

LOCOMOTION ENERGETICS OF THE GHOST CRAB

I. METABOLIC COST AND ENDURANCE

BY ROBERT J. FULL*

*Department of Biological Sciences, State University of New York at Buffalo,
Buffalo, NY 14260, USA**Accepted 13 February 1987*

SUMMARY

Arthropods possess spectacular diversity in locomotor design. Yet it is not clear what unique constraints, if any, variation in design imposes on mechanics, metabolic energy cost or endurance during terrestrial locomotion. In the present study metabolic energy cost and endurance on a treadmill are measured for an arthropod, the eight-legged sideways travelling ghost crab, *Ocypode quadrata* (Fabricius). In a second paper the mechanics of locomotion are determined during walking and running over a force plate.

Severe limitations in O_2 uptake during exercise are not inherent in the design of a crab's O_2 transport system, which consists of gills and an open circulatory system. The ghost crab's capacity to elevate oxygen consumption (\dot{V}_{O_2}) rapidly is correlated with a lesser dependence on anaerobic sources than observed in other crab species. Accelerated glycolysis contributed at the onset of submaximal exercise, before O_2 uptake adjustments were completed, but played only a minor role during steady-state exercise. *O. quadrata* elevated \dot{V}_{O_2} 6.4- to 8-fold above resting rates. The ghost crab's maximal oxygen consumption ($\dot{V}_{O_{2max}}$) was not different from that of an ectothermic vertebrate of the same body mass and temperature, such as a lizard, that uses lungs and a closed circulatory system.

The minimum metabolic energy necessary to move 1 g of crab 1 km (C_{min}) decreased as a function of body mass and age. C_{min} was comparable to that predicted for vertebrates of a similar body mass and, therefore, appears to be relatively independent of locomotor design. This is consistent with the hypothesis that a similarity in the energetic properties of muscle and elastic structures may result in similar metabolic costs of locomotion.

Endurance capacity did not increase with body mass, as predicted from inter-specific comparisons of mammals and lizards. Instead, endurance capacity correlated with the speed at which oxygen consumption was maximal. Mean endurance capacity for ghost crabs was similar to that found for lizards, but was far less than the values predicted for mammals. Ghost crabs could only sustain a slow walk. Running at speeds 20 times faster is possible for short periods, but not without the aid of anaerobic metabolism.

* Present address: Department of Zoology, University of California, Berkeley, CA 94720, USA.

INTRODUCTION

Arthropods have evolved an extraordinary array of solutions to the problems of locomotion on land (Herreid & Fourtner, 1981). They possess different numbers of walking legs (four in a hermit crab to over 180 in a millipede), a variety of leg lengths and positions, numerous stepping patterns, different musculoskeletal arrangements (from muscle levers to hydraulics in spiders), a range of body shapes (long in millipedes and round in some crabs), different styles of locomotion (forwards *vs* sideways travel) and different oxygen transport systems (from gills to tracheae). Nevertheless, each solution must allow for the repeated generation of the necessary propulsive forces. Although the various potentials and limitations of particular locomotor designs have often been hypothesized (Manton, 1977), actual determinations of function that allow comparison are lacking. The following two papers quantify steady-state locomotor performance, so that the effects of variation in design can be delineated. The arthropod selected for this study was the eight-legged sideways travelling ghost crab, *Ocypode quadrata*. The present paper examines metabolic energy input and endurance capacity as a function of speed, body mass and ontogeny. A second paper (Blickhan & Full, 1987) describes the mechanics of locomotion, including the locomotor style, force production, and the mechanical energy output used to move the centre of mass.

Two important variables used to compare locomotor performance are the metabolic energy cost of locomotion and endurance capacity. The metabolic energy required for terrestrial locomotion has been best studied in mammals and birds as a function of body mass and speed (Taylor, Heglund & Maloiy, 1982). Metabolic energy during steady-state, submaximal exercise is derived primarily from aerobic metabolism (Seeherman, Taylor, Maloiy & Armstrong, 1981). In most species, steady-state oxygen consumption increases linearly with an increase in speed and the minimum amount of metabolic energy necessary to move 1 g of animal 1 km (C_{min}) is approached at the higher submaximal speeds (Taylor, Schmidt-Nielsen & Raab, 1970). C_{min} is a regular function of body mass (Taylor *et al.* 1982). Small vertebrates, on a per gram basis, demand more metabolic energy to travel a given distance. Undoubtedly, a suite of size-dependent constraints, such as the cost of muscle force production and the storage of elastic strain energy, determine the scaling of metabolic cost. If size-dependent constraints on metabolic cost are conservative among animals then C_{min} should scale intra- and interspecifically with body mass in a manner relatively independent of locomotor design. Ghost crabs are appropriate for examining intraspecific scaling of energetic cost, because individuals highly adapted for locomotion vary by nearly 40-fold in body mass (Hafemann & Hubbard, 1969; Warner, 1977) and have considerable aerobic capacity, in contrast to other crustaceans (Full & Herreid, 1983). Previous research on interspecific comparisons of mammals, birds, reptiles, an amphibian and some arthropods suggests that C_{min} is relatively independent of locomotor design (Bennett, 1982; Full, 1986; Herreid, 1981; Taylor *et al.* 1982). Determining C_{min} for a ghost crab with its unusual style of

locomotion can be used to examine this hypothesis for an arthropod design that is as large as that of some mammals, birds and reptiles.

Mammals and lizards appear to differ greatly in their maximal capacity to consume oxygen. In both groups, smaller animals attain maximal oxygen consumption ($\dot{V}_{O_2\max}$) at lower speeds than do larger animals (Taylor *et al.* 1980; Garland, 1982, 1983). However, the speed at $\dot{V}_{O_2\max}$ for a lizard is only one-tenth of that predicted for a mammal of the same mass (Garland, 1983). Assuming the capacity to consume oxygen is a major variable determining endurance at speeds near $\dot{V}_{O_2\max}$, then small animals of both groups should have a low endurance capacity. Lizards should fatigue at much lower speeds than mammals (Bennett & Ruben, 1979). If the patterns observed in lizards represent ectotherms in general, then ghost crabs should also fatigue at relatively slow speeds. Moreover, chitinous gills and an open circulatory system in crabs could severely restrict oxygen uptake (Taylor, 1982). If oxygen consumption is severely limited by the crustacean design, then crabs should possess only a modest endurance capacity, even in comparison to other ectotherms, such as lizards.

