

Aerobic response to exercise of the fastest land crab

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FULL, ROBERT J., AND CLYDE F. HERREID II. *Aerobic response to exercise of the fastest land crab*. *Am. J. Physiol.* 244 (Regulatory Integrative Comp. Physiol. 13): R530-R536, 1983.—To view the aerobic response to exercise, the ghost crab *Ocypode quadricaudii* was run in a treadmill respirometer at three velocities (0.13, 0.19, and 0.28 km/h) while oxygen consumption ($\dot{V}O_2$) was monitored. A steady-state $\dot{V}O_2$ that increased linearly with velocity was attained. $\dot{V}O_2$ transient periods at the beginning and end of exercise were extremely rapid with half times from 50 to 150 s. The magnitude of oxygen deficit and debt were small and both showed increases with an increase in velocity. Oxygen debt was measured at each velocity after 4-, 10-, and 20-min exercise bouts. No change in the magnitude of oxygen debt was observed with respect to exercise duration. Maximal $\dot{V}O_2$ was 11.9 times the average resting $\dot{V}O_2$. Oxygen uptake kinetics have shown only very sluggish and reduced rates in five other more sedentary crab species previously tested. The aerobic response pattern observed in the present study is more comparable to that of exercising mammals and highly aerobic ectothermic vertebrates. This suggests that the ghost crab meets the energy demand of sustained exercise by aerobic ATP production in contrast to many other crab species.

crab locomotion; energetics; kinetics of oxygen consumption; maximal oxygen consumption; oxygen deficit and debt

THE AEROBIC RESPONSE to exercise has been studied principally in vertebrates, with humans receiving most attention (2, 30). Rates of oxygen utilization have been examined under steady-state conditions and during transient periods at the beginning and end of exercise. Numerous investigations have viewed the effect of various exercise regimes on the magnitude of oxygen deficit and debt (8, 15, 16, 20, 35). Recent examinations of maximal oxygen consumption have been conducted (21, 31). Study of the various components of the aerobic response to exercise has not only provided extensive information on energy utilization but has also been essential in developing a better understanding of vertebrate metabolic design (3).

Unfortunately, little work has centered on the aerobic response to terrestrial locomotion in the largest and most diverse group of animals, the invertebrates (17-19). Yet the invertebrate design of oxygen transport systems, appendages, and modes of travel provides unusual and diverse solutions to problems of exercise and energy utilization. This is exemplified by five species of land crabs we previously studied (11, 17, 18). Each species used sideways octopedal locomotion while being run on a treadmill.

Oxygen uptake for aerobic energy production occurs in the gill chambers located on either side of the crab. Air or water is drawn into the gill chambers via inspiratory openings along the base of the legs and expired near the mouth. Oxygen diffuses across the gills into an open circulatory system powered by a single-chambered heart. In all five species oxygen uptake kinetics showed sluggish responses both during and after exercise. No steady-state oxygen consumption ($\dot{V}O_2$) was attained during 15- to 20-min exercise bouts. The largest $\dot{V}O_2$ values showed only a modest increase over resting values (e.g., 3-6 times).

These results were unlike the classical mammalian pattern for submaximal exercise: a rapid aerobic on-response, a steady-state $\dot{V}O_2$, and a rapid recovery. Moreover mammals often show a maximal $\dot{V}O_2$ 10 times greater than preexercise values (31). Unfortunately, we could not determine whether the crab data were representative of all crustaceans and an inherent result of the oxygen transport system or whether the species we examined were specialized for short-duration activity requiring anaerobic metabolism. To investigate this problem more fully, we have turned to the ghost crab, an extremely active animal, designated the world's fastest crustacean (14).

In this paper we show that ghost crabs, contrary to data on other studies of land crabs, are highly aerobic during exercise and show responses very much like animals such as mammals, which rely heavily on aerobic ATP production during sustained activity.

