, 1972; Cameron & Mecklenburg, 1973; Cameron, 1975; Mickel & Childress, 1978; Batterton & Cameron, 1978; McMahon *et al.*, 1979; Wood & Randall, 1981). Other studies show alternative responses adopted during exercise. (1) A tachycardia has been observed rather than a bradycardia (McMahon, 1981, McMahon *et al.*, 1979, Wood & Randall, 1981). (2) Oxygen extraction shows a slight reduction during activity in several marine crustaceans (McMahon, 1981). In the exercising land crab, *Cardisoma carnifex*, a large decrease in $\%\ Extr_a$ was reported (Wood & Randall, 1981). (3) In both the water breathing crab, *Callinectes sapidus* and the air breathing *Ocypode*, a rapid increase in $\dot{V}_{O_2}$ occurred at the beginning of exercise (McMahon, 1981, unpublished data). This rapid aerobic adjustment stands in marked contrast to that seen in *Cardisoma guanhumi* (Herreid *et al.*, 1979). It is obvious that we are in need of more experiments where exercise regimes are carefully controlled (quantified intensity and duration) before we begin to understand the patterns of metabolic and physiological adjustments to exercise in arthropods.

The purpose of this study was to examine the locomotion of one of the most terrestrial decapod crustaceans known, the land crab, *Gecarcinus lateralis*.

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This species lives on the upper beaches and in grassy areas sometimes far inland, in the tropical and subtropical Americas (Bliss *et al.*, 1978). *G. lateralis* does not require free water except at the time of reproduction when it migrates to the ocean to deposit eggs. Associated with its terrestriality are morphological adaptations of the respiratory system which include reduced gill area, specialization of gills for water and salt uptake and large branchial chambers whose lining probably has a respiratory function (Copeland, 1968; Diaz & Rodrigues, 1977). In this study we present data for land crabs running on a treadmill while $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were simultaneously measured by use of a respiratory mask and heart rate was monitored. In addition, data on crabs running freely in a treadmill respirometer allowed further examination of the aerobic response pattern resulting from exercise.

MATERIALS AND METHODS

Land crabs, *Gecarcinus lateralis*, were obtained from two separate sources. The first group which was used for experiments with a respiratory mask were captured along the coast of Florida near Boca Raton. The second group which was used for experiments without the mask were obtained from Bermuda. Both sets of animals were maintained in the laboratory at 25°C in good shape on a mixed diet of Purina Puppy Chow, lettuce, fish, clam and egg shell for several months prior to their study. The average mass was 53.4 g ± 8.3 (SD) for the first group and 52.7 g ± 15.4 for the second.

Experiments with a respiratory mask

Two types of experiments were carried out. In the first set of experiments crabs were run on an open treadmill as $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and heart rates were determined simultaneously. In this work the techniques were largely the same as those used for the land crab *Cardisoma guanhumi*, as described by Herreid *et al.* (1979). Briefly, a respiratory mask was sealed over the mouth parts of the crab to capture exhaled gas leaving the gill chamber. The gas leaving the mask passed via a piece of tubing into large thick balloons which served as miniature "Douglas Bags". The tubing was of large bore (7 mm i.d.) to minimize resistance to ventilation. There was no evidence of reversed ventilation in our experiments. Reversed ventilation has been observed only during hypoxia in *Gecarcinus* (O'Mahoney, 1977). Taylor & Davies (1981) have reported reversed beating in *Gecarcinus* infrequently and for normally short durations. Exhaled gas was collected in a balloon for a period of one minute before another balloon was switched into the system via a stopcock. The volume of the balloon was measured with a 50 ml syringe and samples of the gas were periodically used to determine its chemical composition via a 0.5 cc Scholander Gas Analyzer. The method is accurate to ±0.015 volume per cent (Scholander, 1947; Gaudebout & Blayo, 1975). From timed measurements of gas composition and volume, we could determine $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, gill ventilation ($\dot{V}_G$) and O_2 extraction. Values for $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were corrected to STPD. No significant differences were found in the rates of oxygen uptake for *Cardisoma* and *Gecarcinus* when respiratory mask and non-inflating systems were compared (Standaert, 1970; Taylor & Davis, 1981).

Heart rate was determined concurrently with the above tests. Electrocardiograms were obtained by using a pair of electrodes 5–6 mm long made from steel insect pins soldered to 22 gauge stranded, shielded copper wire leads. Two holes were drilled in the dorsal carapace to receive the electrodes, one hole directly above the heart and the other 0.5–1 cm posterior to it. The holes were not drilled deep enough to penetrate the hypodermis. The electrodes were sealed into the holes with "sticky wax" after being pushed through the hypodermis and taped to the carapace. The leads were then carried away above the animal to a Gilson MP5 polygraph where a differential reading between electrodes could be recorded.