MATERIALS AND METHODS

Animals

Ocyropode quadrata (Fabricius) were collected from the beaches surrounding the Duke University Marine Laboratory in Beaufort NC, USA. Plastic containers filled with 50% sea water to a depth of 1 cm were used to house each crab. All animals were kept in an environmental chamber on an L:D 14 h:10 h photoperiod at 24°C and fed fresh fish 2–3 times a week. Only intermoult animals were used. Crabs were divided into three groups based on mass: small (2 g), medium (27 g) and large (71 g).

Aerobic metabolism

Oxygen consumption measurements

Ghost crabs were exercised on a treadmill which was enclosed in a respirometer. Three treadmills were used to accommodate crabs of different size. The chamber volumes were 125, 1432 and 2355 ml for small, medium and large crabs, respectively. \dot{V}_{O_2} was determined by open-flow respirometry. Air flow rate was 50 ml min⁻¹ for the small crabs, 300 ml min⁻¹ for the medium and 400 ml min⁻¹ for the large animals. Air leaving a chamber was dried (Drierite) and CO₂ was removed (soda lime). O₂ concentration was monitored with an oxygen analyser (S3A, Applied Electrochemistry), which was interfaced with an integrating chart recorder (Linear Instruments Model 282). Mass-specific, instantaneous \dot{V}_{O_2} was determined as described previously (Herreid, Prawel & Full, 1981b). All \dot{V}_{O_2} values were corrected to STP.

Sustained exercise

Crabs were given a 30-min rest period on the treadmill before exercise. Animals were exercised for 20 min at a single speed after the rest period. A 30-min recovery

period followed the exercise bout. \dot{V}_{O_2} was measured continuously during rest, exercise and recovery. Steady-state oxygen consumption ($\dot{V}_{O_{2ss}}$) was determined during the final 10 min of a 20-min exercise bout. The range of speeds selected, within a given mass range, was based on the animal's endurance and walking ability. The fastest speed was chosen so that animals could sustain the rate for 20 min, but when exercised longer fatigued shortly thereafter. The slowest speed represented the rate at which an animal could walk and maintain a consistent pace without undergoing extraneous movements. In most cases, each crab was exercised at every speed. An individual was tested only once a day.

Maximal \dot{V}_{O_2}

Maximal oxygen consumption ($\dot{V}_{O_{2max}}$) was determined by a progressive maximal test (Full & Herreid, 1983). Following a 30-min rest period, a crab was exercised at an intermediate to high speed. Upon attaining a steady-state oxygen consumption for 3 min, the speed of the treadmill belt was increased by 0.03 km h^{-1} until a new higher steady-state was attained. Three minutes after the new steady-state had been reached, speed was increased again. $\dot{V}_{O_{2max}}$ was defined as the \dot{V}_{O_2} attained when two consecutive incremental increases in speed resulted in no further increase in \dot{V}_{O_2} .

Anaerobic metabolism

The contribution of anaerobic metabolism to sustained exercise was determined by measuring lactate content. Crabs were given a 30-min rest period on the treadmill before exercise at a single speed. After the rest period or 5, 10, 15 or 20 min of exercise, crabs were quickly removed from the treadmill and frozen in liquid nitrogen (i.e. in 2–3 s). Experiments were immediately terminated if the crabs struggled at any time. After freezing, the whole body of small animals was completely pulverized in a mortar pre-cooled with liquid nitrogen. Animals of intermediate mass (16.3 g) were divided into parts (i.e. body, chelae and walking leg pairs) after the initial freezing. Each part was then pulverized and analysed separately. Tissue powder was placed in a perchloric acid solution and centrifuged. The concentration of L-lactate was determined by a spectrophotometric procedure (Sigma diagnostic kit no. 826-UV). The glycine–hydrazine buffer recommended was modified by adding EDTA and HCl to prevent drift in absorbance readings (Full & Herreid, 1984).

Endurance capacity

After a 10-min rest period on the treadmill, crabs were exercised to fatigue at a selected speed. Speeds ranged from 0.2 to 0.9 km h^{-1} . Crabs maintained a consistent pace without prodding until just before fatigue. An animal was considered fatigued when it failed to maintain pace with the treadmill belt, dragged its abdomen or did not respond to three successive prodding attempts. The experiment was halted if endurance time exceeded 2 h. Experiments during which crabs walked erratically or struggled were aborted.

RESULTS

*Aerobic metabolism**Resting \dot{V}_{O_2}*

The \dot{V}_{O_2} value during the final 15 min of the pre-exercise period was averaged to obtain the resting \dot{V}_{O_2} (Table 1). Mass-specific resting \dot{V}_{O_2} was a function of body mass:

$$\dot{V}_{O_2} = 0.16M_b^{-0.44} \quad (N = 41, \quad r^2 = 0.66),$$

where \dot{V}_{O_2} is in ml O₂ g⁻¹ h⁻¹ and M_b represents body mass in g (Fig. 1).

 \dot{V}_{O_2} kinetics

\dot{V}_{O_2} increased rapidly to a steady-state at the onset of exercise (Fig. 2). The time to attain 50% of the $\dot{V}_{O_{2ss}}$ ($t_{1/2on}$) was independent of speed ($F_{(2,32)} = 1.47$; $P = 0.24$), but was dependent on body mass ($F_{(2,32)} = 9.04$; $P = 0.001$). Crabs of intermediate mass (27 g) had a significantly lower $t_{1/2on}$ (28.2 s; $N = 5$) at high speed (87–92% of $\dot{V}_{O_{2max}}$) compared with medium-sized (2 g) (42.6 s; $N = 5$; $t = 3.0$; $P = 0.02$) and large (71 g) crabs (55.8 s; $N = 4$; $t = 2.5$; $P = 0.02$).

\dot{V}_{O_2} declined rapidly to resting rates after exercise. \dot{V}_{O_2} decreased to 10% of the resting \dot{V}_{O_2} at all speeds within 15 min. The largest crabs (71 g) would not become quiescent, therefore true recovery could not be determined.

 $\dot{V}_{O_{2ss}}$ vs speed

$\dot{V}_{O_{2ss}}$ was calculated by averaging \dot{V}_{O_2} for the last 10 min of exercise. $\dot{V}_{O_{2ss}}$ increased linearly with speed (Fig. 3; Table 1). The slopes of the regression equations, which represent the minimum amount of metabolic energy necessary to move 1 g of crab 1 km (C_{min}), decreased significantly with an increase in body mass (analysis of covariance, $P < 0.001$). y -intercept values were elevated compared to mean resting rates for all groups; 71-g crabs showed the greatest elevation – four-fold.