MATERIALS AND METHODS

Animals. Experiments on the ghost crab *Ocypode quadricaudii* (Milne-Edwards and Lucas) were conducted at the Smithsonian Tropical Research Institute on Naos Island, Panama. This species has two dissimilar types of individuals living on sandy beaches. Larger red crabs ranging up to 30 g were found predominantly during the day. They were poor runners on the treadmill. The mottled grey animals used in the $\dot{V}O_2$ experiments were the smaller members of the same species and more prevalent in the evening. These crabs, both male and female, had an average mass (m) of 2.78 ± 0.61 (SD) g. The crabs were maintained in jars with moist sand at 22°C and fed live and freshly killed fish.

Apparatus. Animals were exercised in a Lucite respirometer that contained a variable-speed treadmill (17, 18). All treadmill experiments were conducted at 22°C. Gas drawn through the chamber at 50 ml/min (\dot{V}_E) was dried by a column containing Drierite. The incurrent

fractional oxygen concentration ($F_{I_{O_2}}$) was compared with the excurrent fraction ($F_{E_{O_2}}$) by a two-channeled Applied Electrochemistry oxygen analyzer, which was interfaced with a Linear Instruments model 282 integrating chart recorder. From the continuous recordings of F_{O_2} , instantaneous $\dot{V}O_2$ was calculated using the method of Bartholomew et al. (1). This procedure provided estimates of rapid changes in metabolic rate when the "washout" response of the system is known. The delay time ranged from 20 to 30 s. The response time of the system (approx 3 min to 50% full-scale deflection) was determined by the addition of gas of a precisely known concentration of oxygen ($20.861 \pm 0.001\%$ O_2 with the remainder being N_2). Mass-specific $\dot{V}O_2$ was calculated by Eq. 3a from Withers (38) where

$$\dot{V}O_2 = \frac{\dot{V}E \cdot (F_{I_{O_2}} - F_{E_{O_2}})}{m \cdot [1 - (1 - RQ) \cdot F_{I_{O_2}}]}$$

Respiratory quotient (RQ) was not determined in this species and was taken to be 1.0. The fractional error in $\dot{V}O_2$ is $\pm 3\%$ if RQ was assumed to be 1.0 but is actually 0.85 or 1.15 (38). All $\dot{V}O_2$ values were corrected to STPD conditions.

Submaximal oxygen consumption. Five animals, whose maximal $\dot{V}O_2$ ($\dot{V}O_{2\max}$) had been determined, were exercised at three velocities: 0.13, 0.19, and 0.28 km/h for 4-, 10-, and 20-min durations. A rest period of 30 min was followed by an exercise bout randomly selected from the above conditions. During the 10- and 20-min runs a steady-state $\dot{V}O_2$ ($\dot{V}O_{2\text{ss}}$) was attained. This was defined as the average $\dot{V}O_2$ over a period of at least 7 min where $\dot{V}O_2$ showed no further increase. When the exercise was finished, a recovery period was begun and lasted 30 min or until the $\dot{V}O_2$ reached prior resting levels. $\dot{V}O_2$ was continuously monitored during rest, exercise, and recovery. In this set of experiments, the volume or equivalent volume of oxygen used during oxygen deficit and debt was determined by planimetry.

Maximal oxygen consumption. $\dot{V}O_{2\max}$ was determined by a progressive maximal test. Following a 30-min rest period, a crab was run at an initial velocity of 0.28 km/h. when a $\dot{V}O_{2\text{ss}}$ had been attained for 3 min, the velocity of the treadmill was increased by approximately 0.03 km/h until a new higher steady state was achieved. Three minutes after this new steady rate occurred, velocity was increased again. $\dot{V}O_{2\max}$ was defined as the $\dot{V}O_2$ attained when two consecutive incremental increases in velocity resulted in no further increase in $\dot{V}O_2$ (i.e., $<0.008\%$ change in $\dot{V}O_2$). $\dot{V}O_{2\max}$ was attained at velocities approaching 0.45 km/h.

Endurance. To evaluate locomotory endurance, after a 5-min rest period 20 ghost crabs were run on the treadmill at a given velocity until fatigued. Running velocities ranged from 0.20 to 0.76 km/h, the latter being the maximum treadmill speed. Fatigue was defined as that time when a crab flipped over onto its carapace and was unable to run. At this time the crabs, normally a grey color, developed a red tint primarily at the base of the eyestalks and walking legs. The color change along with the behavioral response allowed a precise determination of time to fatigue. In this experiment an individual

was tested only once and not used in other experiments. In addition to the treadmill endurance experiments, crabs ranging in size from 8.6 to 31.6 g were run twice on the moist sand of the beach. The average velocity of 10 animals was measured from a standstill start over approximately 10 m.