The basic protocol for the above experiments was as follows. The animal was outfitted with ECG electrodes and the respiratory mask was sealed into place. The crab was placed onto the treadmill in a darkened chamber for 75 min while ECG and $\dot{V}_G$ were determined. At the end of this period, heart rate and ventilation volume had remained constant for 30 min. Values for both measurements were comparable to preliminary tests on 18 animals over the same time period. Ventilation volumes determined were well within the range of previous measurements on *Gecarcinus* over 3 hr (O'Mahoney, 1977). During the next 15 min, ECG, $\dot{V}_G$ and exhaled gas composition of resting crabs were determined. Then, the front of the treadmill was uncovered and the treadmill was turned on. Exercise runs were of 10 min duration. At the end of this time, the treadmill was stopped and the treadmill was again covered while the crab rested for 60 min. Each crab was generally used in three experiments separated by several days: an exercise run at 260 cm/min ($N = 4$), a run at 200 cm/min ($N = 3$) and a control run at 0 cm/min ($N = 2$). In the later experiment, the crab was not exercised nor was the treadmill turned on. The top of the treadmill chamber was simply removed admitting light and the investigator moved about in front of the crab as in a normal experiment, occasionally prodding the animal. A running speed of 260 cm/min was the highest value the crabs could sustain for a 10 min bout without showing distress, and is comparable to moderate locomotion we have observed in the wild.

Experiments with a respirometer treadmill

In a second type of experiment we used a small treadmill completely enclosed within an airtight lucite respirometer. The treadmill was driven by a DC gear motor located outside the chamber and controlled by a veriac. The top of the chamber had inlet and outlet ports through which air could be ventilated. Room air was continuously drawn through the 1700 ml working section of the chamber at 300 ml/min and passed through a drierite filter to remove water vapor. The gas was then passed through a flow meter and pump before entering one sensor cell of an S-3A Applied Electrochemistry O_2 Analyzer which can detect differences of 0.001 per cent O_2. The analyzer was electrically interfaced with a Linear Instruments Model 282 Integrating Chart Recorder. As a reference gas, room air was directly passed at 300 ml/min via a drying filter and into the second sensor cell of the analyzer. The analyzer detected differences in O_2 composition between the room air and the gas leaving the respirometer. Multiplying this value by the flow rate through the chamber allowed us to calculate the $\dot{V}_{O_2}$ for the crabs corrected to conditions of STPD. All data are presented in terms of instantaneous $\dot{V}_{O_2}$ (Bartholomew *et al.*, 1981); they reflect the immediate response of the crab and are not a function of the washout characteristics of the chamber.

The protocol for the experiments using the enclosed treadmill was as follows. The crabs were placed in the respirometer for 45 min at rest. At this point the treadmill was turned on. The animals usually maintained their position on the latex treadmill belt without any problem. Crabs were exercised for 20 min which was followed by a recovery period of over 60 min. Each of the five animals were exercised at three speeds (270, 210 and 150 cm/min), separated by several days rest.

RESULTS

Gecarcinus lateralis used all eight legs as it travelled sideways on the treadmill in the alternating tetrapod

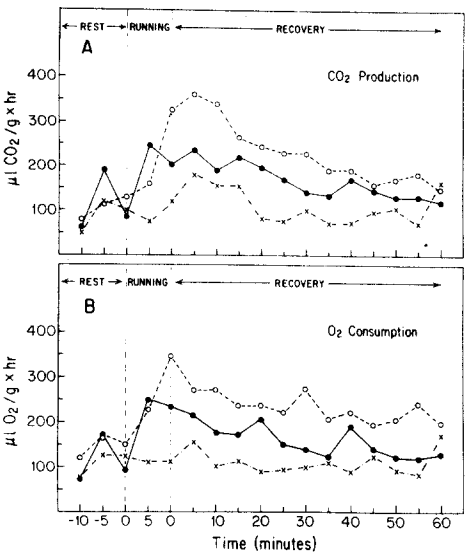

Fig. 1. CO_2 production and O_2 consumption of land crabs *Gecarcinus lateralis* during rest, exercise and recovery. The three curves represent the average data for crabs wearing a respiratory mask while running on a treadmill at three speeds: zero speed, lower curve; 200 cm/min, middle curve; 260 cm/min, upper curve.

gait so typical of crabs. An animal walked with either the right or left side leading, occasionally switching sides, especially at the highest speed. The chelipeds were used in locomotion most often at fast speeds or at the end of a run. At the lowest treadmill speeds the crabs were apt to be erratic in their movements, sometimes wandering about or riding the treadmill belt a bit before accelerating forward. Otherwise they were good subjects for the treadmill study.