Maximal \dot{V}_{O_2}

Mass-specific $\dot{V}_{O_{2max}}$ decreased as a function of body mass (Fig. 1):

$$\dot{V}_{O_{2max}} = 1.70M_b^{-0.30} \quad (N = 15; \quad r^2 = 0.95).$$

$\dot{V}_{O_{2max}}$ was attained after 2–3 consecutive increases in speed. The speed at which $\dot{V}_{O_{2max}}$ was reached ($v\dot{V}_{O_{2max}}$) was a complex function of body mass. $v\dot{V}_{O_{2max}}$ was significantly greater for 27-g crabs of intermediate mass when compared to 71-g crabs ($t = 7.2$; $P < 0.001$). Small crabs (2 g) attained $\dot{V}_{O_{2max}}$ at the lowest speeds (Table 1).

The regression equations relating $\dot{V}_{O_{2max}}$ and $\dot{V}_{O_{2rest}}$ to body mass were significantly different ($t = 17.3$; $P < 0.003$). Large crabs (71 g) had greater aerobic factorial scopes ($\dot{V}_{O_{2max}}/\dot{V}_{O_{2rest}}$).

Table 1. Aerobic metabolism of the ghost crab at rest and during exercise as a function of body mass

Body mass (g)	$\dot{V}_{O_2,rest}$ (ml O ₂ g ⁻¹ h ⁻¹)	$\dot{V}_{O_2,ss}$ (ml O ₂ g ⁻¹ h ⁻¹) vs speed (v, km h ⁻¹)	y-int/ $\dot{V}_{O_2,rest}$	$\dot{V}_{O_2,max}$ (ml O ₂ g ⁻¹ h ⁻¹)	$\dot{V}_{O_2,max}/\dot{V}_{O_2,rest}$	$v\dot{V}_{O_2,max}$ (km h ⁻¹)
2.1 ± 0.26 (N = 5)	0.25 ± 0.02 (N = 15)	$\dot{V}_{O_2,ss} = 3.7v + 0.44$ (N = 15; r ² = 0.67)	1.7	1.60 ± 0.08 (N = 5)	6.4	0.33 ± 0.01 (N = 5)
26.9 ± 0.74 (N = 5)	0.12 ± 0.02 (N = 13)	$\dot{V}_{O_2,ss} = 0.86v + 0.18$ (N = 15; r ² = 0.76)	1.5	0.77 ± 0.02 (N = 5)	6.5	0.63 ± 0.01 (N = 5)
70.9 ± 3.49 (N = 5)	0.07 ± 0.006 (N = 14)	$\dot{V}_{O_2,ss} = 0.45v + 0.28$ (N = 21; r ² = 0.42)	4.0	0.56 ± 0.02 (N = 5)	8.0	0.56 ± 0.01 (N = 5)

All values are ± one standard error.

$\dot{V}_{O_2,rest}$, average oxygen consumption of an inactive animal during the 15 min prior to exercise.

$\dot{V}_{O_2,ss}$, average steady-state oxygen consumption determined during the final 10 min of a 20-min exercise bout.

y-int, y-intercept of the $\dot{V}_{O_2,ss}$ vs speed function.

$\dot{V}_{O_2,max}$, maximal \dot{V}_{O_2} attained when two increases in speed resulted in no further increase in \dot{V}_{O_2} .

$v\dot{V}_{O_2,max}$, speed at which maximal \dot{V}_{O_2} was attained.

Net lactate production

Whole body lactate (WBL) content in the 2-g crabs did not continue to increase after $\dot{V}_{O_{2ss}}$ had been attained, even at speeds eliciting 92% of $\dot{V}_{O_{2max}}$ (Fig. 4A). Pre-exercise WBL was $2.10 \pm 0.36 \mu\text{mol g}^{-1}$ ($N = 3$). No increase in WBL over pre-exercise levels occurred at the slow (57% of $\dot{V}_{O_{2max}}$; $F_{(2,6)} = 1.9$; $P = 0.22$) and medium (72% of $\dot{V}_{O_{2max}}$; $F_{(2,6)} = 3.7$; $P = 0.09$) exercise speeds. WBL content increased during the first 10 min of exercise at the fastest speed (92% of $\dot{V}_{O_{2max}}$), but decreased as exercise continued past 10 min.

WBL content of 16-g crabs depended on speed ($F_{(2,10)} = 40.6$; $P < 0.001$) and exercise duration ($F_{(1,10)} = 14.0$; $P < 0.005$). WBL increased over resting levels at 0.4 and 0.6 km h^{-1} (Fig. 4B). WBL content at 0.4 km h^{-1} after 20 min of exercise was not significantly greater than levels measured after 10 min ($t = 1.98$; $P = 0.073$). Net WBL production did not occur during $\dot{V}_{O_{2ss}}$ in 16-g crabs until exercise exceeded 68% of $\dot{V}_{O_{2max}}$ (Fig. 4B). This is actually a conservative estimate, because these crabs were smaller than the intermediate group (27 g) used for \dot{V}_{O_2} measurements and were therefore exercising at speeds closer to their maximal aerobic speed (i.e. >68% of $\dot{V}_{O_{2max}}$). WBL increased throughout the exercise period at 0.6 km h^{-1} . WBL was significantly greater during exercise at 0.6 km h^{-1} than at 0.4 km h^{-1} after both 10 ($t = 3.58$; $P = 0.005$) and 20 min ($t = 4.83$; $P = 0.001$).

Metabolic energy cost

The metabolic energy cost of locomotion for the ghost crab was dependent on body mass and speed (Fig. 3). Smaller, younger crabs used higher rates of oxygen

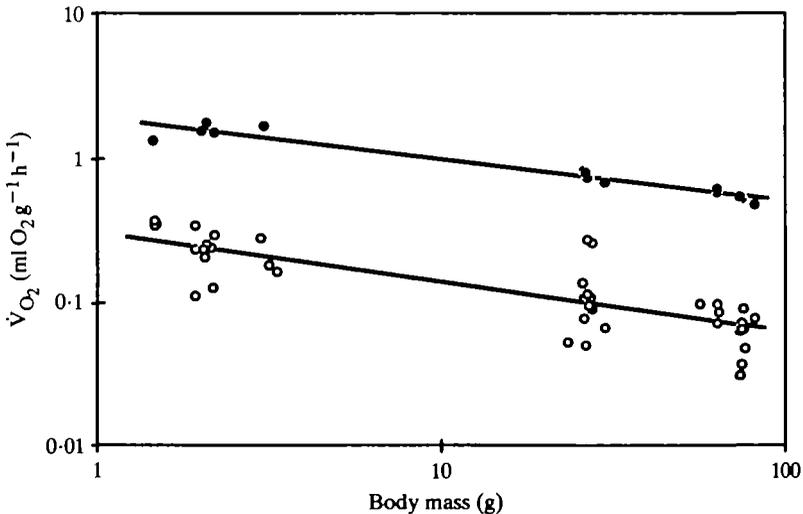


Fig. 1. Resting (○) and maximal (●) oxygen consumption (\dot{V}_{O_2}) of ghost crabs as a function of body mass. Ghost crabs have the capacity to elevate oxygen consumption six- to eight-fold over resting rates, typical of many vertebrates.