RESULTS

Submaximal oxygen consumption. In the experiments where a $\dot{V}O_{2\text{ss}}$ was attained, ghost crabs utilized 0.12 ± 0.06 (SD) $\text{ml } O_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ during the rest period before exercise. Figure 1 shows the aerobic response to exercise at a velocity of 0.19 km/h for 4-, 10-, and 20-min durations. As exercise began, $\dot{V}O_2$ showed a rapid increase from the resting value. All animals during the 10- and 20-min exercise periods established a $\dot{V}O_{2\text{ss}}$ at each of the velocities tested. Sixty percent of the animals running for 4 min arrived at a $\dot{V}O_{2\text{ss}}$ value at the 4th min that was comparable to the $\dot{V}O_{2\text{ss}}$ found for 10- and 20-min runs.

After exercise, $\dot{V}O_2$ declined toward the previous resting $\dot{V}O_2$. Both the intensity and duration of the exercise period had an effect on the $\dot{V}O_2$ level attained during 30 min of recovery. All of the crabs exercising for 4 min at

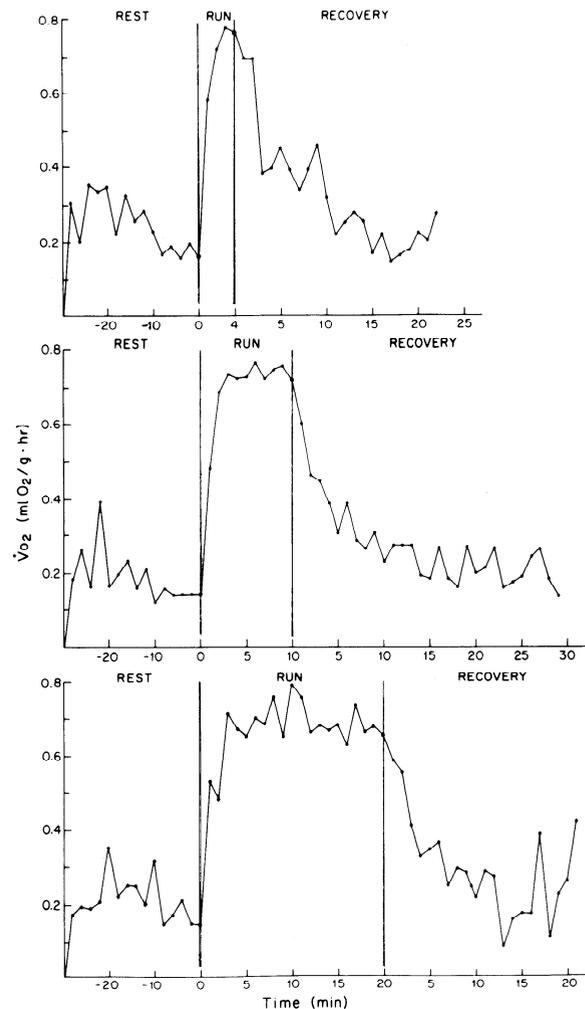


FIG. 1. Oxygen consumption ($\dot{V}O_2$) of a ghost crab run for periods of 4, 10, and 20 min at 0.19 km/h.

the slowest (0.13 km/h) and intermediate (0.19 km/h) velocities reached complete recovery within 30 min. None of the 20-min duration experiments at the fastest velocity (0.28 km/h) showed a complete recovery pattern in 30 min. In nearly all of the incomplete recovery patterns, $\dot{V}O_2$ seemed to approach an asymptote of a new higher resting $\dot{V}O_2$. Within 30 min, the recovery $\dot{V}O_2$ of all animals in every experimental condition declined to 90% of the resting $\dot{V}O_2$.