Figure 1 displays the $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ value for *G. lateralis* during rest, exercise and recovery while using the respiratory mask. Resting rates for the 15 min just prior to exercise in the nine experiments were $\dot{V}_{O_2} = 108 \pm 50$ μl O_2/g per hr and $\dot{V}_{CO_2} = 104 \pm 42$ μl CO_2/g per hr. The mean respiratory exchange ratio (R) of the individual crabs was 0.85. These values are quite comparable to the same parameters measured for *G. lateralis* by Cameron (1975) and O'Mahoney (1977).

During the 10 min exercise bout, $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ increased. In the case of the highest speed (260 cm/min), the peak $\dot{V}_{O_2}$ was about 3.5 times higher than at rest. The peak $\dot{V}_{CO_2}$ was somewhat delayed compared to the peak $\dot{V}_{O_2}$, causing R values to frequently rise above 1 during the recovery process (see Herreid *et al.*, 1979). Both $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ did not return to resting rates immediately after exercise. At the 200 cm/min

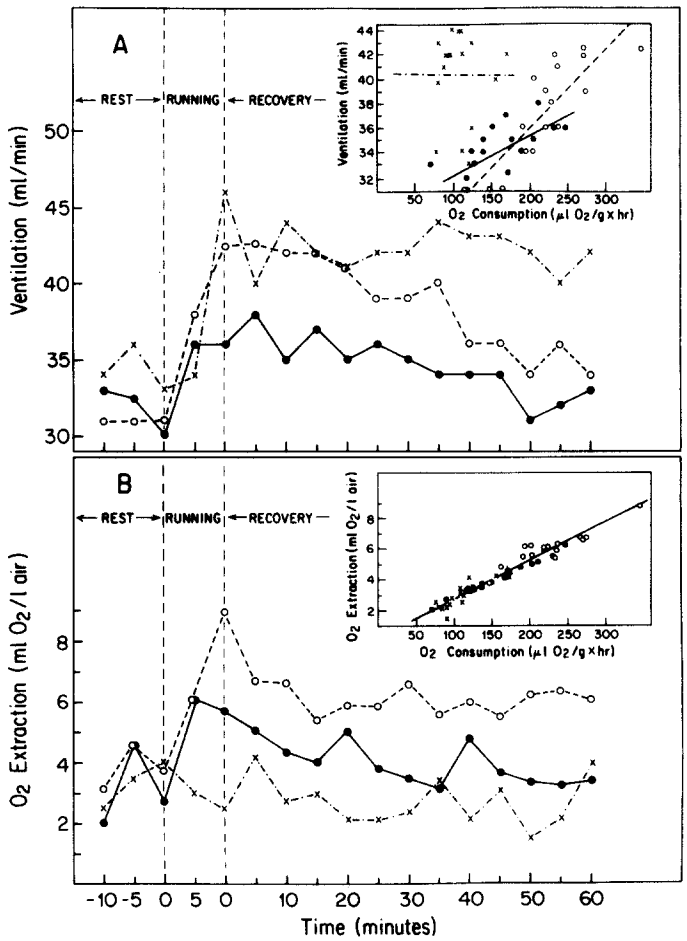

Fig. 2. Ventilation rate and O_2 extraction by land crabs as they exercised on a treadmill. The data were collected at the same time as those presented in Fig. 1. The symbols represent experiments at zero (X symbols), 200 cm/min (solid circles) and 260 cm/min (open circles).

speed it took over 30 min before resting rates were approached, whereas at 260 cm/min running speeds it was at least 45 min or even longer before this point was reached.