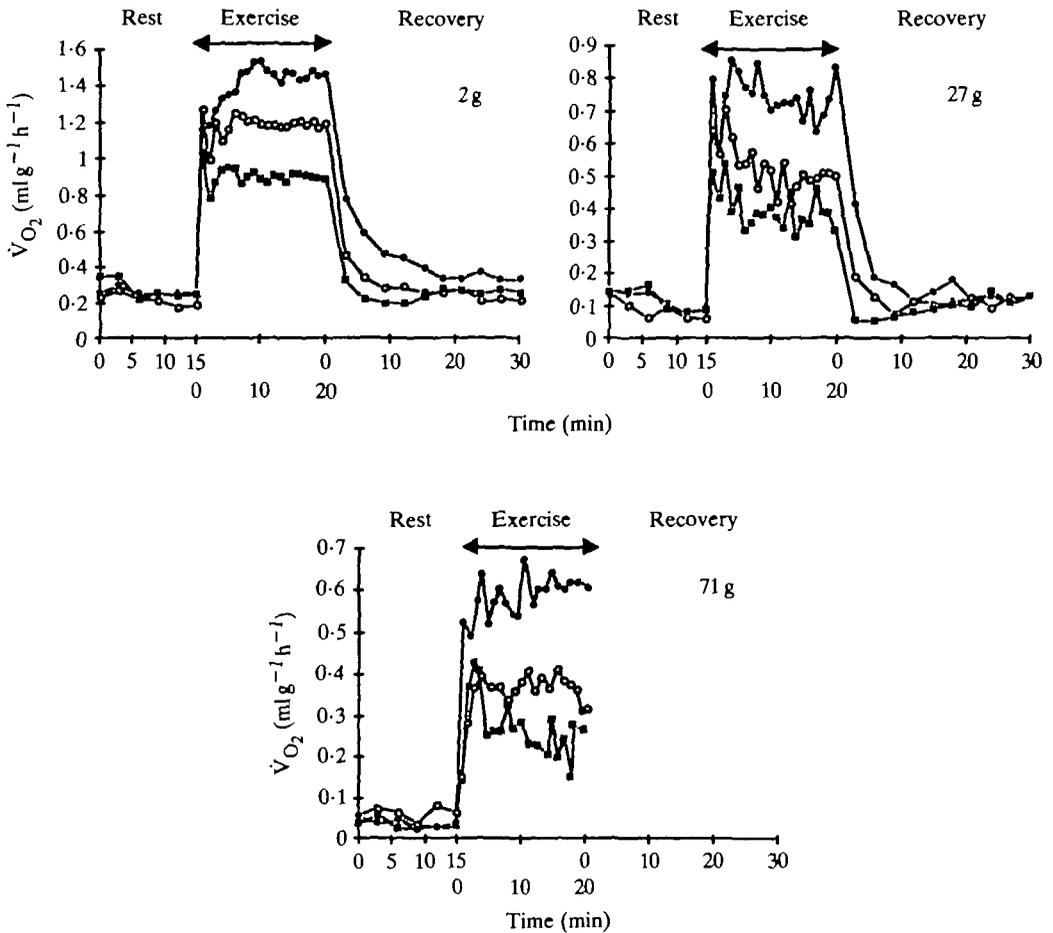


Fig. 2. Oxygen consumption (\dot{V}_{O_2}) kinetics during rest, exercise and recovery for crabs grouped by body mass. Low (■), medium (○) and high (●) exercise speeds are represented. Ghost crabs increase \dot{V}_{O_2} in time periods comparable to those observed in mammals and insects. (No recovery data were obtained on 71-g crabs because they would not become quiescent after exercise.)

consumption on a per gram basis at any speed. Elevated costs were due to (1) higher resting metabolic rates, (2) elevated y-intercepts (i.e. the intercept of the $\dot{V}_{O_{2,ss}}$ vs speed function compared to $\dot{V}_{O_{2,rest}}$) and (3) a steeper incremental increase in $\dot{V}_{O_{2,ss}}$ with an increase in speed (C_{min} , minimum cost of locomotion). Each component increased the total metabolic energy required to travel a given distance. Smaller crabs (2g) had the highest mass-specific $\dot{V}_{O_{2,rest}}$ and, therefore, the highest total mass-specific cost of locomotion at each speed ($C_t = \dot{V}_{O_{2,ss}}/\text{speed}$; Fig. 5). The largest crabs (71g) with the lowest mass-specific $\dot{V}_{O_{2,rest}}$ had the lowest C_t values, except at the low speeds. For crabs of all masses, C_t decreased with speed, because $\dot{V}_{O_{2,rest}}$ and the y-intercept became a smaller percentage of the total metabolic cost at the higher speeds.

Endurance capacity

Endurance time (T_{end}) decreased as exercise speed increased (Fig. 6). Crabs of intermediate mass (27 g) showed the greatest endurance capacity over the range of speeds tested ($T_{\text{end}} = 0.036v^{-4.02}$ where T_{end} is in h and v is in km h^{-1} ; $r^2 = 0.81$; analysis of covariance, $P < 0.001$), whereas the 2-g crabs had the poorest capacity ($T_{\text{end}} = 0.0097v^{-2.96}$; $r^2 = 0.82$). Large crabs (71 g) showed less stamina ($T_{\text{end}} = 0.019v^{-3.35}$; $r^2 = 0.80$) than 27-g animals.