The time it takes to arrive at 50% of the $\dot{V}O_{2\text{ss}}$ ($t_{1/2\text{on}}$) was used to evaluate the initial $\dot{V}O_2$ transient at the start of exercise for the 20-min duration experiments (Fig. 2). A one-way analysis of variance (ANOVA) showed that $t_{1/2\text{on}}$ values were longer the greater the velocity [$F(2, 12) = 5.13, P = 0.05$]. The time to 50% recovery ($t_{1/2\text{off}}$)

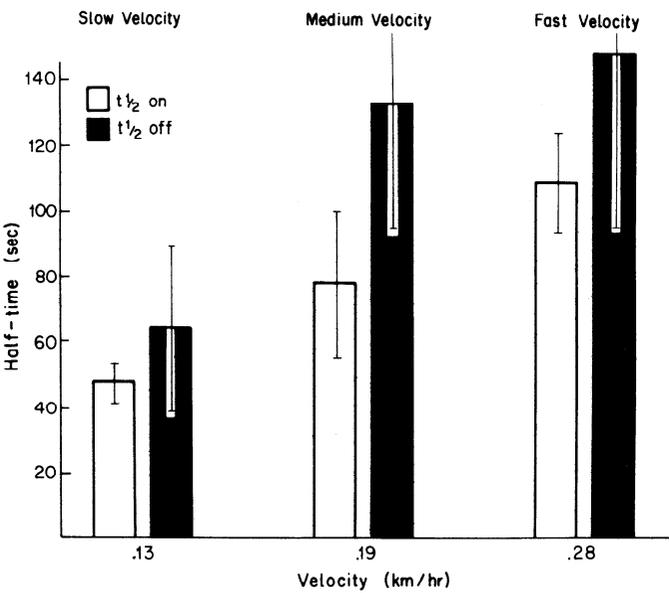


FIG. 2. Time to reach 50% steady state $\dot{V}O_2$ ($t_{1/2\text{on}}$) and 50% recovery ($t_{1/2\text{off}}$) at slow, medium, and fast velocities of a 20-min run. Each bar represents mean \pm SE of 5 animals.

was also calculated. The mean $t_{1/2\text{off}}$ values appeared longer at the greater velocities of locomotion, but such differences were not significant at the 95% level in a one-way ANOVA. The $t_{1/2\text{off}}$ value was not significantly longer than the $t_{1/2\text{on}}$ value at any velocity when a paired t test was conducted.

In addition to evaluating half time, the size of the oxygen deficit and debt was calculated to better describe the $\dot{V}O_2$ transients of exercise (Fig. 3). Oxygen deficit was defined as the volume of oxygen represented by the area between the observed increase in $\dot{V}O_2$ and the theoretical instantaneous rise to a steady state (30). A one-way ANOVA on the 20-min runs showed that the magnitude of the deficit was greater the more intense the exercise [$F(2, 12) = 19.8, P = 0.001$]. Oxygen debt was operationally defined as the area under the recovery $\dot{V}O_2$ curve (above the resting $\dot{V}O_2$). Since complete recovery was not seen in all experimental conditions, the volume of oxygen used in the oxygen debt period was calculated to 90% of the resting $\dot{V}O_2$. A 3 \times 3 ANOVA showed an increase in oxygen debt with increasing velocity at all durations tested [$F(2, 12) = 8.98, P = 0.004$]. Oxygen debt at a given velocity was not found to be different when 4-, 10-, and 20-min duration runs were compared. The ratio of oxygen deficit to oxygen debt was near 0.4 for the three velocities tested after the 20-min exercise bout.

Oxygen consumption vs. velocity. $\dot{V}O_{2\text{ss}}$ increased in a linear manner with velocity (Fig. 4). The least-squares regression line was $\dot{V}O_{2\text{ss}} = 1.9V + 0.38$, where V is velocity in kilometers per hour. If the net volume of oxygen (total volume - resting $\dot{V}O_2$) used during the exercise period is added to the net volume of oxygen used during recovery, a value defined as the cum net $\dot{V}O_2$ can be calculated. This value has been used in other crab species to estimate the energy required to locomote at a given velocity (11, 17, 18). The cum net $\dot{V}O_2$ also varies linearly with velocity and is not different from the $\dot{V}O_{2\text{ss}}$ regression line (Fig. 4).