Figure 2 illustrates some of the compensatory mechanisms the crab used during exercise and recovery. Figure 2A shows how ventilation volume ($\dot{V}_G$) changed with rest, running and recovery. The average resting $\dot{V}_G$ for nine experiments under ambient conditions (BTPW) was 32 ± 1.9 ml air/min, which was comparable to data collected on 18 *G. lateralis* on other occasions (30.4 ± 0.5 ml air/min. It will be seen from the figure that $\dot{V}_G$ was raised in all experiments, higher $\dot{V}_G$ rates being prevalent at 260 cm/min running than at 200 cm/min. However, it should be noted that the peak $\dot{V}_G$ for the highest running rate was only 1.4 times higher than at rest. Thus, the increased $\dot{V}_G$ was quite insufficient by itself to account for the increased $\dot{V}_{O_2}$ we mentioned earlier. One unusual feature of the graph should be noted: the $\dot{V}_G$ of the crabs at zero speed was raised dramatically during the experiment and remained elevated thereafter. There was no obvious explanation for this pattern, except to note that as a result of the small sample size ($N = 2$), a single animal showed this elevation. In experiments on 4 animals of a third population (otherwise not reported on here) an elevation was not seen during the complete zero speed period ($\dot{V}_G = 31.3 \pm 1.0$). Figure 2A (insert) also displays the relationship between $\dot{V}_G$ and $\dot{V}_{O_2}$. The least squares regression lines and correlation coefficients were calculated for each of the three speeds. For zero speed $\dot{V}_G = 40.6 + 0.00\ \dot{V}_{O_2}$, $r = 0.01$. There is no evidence that there is any consistent change in $\dot{V}_G$ with a change in $\dot{V}_{O_2}$ at rest. This situation changes when exercise is involved: at 200 cm/min $\dot{V}_G = 29.4 + 0.03\ \dot{V}_{O_2}$, $r = 0.70$; at 260 cm/min $\dot{V}_G = 23.0 + 0.06\ \dot{V}_{O_2}$, $r = 0.84$. In both these cases increased $\dot{V}_{O_2}$ is correlated with a compensatory increase in $\dot{V}_G$.

Figure 2B shows the changes in O_2 extraction ($Extr_a$) during the experiment. The resting $Extr_a$ averaged 3.45 ± 0.92 ml O_2/l air ventilated. This is equivalent to a per cent utilization of 1.6% of the oxygen present. The values are quite comparable to other land Crustacea (Cameron, 1975). O_2 extraction increased significantly during exercise, rising to 2.4

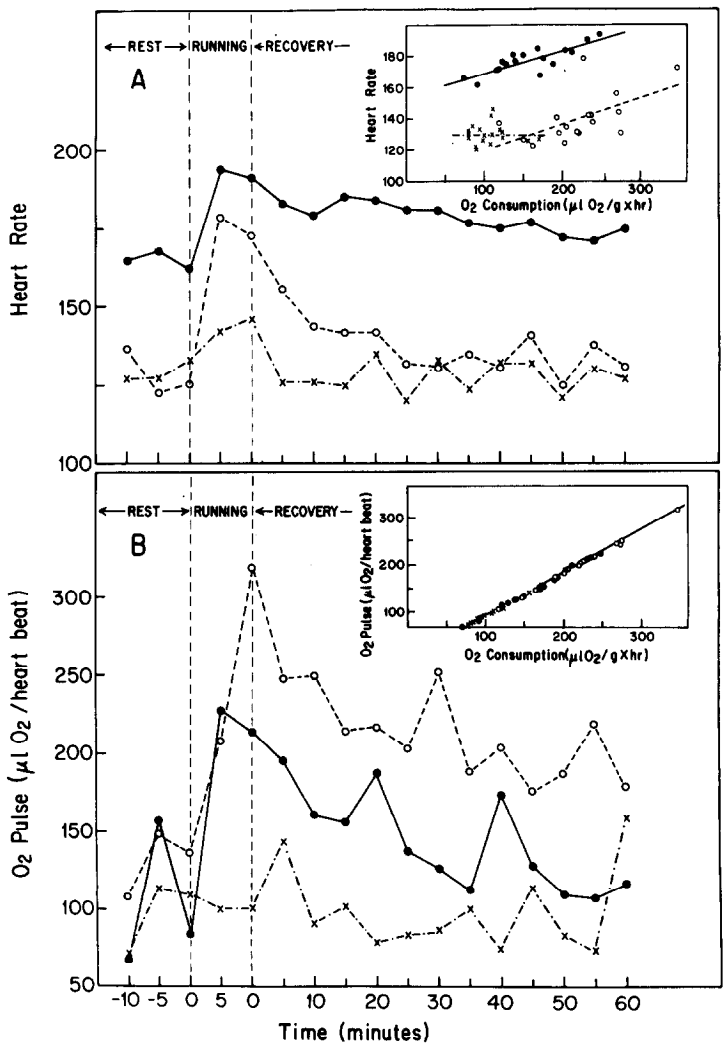

Fig. 3. Heart rate (beat/min) and O_2 pulse of land crabs exercising on a treadmill. The data were collected at the same time as those in Figs. 1 & 2. The symbols represent experiments at zero speed (X symbols), 200 cm/min (solid circles) and 260 cm/min (open circles).