DISCUSSION

Submaximal exercise

Aerobic metabolism

The ghost crab's rapid adjustment of O_2 uptake from the environment during submaximal exercise was comparable to other gas transport systems in meeting the O_2 demands of aerobic pathways in muscle, despite its reliance on gills and an open circulatory system. A $\dot{V}_{\text{O}_{2\text{ss}}}$ value was observed at all speeds (Fig. 2). The time required to attain 50% of $\dot{V}_{\text{O}_{2\text{ss}}}$ ($t_{1/2\text{on}} = 30\text{--}60\text{ s}$) was well within the range observed for mammals ventilating lungs ($t_{1/2\text{on}} = 25\text{--}90\text{ s}$; Cerretelli *et al.* 1979; Marconi *et al.* 1982), insects using tracheae ($t_{1/2\text{on}} = 30\text{--}180\text{ s}$; Herreid & Full, 1984)

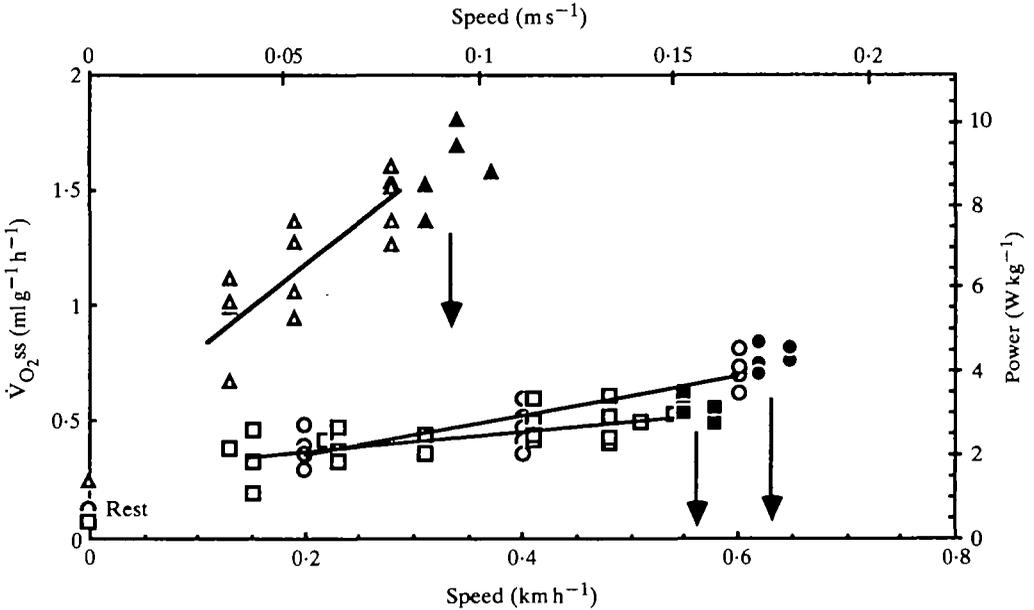


Fig. 3. Steady-state oxygen consumption ($\dot{V}_{\text{O}_{2\text{ss}}}$; open symbols) as a function of speed for 2- (Δ), 27- (\circ) and 71-g (\square) crabs. Resting rates are shown at zero speed. Closed symbols represent maximal oxygen consumption ($\dot{V}_{\text{O}_{2\text{max}}}$). Maximum aerobic speed is indicated by arrows. Maximum aerobic speed is the highest in crabs of intermediate mass (27 g). The minimum cost of transport (slope of line) decreases with an increase in body mass. The right-hand ordinate was calculated by using the conversion $1 \text{ ml O}_2 = 20.1 \text{ J}$.

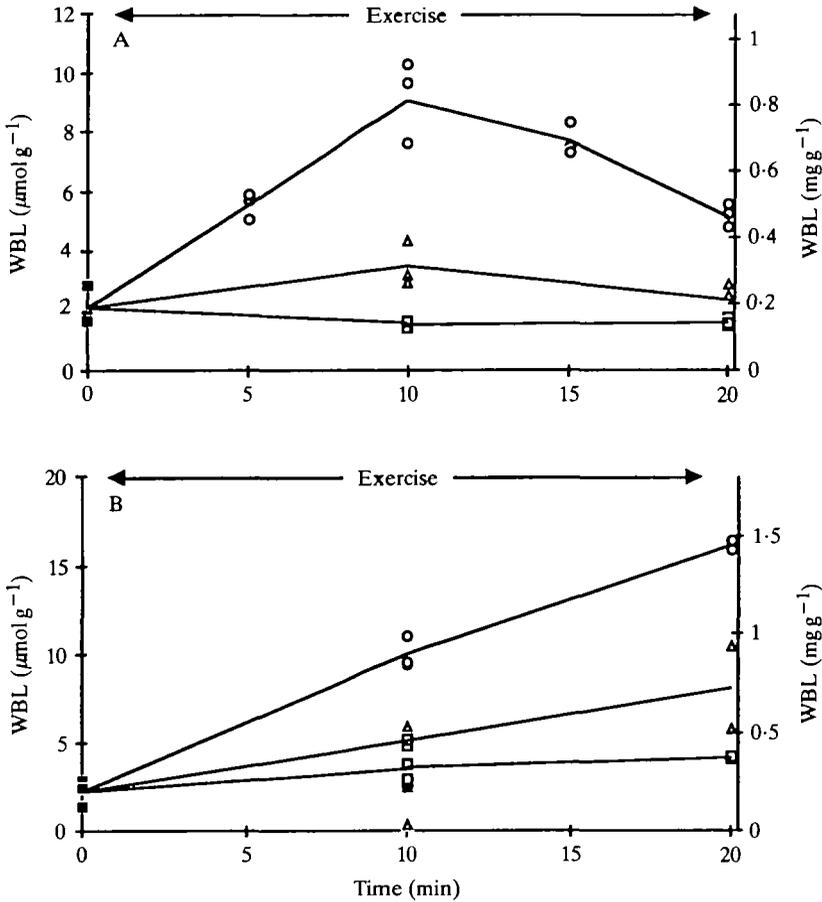


Fig. 4. (A) Whole body lactate content (WBL) during rest (■) and during exercise for 2-g crabs at 0.13 (□), 0.19 (△) and 0.28 km h⁻¹ (○). (B) Whole body lactate content during rest (■) and during exercise for 16-g crabs at 0.2 (□), 0.4 (△) and 0.6 km h⁻¹ (○). Each point represents a single animal. Both plots show that accelerated glycolysis plays only a minor role in energy production during submaximal exercise.

and another species of ghost crab, *O. gaudichaudii*, depending on gills ($t_{1/2on} = 50\text{--}150$ s; Full & Herreid, 1983). The \dot{V}_{O_2} kinetics of *O. quadrata* remained rapid as speed was increased to workloads near $\dot{V}_{O_{2max}}$. Furthermore, effective O_2 transport during submaximal exercise appears to be maintained as *O. quadrata* increases in body mass; $t_{1/2on}$ values for crabs varying in mass from 2 to 71 g were within the ranges for mammals and insects. It should be noted, however, that 71-g crabs did have significantly slower adjustments to $\dot{V}_{O_{2ss}}$ than smaller crabs, especially at speeds approaching $\dot{V}_{O_{2max}}$.