The slope of the velocity vs. $\dot{V}O_{2\text{ss}}$ relationship has

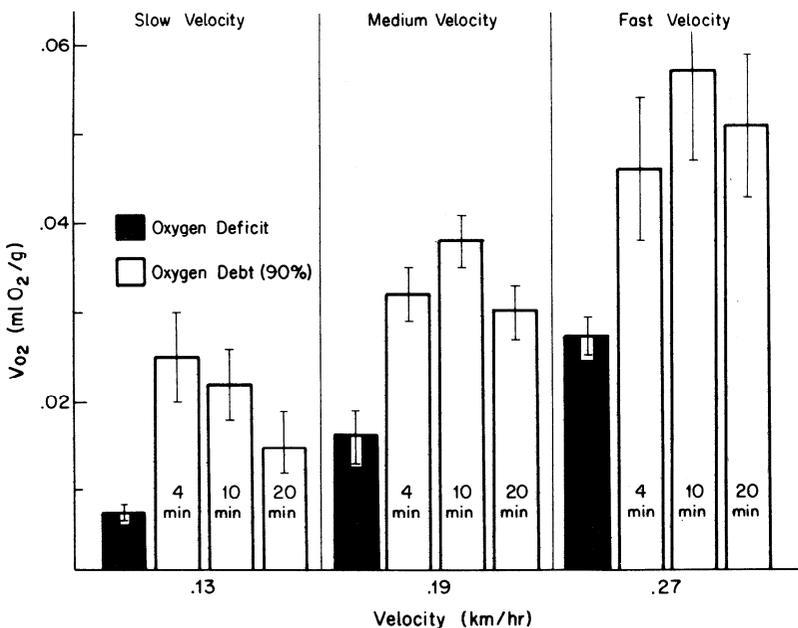


FIG. 3. Magnitude of oxygen deficit and debt at slow, medium, and fast velocities with oxygen debt measured after 4, 10, and 20 min of exercise. Each bar represents mean \pm SE of 5 animals.

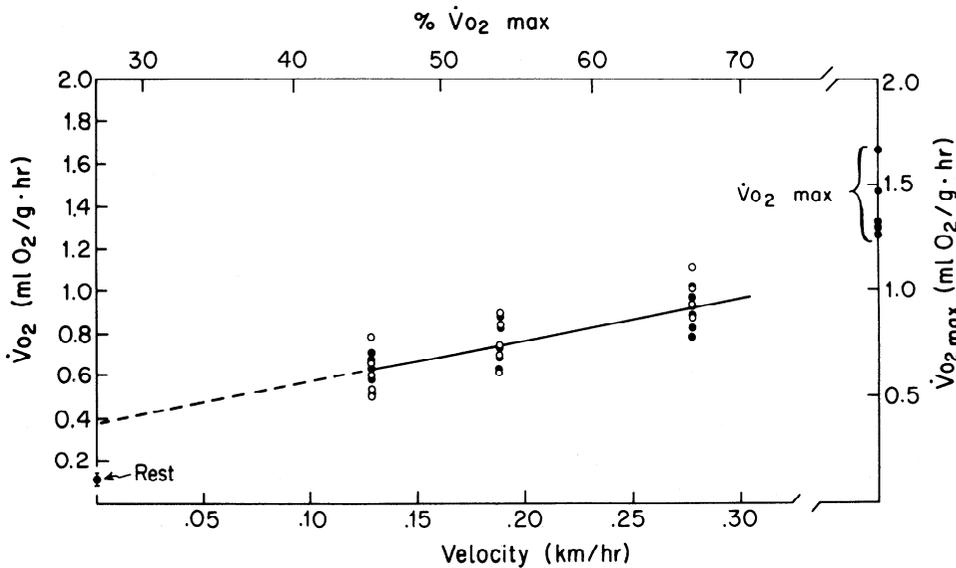


FIG. 4. Steady-state oxygen consumption (closed circles) and cum net $\dot{V}O_2$ (open circles) for 5 ghost crabs as a function of velocity. Maximal oxygen consumption ($\dot{V}O_{2\max}$) is plotted for comparison on right. $\% \dot{V}O_{2\max}$ scale represents rate of steady-state oxygen utilized at a given velocity compared with $\dot{V}O_{2\max}$.