times the resting value at the end of the fast run. Although the $Extr_a$ at the 200 cm/min speed dropped back to resting levels within 30 min after the run ceased, this was not the case for the run at 260 cm/min where $Extr_a$ was still elevated after 1 hr of recovery. Perhaps the most cogent point about Fig. 2B is seen in the insert, where $Extr_a$ is plotted against $\dot{V}_{O_2}$. It is clear that the two variables are closely related at all levels of activity. In fact, all of the data for rest, exercise and recovery are well represented by the least squares regression equation $Extr_a = 0.03 + 0.02\ \dot{V}_{O_2}$, $r = 0.97$.

Heart rates (F_H) in *G. lateralis* collected during the tests are illustrated in Fig. 3A. Resting values fall into two groups: crabs tested at zero and high speeds had an average resting rate of 129 beats/min prior to running whereas those at the intermediate speed (200 cm/min) averaged a much higher 166 beats/min. There was no apparent reason for the difference. Preliminary experiments on 18 animals after 75 min of rest showed rates of 151 ± 7 beats/min. We must simply conclude that heart rate is quite variable among these crabs.

Once the running test began, heart rates increased over resting rates: zero speed, 1.1 times; intermediate speed, 1.2 times; high speed, 1.4 times. Recovery was complete within 5 min after the zero speed test and largely complete within 10 min after the intermediate and high speed runs were finished. The insert in the figure shows how heart rate is related to $\dot{V}_{O_2}$. The least squares regression line for zero speed is $F_H = 130.6 - 0.009\ \dot{V}_{O_2}$, $r = -0.03$, suggesting no relationship. However, during the intermediate and high speeds, heart rate clearly accelerated as O_2 consumption rose: in the 200 cm/min running test, $F_H = 154.7 + 0.15\ \dot{V}_{O_2}$, $r = 0.58$. Finally, we should mention that there were no examples of cardiac arrest during the experiments, in contrast to our experience with *Cardisoma guanhumi* (Herreid *et al.*, 1979).

Figure 3B shows how the O_2 pulse varied throughout the experiment. O_2 pulse is the amount of oxygen passing through the body per heart beat (Maynard, 1960). It is simply calculated by dividing O_2 consumption/crab per min by heart beats/min. The resting O_2 pulse in the 15 min prior to exercise was 111 ± 33 μl O_2/heart beat. Little change was evident in the control experiment at zero speed. However, large increases in O_2 pulse values occurred during the runs at 200 and 260 cm/min, where the measurements reached peak values 2–3 times the resting rate. The return to resting levels during recovery depended upon the intensity of exercise. Recovery from the run at the 200 cm/min speed was apparently complete within 30 min whereas at the 260 cm/min speed the O_2 pulse was still elevated 1 hr after the run. As the insert in Fig. 3B shows, not surprisingly, the O_2 pulse is directly related to O_2 consumption.

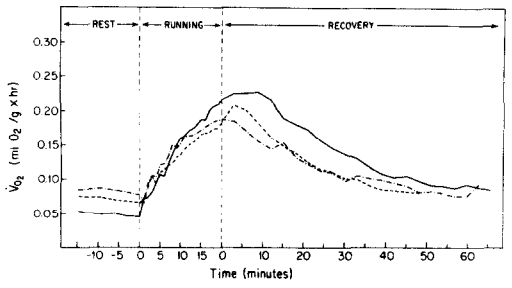

Fig. 4. O_2 consumption of five land crabs running freely on a treadmill. The three curves represent data collected at three speeds: 270 cm/min (solid line), 210 cm/min (dashed line) and 150 cm/min (dot-dashed line).

Experiments were conducted on five *G. lateralis* running freely on a treadmill enclosed within a respirometer. The purpose of these experiments was to obtain a more detailed picture of the $\dot{V}_{O_2}$ during exercise than was possible in the previous work. Moreover, in these experiments we ran the crabs for 20 min and could compare some effects of the respiratory mask on running performance. Unfortunately, because of the limitations of sample size and the fact that the crabs were from two different populations, direct comparisons between the mask and free running experiments should be approached cautiously. The results of the free running tests are depicted in Fig. 4. The pattern is similar to Fig. 1, although both resting $\dot{V}_{O_2}$ and peak values appear to be somewhat lower during free running experiments.