The slowest \dot{V}_{O_2} kinetics of ghost crabs were considerably faster than the sluggish responses seen in five other species of terrestrial and semiterrestrial crabs. In species of *Cardisoma*, *Uca* and *Gecarcinus* \dot{V}_{O_2} never attains a steady state during 10–20 min of treadmill exercise, even at slow speeds (Full & Herreid, 1984; Herreid, Lee & Shah, 1979; Herreid, O'Mahoney & Full, 1983; Wood & Randall, 1981a). In

humans, prolonged delays in achieving $\dot{V}_{O_{2ss}}$ (i.e. \dot{V}_{O_2} drift) have been correlated with increasing blood lactate levels and may result from hormonal and temperature changes (Davis, 1985). The actual mechanism behind the difference between ghost crabs and other crab species remains obscure. Nevertheless, the ghost crab's capacity to elevate \dot{V}_{O_2} rapidly was associated with a lesser dependence on anaerobic sources.

Anaerobic metabolism

Using net lactate production as an index, accelerated glycolysis in ghost crabs appears to play only a minor role in energy production during steady-state submaximal exercise, even at speeds at which 70–90% of $\dot{V}_{O_{2max}}$ was required (Fig. 4). These findings are consistent with previous studies on mammals and lizards (Seeherman *et al.* 1981; Seeherman, Dmi'el & Gleeson, 1983).

Rapid glycolysis can also contribute at the onset of submaximal exercise before O_2 uptake adjustments are completed. WBL content during submaximal exercise in ghost crabs increased during the first 10 min of exercise (Fig. 4); thereafter, WBL content declined or remained the same as a $\dot{V}_{O_{2ss}}$ was established. Studies on humans (Cerretelli, Pendergast, Paganelli & Rennie, 1979), mammals (Seeherman *et al.* 1981), lizards (Gleeson & Bennett, 1982), anuran amphibians (Taigen & Beuchat, 1984) and lungless salamanders (Full, 1986) have also shown lactate accumulation at

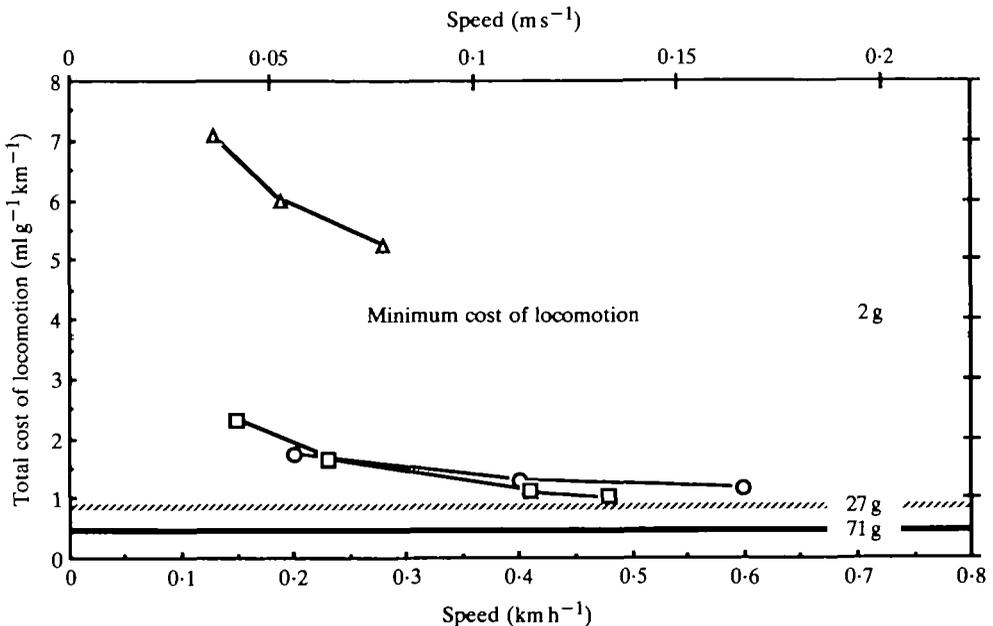


Fig. 5. Mass-specific cost of locomotion (C_t) as a function of speed for 2- (Δ), 27- (\circ) and 71-g (\square) crabs. The minimum mass-specific cost of locomotion (i.e. C_{min} , the slope of the steady-state oxygen consumption vs speed function) for each body mass is represented by a horizontal line and decreases with an increase in body mass. Large crabs (71 g) have total energetic costs similar to crabs of medium size (27 g) at slow speeds because 71-g crabs have an elevated y-intercept that is unusually high (see Fig. 3).

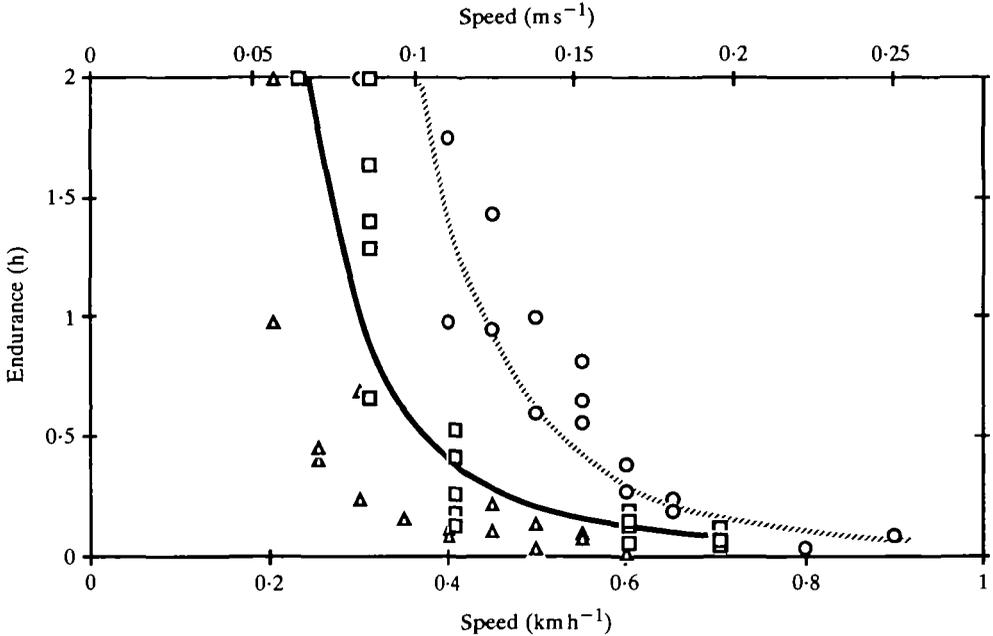


Fig. 6. Endurance time as a function of speed for 2- (Δ), 27- (\circ) and 71-g (\square) crabs. Endurance capacity was correlated with maximum aerobic speed (see Fig. 3). Crabs of 27 g showed the greatest endurance capacity. (Experiments were terminated after 2 h if the crab had not yet become fatigued.)