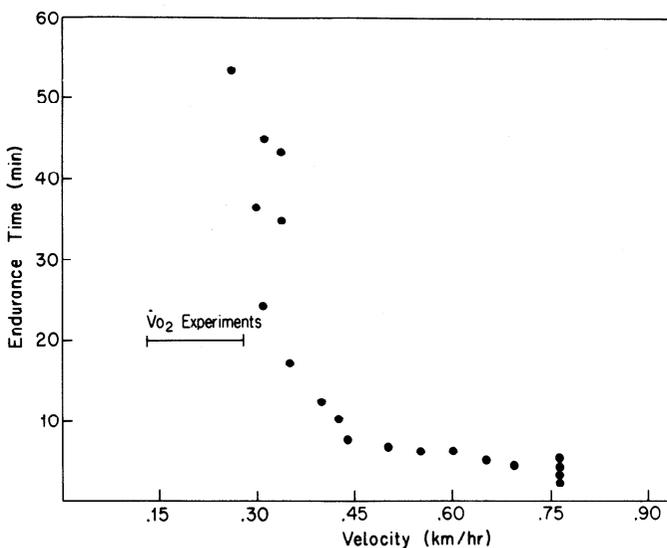


FIG. 5. Endurance time as a function of velocity. Horizontal bar indicates range of velocities used in submaximal steady-state $\dot{V}O_2$ experiments. At velocities less than 0.20 km/h, crab did not fatigue during 60-min test period.

been defined as the minimum cost of locomotion (M_{run}) by Taylor et al. (32). Therefore, the M_{run} of ghost crab is $1.9 \pm 0.9 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{km}^{-1}$ ($\pm 95\%$ confidence interval).

In Fig. 4 $\dot{V}O_{2\max}$ is compared with $\dot{V}O_{2\text{ss}}$ attained at various velocities. The mean $\dot{V}O_{2\max}$ $1.37 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, was 11.9 times the mean resting $\dot{V}O_2$. Notice also that the regression line in Fig. 4 extrapolates to a point on the Y-axis that is almost four times higher than actual resting $\dot{V}O_2$. This discrepancy is common among vertebrate and invertebrate runners and probably has multiple causes (17).

Endurance. As a test of endurance, ghost crabs were run on a treadmill at various velocities until fatigued. Figure 5 shows the time to fatigue as a function of velocity. At velocities less than 0.20 km/h crabs did not become fatigued during the 1-h run. From velocities of 0.20 to 0.34 km/h the crabs' times to fatigue were extremely variable but still longer than 20 min. Fatigue occurred in less than 20 min at velocities greater than

0.34 km/h. At 0.76 km/h fatigue was observed in approximately 5 min or less.

In the experiments on the beach with larger animals, average sprinting velocity was 5.4 km/h. The fastest velocity attained was 8.5 km/h by an 9.6-g crab.

DISCUSSION

Aerobic factorial scope. The morphological and physiological design of the ghost crab is strikingly different from that of vertebrates. Yet the reliance on aerobic metabolism is more like that of active vertebrates than of other land crab species previously surveyed (11, 17, 18). For example, numerous studies have been conducted on vertebrates comparing the ratio of active to resting $\dot{V}O_2$. This dimensionless number is called the aerobic factorial scope. It is an indicator of the animal's capacity to support activity aerobically. Values for vertebrates in general range from 5- to 15-fold (2, 21, 31). Crustaceans studied thus far have shown only modest increases in $\dot{V}O_2$ during activity. Aerobic factorial scope values range from 3 to 6 (17, 18, 36). In the present study, the ghost crab showed a substantial aerobic capacity to support activity: aerobic factorial scope values approach 12-fold (Fig. 4).