O_2 consumption at rest for free crabs was 69 ± 16 μl O_2/g per hr. Once exercise began, $\dot{V}_{O_2}$ increased throughout the run. We could not identify a steady-state $\dot{V}_{O_2}$ during exercise and it was not possible to force the crabs to continue running for more prolonged periods without their showing fatigue. The peak $\dot{V}_{O_2}$ in freely running crabs was about 3 times the resting rate. Judging by the increase in $\dot{V}_{O_2}$, the physiological adjustment to exercise is relatively slow. The times to reach one-half of the peak $\dot{V}_{O_2}$ ($t_{1/2}$ on-response) were 6.7, 10.3 and 9.0 min for the three running speeds of 270, 210 and 150 cm/min, respectively. Recovery was slow as well. The half times to decline from peak $\dot{V}_{O_2}$ to resting values ($t_{1/2}$ off-response) were 19.3, 18.0 and 26.3 min, for fast, medium and slow speeds, respectively.

Many species display a $\dot{V}_{O_2}$ which is a function of running speed (e.g., Taylor *et al.*, 1970). To demonstrate this point, ideally, one would like to compare $\dot{V}_{O_2}$ measured under steady-state conditions to the intensity of exercise. Since this is not possible, we have plotted the cumulative net O_2 consumption against the velocity for the treadmill respirometer experiments. Cumulative net O_2 consumption is defined here as the total O_2 used during the run and recovery period minus the resting O_2 consumption. The total O_2 consumption was obtained by integrating the area under the $\dot{V}_{O_2}$ curve for each individual crab during the run and recovery. Figure 5 shows the results of this procedure. The least squares regression line and correlation coefficient are $\dot{V}_{O_2} = -0.15 + 3.01$ V, $r = 0.74$. Using a variation of the method of calcalculating the minimum cost of transport (Taylor *et al.*, 1970), we can calculate a cumulative net cost of transport value by using the slope of the above regression line, i.e. 3.01 ml O_2/g per km. We will discuss the validity of this technique below.

DISCUSSION

This is our second attempt to analyze the aerobic response to locomotion in terrestrial carbs. In many respects, the data presented here for *Gecarcinus later-*

alis are quite similar to that for *Cardisoma guanhumi* (Herreid *et al.*, 1979). Both species display a slow $\dot{V}_{O_2}$ on-response to exercise; $t_{1/2}$ on-response for *C. guanhumi* at 300 cm/min was about 4 min, and for *G. lateralis* at 260 cm/min (Fig. 4) was about 6 min. These times are much slower than those reported for mammals such as dogs and humans and for insects where $t_{1/2}$ on-responses are measured in seconds (Chadwick & Gilmour, 1940; Krogh & Weis-Fogh, 1951; Cerretelli *et al.*, 1979, Herreid *et al.*, 1981).

Another point of similarity between *Gecarcinus* and *Cardisoma* is the fact that steady-state $\dot{V}_{O_2}$ values were not evident (Fig. 1). This was the case even when 20 min exercise bouts were performed (Fig. 4). Again, this is distinctly different from the pattern in mammals, birds and insects (e.g., Cerretelli *et al.*, 1979; Herreid *et al.*, 1981).

The speed of the on-response and the lack of a steady-state $\dot{V}_{O_2}$, depends upon many factors, including the intensity of exercise, the amounts of ATP and phosphagen stored in the muscle, the magnitude of the O_2 stores in the tissue and blood, the degree of anaerobic metabolism, the sensitivity of the receptor systems involved in detecting changes caused by exercise and the nature of the O_2 conductance system. We are relatively ignorant of these important features of the crustacean system, so it is not easy to account for these land crabs' sluggish aerobic response to exercise. Nevertheless, it does seem that their O_2 conductance system (*à la* Piiper *et al.*, 1971; Herreid, 1980) is clearly inferior to that of a mammal or an insect which are capable of much higher metabolic rates (Herreid, 1981). But a low O_2 conductance system, although it sets the limits for $\dot{V}_{O_2}$, does not necessarily demand that the O_2 on-response must be slow. In fact, the swimming blue crab, *Callinectes sapidus*, has a rapid on-response (McMahon, 1981). In such cases, other differences must be present.