the beginning of submaximal exercise (i.e. $>50\% \dot{V}_{O_{2max}}$). Other crab species, such as *U. pugilator*, rely on rapid glycolysis early in exercise to a much greater extent. These crabs require near maximal rates of \dot{V}_{O_2} at all speeds and are unable to increase \dot{V}_{O_2} rapidly to a steady state during 10–20 min of exercise. The delay is similar to that measured in sedentary humans forced to exercise (Cerretelli *et al.* 1977, 1979). Just as in these untrained subjects, crabs also depend more on accelerated glycolysis to power exercise before $\dot{V}_{O_{2ss}}$ is attained. In fiddler crabs, 40–70% of the ATP requirement for a 15-min exercise bout is supplied by anaerobic metabolism (Full & Herreid, 1984).

Based on the patterns of aerobic and anaerobic metabolism in ghost crabs, it appears that any limitation in the rate of O_2 uptake during submaximal exercise is not necessarily inherent in the design of the crab's O_2 transport system. This conclusion is perhaps less surprising in the light of recent studies of lungless salamanders exercising on treadmills (Full, 1986). The increase in O_2 uptake for these diffusion-limited, lungless vertebrates is also relatively rapid ($t_{1/2O_2} = 100$ s), and accelerated glycolysis contributes little during $\dot{V}_{O_{2ss}}$ until $>85\%$ of $\dot{V}_{O_{2max}}$ is attained.

Maximal exercise

Extraordinarily different O_2 transport systems appear to have a similar capacity to increase O_2 delivery above resting rates. Ghost crabs depend on gills and an open circulatory system for O_2 transport during exercise. Yet $\dot{V}_{O_{2max}}$ is not different from

that predicted for an ectotherm, such as a lizard, of the same body mass and temperature (Bennett, 1982). *Ocypode quadrata* had the capacity to elevate its \dot{V}_{O_2} 6.4- to 8-fold over resting rates (Table 1). The capacity to increase \dot{V}_{O_2} was somewhat less than that of the ghost crab, *O. gaudichaudii* (12-fold; Full & Herreid, 1983), but was well within the range (5- to 15-fold) reported for mammals (Taylor *et al.* 1980), reptiles (Bennett, 1982) and even a lungless salamander (Full, 1986).

It should be emphasized that the factorial increase in \dot{V}_{O_2} depends on the ratio of $\dot{V}_{O_{2max}}$ to $\dot{V}_{O_{2rest}}$. Similar aerobic factorial scopes do not necessarily indicate a similar $\dot{V}_{O_{2max}}$. Factorial scopes can be elevated if $\dot{V}_{O_{2rest}}$ is low. For example, ghost crabs and lungless salamanders (Full, 1986) have a similar aerobic factorial scope, yet the $\dot{V}_{O_{2max}}$ of the salamander is only half that predicted for a ghost crab of a similar mass and body temperature. The high factorial scope is due to the fact that plethodontid salamanders have a very low $\dot{V}_{O_{2rest}}$ (Feder, 1976). Similar factorial scopes can also result from proportional increases in both $\dot{V}_{O_{2rest}}$ and $\dot{V}_{O_{2max}}$. The aerobic factorial scope of the ghost crab was comparable to that measured in mammals, even though the absolute $\dot{V}_{O_{2max}}$ is 20-fold greater in the mammal.

Above $\dot{V}_{O_{2max}}$, rapid glycolysis contributes throughout the exercise period in mammals (Seeherman *et al.* 1981), lizards (Seeherman *et al.* 1983) and lungless salamanders (Full, 1986). A similar dependence most probably existed for the 16-g *O. quadrata* at high speeds (0.6 km h^{-1}); WBL increased linearly during 20 min of exercise, but no direct measurements of $\dot{V}_{O_{2max}}$ were available for that body mass (Fig. 4B). Full & Prestwich (1986) have shown that both rapid glycolysis and depletion of high-energy phosphates contribute in ghost crabs at speeds demanding energy well above $\dot{V}_{O_{2max}}$ (i.e. $1.4\text{--}2.3 \text{ km h}^{-1}$ for a 27-g crab). Other crustacean species also show increases in lactate levels during vigorous exercise, presumably at or above $\dot{V}_{O_{2max}}$ (Burke, 1979; McDonald, McMahon & Wood, 1979; Wood & Randall, 1981b). Unfortunately, activity levels have seldom been quantified. During controlled exercise in fiddler crabs, WBL content increases at a constant rate throughout the exercise period at even relatively slow speeds ($0.06\text{--}0.16 \text{ km h}^{-1}$; Full & Herreid, 1984). In contrast to ghost crabs, other crustaceans have a relatively modest capacity to increase \dot{V}_{O_2} above their resting rates (i.e. 2- to 6-fold; McMahon, 1981). Consequently, they always appear to be exercising near $\dot{V}_{O_{2max}}$, even at relatively low levels of activity.

Metabolic energy cost

Small animals, regardless of their locomotor design, appear to demand more energy than larger animals to transport 1 g of body mass over a distance. Evidence for this statement has come from interspecific comparisons of adult mammals, birds, reptiles and some arthropods (Herreid, 1981; Bennett, 1982; Taylor *et al.* 1982). The present study suggests a similar intraspecific trend.