Oxygen deficit. Most mammals show relatively rapid $\dot{V}O_2$ kinetics with small oxygen deficits, $t_{1/2\text{ on}} = 14\text{--}40 \text{ s}$ (7, 24). Similar rapid aerobic responses at the beginning of exercise have been observed for cockroaches (19) and some lizards (12, 26). However, five species of crabs exercising on treadmills for 15–20 min have shown an aerobic response pattern where $\dot{V}O_2$ does not attain a steady state and peak $\dot{V}O_2$ may occur after the run (11, 17, 18). No true oxygen deficit can be determined in these invertebrates. Various factors potentially contribute to this delayed rise in $\dot{V}O_2$: 1) rate of elevation of respiration and circulation, 2) rate of oxygen delivery by diffusion, 3) size of oxygen and phosphate stores, 4) activated muscle fiber type, and 5) changes in ATP, ADP, and P_i concentration, which affect mitochondrial respiration rate. Similar factors could be involved in the delayed aerobic response of crustaceans. Investigations of the

land crab *Cardisoma guanhumi*, which never attains a $\dot{V}O_{2\text{ss}}$ during locomotion, have revealed a slow rise in ventilation rate, indicating that respiration and/or circulation may be a serious limitation for oxygen conductance in this species (18). The rate of oxygen diffusion across the chitin layer of crustacean gills is often suggested as a possible limitation (25). Information for crustaceans at the level of the muscle with respect to fiber type and higher-energy phosphates is lacking.

A sluggish aerobic response is not characteristic of the ghost crab. A rapid increase in $\dot{V}O_2$ to steady state is observed with $t_{1/2\text{on}}$ only slightly slower than some mammals and cockroaches (Figs. 1 and 2). In exercising humans, the $t_{1/2\text{on}}$ can be altered by changes in work intensity. When work is increased, $t_{1/2\text{on}}$ has been shown to increase along with oxygen deficit, indicating a greater utilization of oxygen stores, high-energy phosphates, and/or anaerobic ATP production (15, 20). A similar pattern with increasing velocity has been described for the exercising ghost crab (Fig. 3). However, even at the highest sustained velocities, aerobic energy production still contributes extensively.

The data presented for the ghost crabs do not support a common view of the crustacean oxygen transport system as relatively inefficient. The high aerobic factorial scope and the rapid rise in exercising $\dot{V}O_2$ to a steady state suggests that the ghost crabs rely primarily on aerobic ATP production for locomotion at sustained velocities just as do mammals and reptiles. However, it is important to stress that the absolute $\dot{V}O_2$ for crabs is markedly lower than that of mammals; e.g., the resting $\dot{V}O_2$ for ghost crabs was $1/25$ of the value predicted for a resting mammal of the same size.

Aerobic recovery. In vertebrates the time required for $\dot{V}O_2$ to return to preexercise levels is highly variable. The range of time for oxygen debt varies from 30 min in exercising humans to 10 h in swimming fish (2, 15). Unfortunately, only in exercising humans have the relationships between work level and oxygen debt been rigorously examined. In humans, oxygen debt has been classically shown to be best described by a two-component exponential curve (23). The first component being rapid with a $t_{1/2}$ of near 30 s, while the second component is slower with $t_{1/2}$ as great as 30 min (15, 35). Hagberg et al. (15) found that the rapid component of oxygen debt increased with work intensity but not duration. The slow component was not altered by exercise intensity or duration at less than 65% $\dot{V}O_{2\text{max}}$ but was five times greater after 20 min of exercise at 80% $\dot{V}O_{2\text{max}}$. At heavier work rates, $\dot{V}O_2$ has been reported to remain elevated for several hours, reaching an apparent recovery asymptote above preexercise rates (35). A remarkably similar aerobic pattern of recovery exists in the ghost crab. The magnitude of oxygen debt (to 90% recovery) increased with increasing velocity, but no trend was seen with different durations of exercise (Fig. 3). Although the slow component of recovery was not directly evaluated, increased intensity and duration of exercise prolonged complete recovery, and at faster running velocities an elevated recovery asymptote was found. The above aerobic recovery patterns stand in marked contrast to previously

studied running crabs. The majority of crabs have shown a nearly monoexponential curve with $t_{1/2\text{off}}$ ranging from 15 to 20 min with complete recovery taking several hours (11, 17, 18, 29, 36). The explanation for the observed differences in the aerobic recovery pattern is not clear.