When $\dot{V}_{O_2}$ is inadequate to meet the energetic demands of locomotion, such as the case during the onset of exercise, three alternatives are available: phosphagens, O_2 reserves and anaerobic fermentations. Unfortunately, we have only meager information on these alternatives in crabs. (1) Arginine phosphate levels (AP) in crustaceans have been measured in lobster abdominal muscle (Beis & Newsholme, 1975). The value of 33.4 μmol AP/g muscle is high compared to phosphagen contents of other animals. If the levels in the locomotor muscles of land crabs are also high, the phosphagen stores may be of great significance during the onset of exercise. (2) Crabs have a high blood volume, roughly 30% of their body weight (Prosser, 1973). Therefore, even if they do have a low carrying capacity, the total O_2 content of their hemolymph could be important. (3) Anaerobic fermentation leads to the development of lactate during strenuous exercise in crustaceans (e.g., Phillips *et al.*, 1977). Even moderate exercise in *Cardisoma carnifex* (Wood & Randall, 1981) also leads to increases in hemolymph lactate and pyruvate. Smatresk *et al.* (1979) found *G. lateralis* only produced modest amounts of lactate after strenuous exercise, but they found evidence that the crab produced another unidentified metabolic acid as well. Estimates of maximal phosphate and O_2 utilization in *Gecarcinus* suggest that anaerobic fermentation contributes

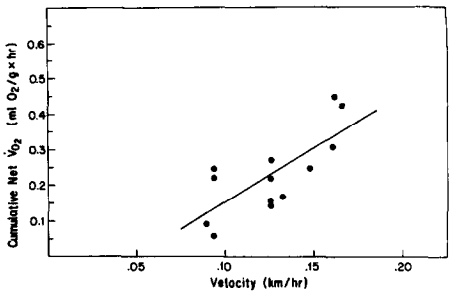

Fig. 5. Cumulative net cost of locomotion as a function of running velocity of land crabs. Each point represents a single crab's net O_2 consumption (above the resting rate) during exercise and recovery. The slope of the regression line may be analagous to the minimum cost of transport.

over 30% of the energy required during exercise (Herreid, 1981).

Peak $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ are related to the intensity of exercise in crabs (Fig. 1; Herreid *et al.*, 1979). The peak values from these experiments on individual crabs ranged up to 3 times higher than those at rest. In *C. guanhumi* we noticed a peak of 5 times that of rest. These aerobic factorial scope values seem quite comparable to small mammals and birds but are definitely inferior to those seen in flying insects. The latter can increase $\dot{V}_{O_2}$ to from 25 to 150 times resting rate, due to the prodigious metabolic rate of the flight muscle (Polacek & Kubista, 1960; Weis-Fogh, 1967) and the differences in body temperatures at rest and in flight (e.g., Bartholomew & Casey, 1978).

Let us now turn to the physiological compensation for exercise in land crabs. *G. lateralis* showed an increase in both ventilation volume and extraction of O_2 (Fig. 2) with exercise. Discounting the unusual values seen in $\dot{V}_G$ at zero speed as being anomalous (see Results section), the pattern is largely predictable. Both $\dot{V}_G$ and $Extr_a$ were directly related to intensity of exercise. This is most easily seen by comparing these parameters with $\dot{V}_{O_2}$ in the inserts of Fig. 2. Note that $\dot{V}_G$ is much less closely coupled to $\dot{V}_{O_2}$ than is $Extr_a$. Ventilation does not change consistently with $\dot{V}_{O_2}$ during rest, a point also seen in other experiments not shown. Furthermore, the scatter of data for $\dot{V}_G$ is greater than that for $Extr_a$ during exercise at 200 and 260 cm/min. Moreover, the magnitude of change for $\dot{V}_G$ is less than that of $Extr_a$ during the experiments, i.e., a tripling of the $\dot{V}_{O_2}$, say from 100 to 300 μl O_2/g per hr, produced an increase of $\dot{V}_G$ of only 1.3 times, whereas $Extr_a$ increased 2.5 times. Clearly, changes in $Extr_a$ are of greater importance in meeting the O_2 demand of exercise in this species. The opposite is true for *C. guanhumi* (Herreid *et al.*, 1979) where we noticed that an increase in $\dot{V}_{O_2}$ was almost solely due to changes in $\dot{V}_G$. In *Cardisoma carnifex*, a near four-fold decrease in % $Extr_a$ was reported during exercise, although there is some doubt about the validity of the resting values (Wood & Randall, 1981). Clearly, these species, although closely related, are using different strategies for coping with the aerobic demands of exercise.

Since $Extr_a$ increases so closely with $\dot{V}_{O_2}$ in *G. lateralis*, major changes must occur in the circulatory transport of O_2. We noted an increase in heart rate,

but other changes must be occurring as well since the O_2 pulse measured in μl O_2/heart beat increased dramatically with exercise (Fig. 3). This rise is probably due to an increased stroke volume, a typical response in crustaceans (McMahon, 1981) and to an increased A–V difference in O_2 content. Several authors have indicated that exercise in crabs increases the ΔpO_2 between the arterial and venous blood primarily by decreasing the venous pO_2 (e.g., Johansen *et al.*, 1970; McMahon *et al.*, 1979; Wood & Randall, 1981). This shifts the pO_2 into the steep part of the O_2 dissociation curve, where considerably more O_2 may be unloaded than at rest. Also, crabs show a distinct Bohr shift, so that metabolic and respiratory acidosis which accompanies exercise has the added effect of unloading more O_2 (Johansen *et al.*, 1970; Mangum & Weiland, 1975; McMahon *et al.*, 1979).

What is the energetic cost of transport in crabs? This question is addressed with difficulty because of the likely large contribution of non-aerobic metabolism and the long lag time before $\dot{V}_{O_2}$ reaches high levels. If we assume that the post-exercise recovery O_2 (O_2 debt) is a measure of the anaerobic contribution plus the repayment of an O_2 deficit, then we can justifiably include the recovery O_2 in our calculation of the cost of transport. This approach has been used to calculate a net cumulative cost of transport for *C. guanhumi* and slugs (Herreid *et al.*, 1979; Denny, 1980). Unfortunately, there is little evidence to justify this procedure. It does seem likely that part of the recovery O_2 is a repayment of the O_2 deficit where ATP, phosphagens and O_2 stores in the body are replaced. In mammals, this accounts for the first 20–30 sec, or the fast component, of the post-exercise recovery. It may be considerably longer in these poikilothermic crustaceans. However, the remaining part of the O_2 debt may not be directly related to the energy expenditure in locomotion at all. Originally, most lactate produced during exercise in vertebrates was believed to be reconverted into glycogen during rest at the cost of excess O_2. If this were the case in crabs, then we could justify including recovery O_2 in our calculations. Unfortunately, this is probably not the situation. Phillips *et al.* (1977), using radioactively labelled lactate, noted little conversion of lactate into glucose or glycogen in crustaceans. Also, we should emphasize that the bulk of the lactate in mammals is not involved in gluconeogenesis either. It is simply oxidized during recovery at the cost of no extra O_2 (e.g., Brooks *et al.*, 1973). Thus, we need to find other reasons for the elevated post-exercise $\dot{V}_{O_2}$. In mammals, 70% of the recovery O_2 can be due to a rise in body temperature. This produces a rise in resting tissue $\dot{V}_{O_2}$ by a Q_{10} effect and because there is a decrease in the efficiency of ATP generation (Brooks *et al.*, 1971a, 1971b, 1973; Segal & Brooks, 1979; Hagberg *et al.*, 1980). Such an explanation cannot be put forward for poikilothermic crabs. We can calculate the heat production of a running 50 g crab by assuming an average $\dot{V}_{O_2}$ of 250 μl/g per hr. If this $\dot{V}_{O_2}$ occurred for the duration of a 20 min run, a crab would use about 4.1 ml O_2. Assuming an energy equivalent of 4.8 cal/ml O_2, the total heat production would be 20 cal. This would amount to a maximum temperature rise of perhaps 0.3°C, assuming a specific heat of 0.83. The real temperature increase is probably a fraction of this value because of the large evaporative water loss in crabs (Herreid, 1969).

With the above caveats in minds we can now plot the net cumulative cost of transport for *G. lateralis* using the data from Fig. 4. Firstly, notice that the regression line does not pass through the origin (Fig. 5). This may be due to a curvilinear relationship between $\dot{V}_{O_2}$ and velocity, a large anaerobic contribution at these speeds or invalid assumptions concerning the magnitude of oxygen debt representing the total non-aerobic energy used during locomotion. Secondly, the slope of the curve $\dot{V}_{O_2}$ vs velocity is 3.01 ml O_2/g per km. When this is compared to the minimum cost of transport (see Taylor *et al.*, 1970) developed for birds and mammals by Fedak & Seeherman (1997), we obtain an almost identical value. Data on *C. guanhumi* are also similar to the higher vertebrates (Herreid *et al.*, 1979). Although we should approach such data with caution in the light of our ignorance about post-exercise O_2, nevertheless to date, we have no reason to believe that crabs are unique in their energy expenditure during locomotion even though they have a gill/hemolymph O_2 conductance system and run sideways on eight legs.

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