Traditional interpretations of oxygen debt with respect to a two-component model have been challenged (4, 5, 12). In fact, it has been suggested that the term oxygen debt be changed to excess postexercise oxygen consumption (4, 5). Studies of oxygen debt in mammals have shown it to be a result of a number of factors, which include 1) repayment of tissue and blood oxygen stores, 2) replenishment of phosphagens, 3) a Q_{10} effect of elevated body temperature, 4) removal of anaerobic end-products, 5) increased respiratory and cardiovascular work during recovery, 6) elevated metabolism due to hormones, and 7) energy for ion redistribution and tissue repair (30). Oxygen debt, therefore, is not a simple repayment of the oxygen deficit incurred early in exercise. Both fast and slow components of oxygen debt possess multiple contributors. In locomoting crabs, body temperature does not show a significant increase due to the low metabolic rates. Crabs with large oxygen debts have shown elevated ventilation rates and volumes well into recovery, but this additional cost has not been evaluated. Lactic acid has been shown to be produced in a number of crustaceans after exercise, but its subsequent fate is unknown (27, 29, 37). Additional research is required before differences in oxygen debt can be clarified.

Endurance. How does the aerobic response to exercise relate to a ghost crab's performance? As work rate increases in exercising humans, a level is reached beyond which performance time declines in an exponential fashion (34). This also seems to be true for a locomoting lizard (21) and the land crab *C. carnifex* (36). A similar relationship for the ghost crab is shown in Fig. 5. One often sees a ghost crab sprinting across the beach. These rapid rates of locomotion during escape can be maintained for only short periods of time. But at velocities less than 0.30 km/h, locomotor activity could be sustained for well over 40 min. At low intensity, exercise activity is fueled primarily by aerobic metabolism. It is at these low velocities that a $\dot{V}O_{2\text{ss}}$ is attained and the cost of transport may be estimated. The low range of velocities may correspond to the exercise intensity level of burrow excavation and sand pellet feeding, which are behaviors of somewhat extended duration. An increase in velocity is accompanied by an increase in the magnitude of the oxygen deficit. Therefore, the contribution of oxygen and energy-rich phosphate stores along with anaerobic energy production is likely to be greater as exercise levels are increased. At exercise intensities greater than 0.30 km/h (70% $\dot{V}O_{2\text{max}}$) the time to fatigue declines sharply. A similar situation may exist during rapid escape behavior on the beach. The reason for the limited ability to sustain activity at these higher work levels is not clear.

Cost of transport. M_{run} for ghost crabs was calculated from the $\dot{V}O_2$ vs. velocity regression slope (Fig. 4) to be $1.9 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{km}^{-1}$; i.e., it requires 1.9 ml O_2 to move 1 g of crab 1-km distance. Since other species of crabs have not produced steady-state values during exercise, this is

the first time we have attained adequate data for a determination of M_{run} in eight-legged animals. Previously our best estimations of M_{run} (17, 18) utilized the total amount of oxygen over resting levels during both exercise and recovery (cum net $\dot{V}O_2$). This method assumes that the total amount of oxygen used during recovery is due to excess oxygen used to replenish oxygen stores, energy-rich phosphate stores, and removal of lactate formed in anaerobic ATP production. As discussed earlier, this assumption is only partially true for vertebrates and may not be valid for crustaceans. Thus it may be significant that for the ghost crab the two methods cum net $\dot{V}O_2$ and $\dot{V}O_{2\text{ss}}$ evaluation yield the same values for M_{run} (Fig. 4).

How does the crab cost of transport compare with pedestrian birds, lizards, and mammals? From the equation developed for two- and four-legged vertebrates (10), we predict that a 2.8-g animal would have an M_{run} of 2.9 ml $O_2 \cdot g^{-1} \cdot km^{-1}$. The M_{run} of the ghost crab falls within

the spread of this predicted value. We have previously noted a similar agreement between vertebrate runners and six-legged cockroaches (19). The data support our contention (17, 19) that the minimum cost of pedestrian locomotion does not depend on the number of legs or on the nature of the respiratory and circulatory system, all of which differ radically among the species tested. Instead, it is dependent on two major factors: 1) the body mass, where small animals have higher costs than large, and 2) the mode of locomotion, where pedestrian travel among most species is metabolically more expensive than either swimming or flying (28, 33).

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