Elevated costs in small ghost crabs resulted from (1) higher resting metabolic rates, (2) elevated y-intercepts (i.e. the intercept of the $\dot{V}_{O_{2ss}}$ vs speed function compared to $\dot{V}_{O_{2rest}}$) and (3) a steeper incremental increase in $\dot{V}_{O_{2ss}}$ with an increase in speed (C_{min}). Metabolic maintenance costs are often subtracted in order to

compare animals of different body masses and temperatures. Certainly, the validity of these baseline subtractions is somewhat questionable (Stainsby, Gladden, Barclay & Wilson, 1980). For example, the resting metabolic component is often assumed to remain constant during exercise, even though this assumption is largely untested. Even with $\dot{V}_{O_2\text{rest}}$ removed, the 2-g crabs still demanded more energy than the larger crabs to move 1 g of their mass 1 km. This energy cost represents the net cost of transport (C_{net}), the amount of energy over rest required to move 1 g of animal 1 km. Surprisingly, the largest crabs (71 g) had a greater C_{net} than 27-g crabs at speeds up to 0.5 km h^{-1} . Intraspecific scaling of C_{net} did not follow interspecific trends (i.e. a decrease with increased body mass). The largest crabs (71 g) actually required higher net mass-specific rates of oxygen consumption at low speeds compared to crabs less than half their mass (Fig. 3). This resulted in the relatively large y-intercept to $\dot{V}_{O_2\text{rest}}$ ratio of 4.0 (Table 1). In birds and mammals, this ratio ranges from 0.4 to 2.3 (Fedak, Pinshow & Schmidt-Nielsen, 1974; Taylor *et al.* 1970). The reason for the relatively high energy costs at low speeds in large crabs (71 g) is unknown.

C_t and C_{net} both decreased at the high speed to a minimum (C_{min}) which equals the slope of the $\dot{V}_{O_2\text{ss}}$ vs speed relationship (Fig. 5). Two points are apparent from the C_{min} determination for ghost crabs. (1) The relationship between C_{min} and body mass was similar to that found for interspecific comparisons of adult mammals, birds, reptiles and some other arthropods (Herreid, 1981; Bennett, 1982; Taylor *et al.* 1982). A smaller crab requires a greater minimum amount of energy to move 1 g of its body 1 km. As ghost crabs grow larger, the energy cost of moving 1 g of their body a given distance at speeds near $\dot{V}_{O_2\text{max}}$ declines. (2) C_{min} appears to be relatively independent of locomotor design, even when sideways travelling octapedal arthropods are considered. C_{min} for ghost crabs fell within the 95% confidence interval of the relationship given for vertebrates (Fedak & Seeherman, 1979; Taylor *et al.* 1982). Additional support for this conclusion is found for six-legged insects (Herreid, 1981; Herreid, Full & Prawel, 1981a; Lighton, 1985), small Panamanian ghost crabs (Full & Herreid, 1983) and four-legged hermit crabs (Herreid & Full, 1985).

The present results are consistent with the hypothesis that the time course of force development and decay is the primary determinant of the metabolic cost of locomotion (Taylor, 1985), although this does not rule out the possibility that other size-dependent constraints are involved. Even though drastically different in design, crabs and vertebrates of a similar mass cycle their limbs, and therefore operate their muscles, at similar frequencies (Blickhan & Full, 1987).

Endurance

Endurance capacity correlates with the speed at which $\dot{V}_{O_2\text{max}}$ is attained. However, endurance capacity may not be a simple function of body mass within a species as has been described for interspecific comparisons. Endurance capacity in ghost crabs decreased exponentially with an increase in speed, just as is found in humans (Wasserman, VanKessel & Burton, 1967), lizards (John-Alder & Bennett, 1981) and other crab species (Wood & Randall, 1981a; Full & Herreid, 1983, 1984).

Yet endurance capacity did not increase regularly with body mass (Fig. 6). Instead, endurance capacity was correlated with the speed at which $\dot{V}_{O_2\max}$ was attained ($v\dot{V}_{O_2\max}$). In lizards (Bennett & John-Alder, 1984) endurance capacity also correlates with $v\dot{V}_{O_2\max}$. At speeds approaching the $v\dot{V}_{O_2\max}$, anaerobic metabolism supplements aerobic sources and endurance capacity declines. In mammals $v\dot{V}_{O_2\max}$ increases as a function of body mass (Taylor *et al.* 1980). Smaller mammals attain $\dot{V}_{O_2\max}$ at lower speeds, primarily due to a higher mass-specific C_{\min} . Lizards show a similar increase of $v\dot{V}_{O_2\max}$ with body mass, except that the absolute $v\dot{V}_{O_2\max}$ is only one-tenth of that predicted for a mammal of the same mass (Garland, 1982, 1983).

The ontogenetic comparison in ghost crabs did not follow the same relationships observed interspecifically for lizards and mammals. Crabs of intermediate mass (27 g) had the highest $v\dot{V}_{O_2\max}$ and the best endurance capacity. The 2-g crabs had a high mass-specific C_{\min} , as do other small animals, and therefore had a lower $v\dot{V}_{O_2\max}$ and the poorest endurance. The largest crabs (71 g) had a low mass-specific C_{\min} , but used large amounts of energy even at slow speeds (i.e. an elevated y-intercept). As a result, 71-g crabs attained $\dot{V}_{O_2\max}$ at lower speeds than did 27-g crabs. The largest crabs (71 g) were able to sustain speeds for only 1/2–1/3 as long as a crab half their mass (e.g. 0.4 km h⁻¹ for 30 min).

Overall $\dot{V}_{O_2\max}$ and $v\dot{V}_{O_2\max}$ for ghost crabs were similar to values found for lizards (Garland, 1982, 1983), but were much lower than the values predicted for mammals. Ghost crabs (30–70 g) use a walking gait as speed is increased up to 1.4 km h⁻¹, where they switch to a slow run (Blickhan & Full, 1987). In marked contrast to mammals, ghost crabs attained $\dot{V}_{O_2\max}$ at speeds ($v\dot{V}_{O_2\max} \approx 0.6$ km h⁻¹) below this transition from a walk to a slow run, at approximately the mid-speed used for a walk. For animals locomoting within a gait, such as walking in humans (Margaria, Cerretelli, Aghemo & Sassi, 1963) and horses (Hoyt & Taylor, 1981), the minimum energy cost to travel a given distance is found near the mid-speed for that gait. This speed is also the operating speed preferred by the animal. At higher or lower speeds within the gait, the metabolic cost per unit distance increases. A similar situation could exist in crabs. The speed at which $\dot{V}_{O_2\max}$ was attained corresponds to the range of speeds over which a pendulum-like mechanism minimizes mechanical and probably metabolic energy (Blickhan & Full, 1987). At faster walking speeds, the energy-conserving mechanism becomes less effective in minimizing energy cost, and additional metabolic energy must be supplied by anaerobic sources because $\dot{V}_{O_2\max}$ is exceeded. Ghost crabs can change gaits and run at speeds 20 times faster, but only for short periods and with the aid of anaerobic metabolism.

Many thanks to C. F. Herreid for all phases of this work and to William Kirby-Smith for the collection of animals.

REFERENCES

- BENNETT, A. F. (1982). The energetics of reptilian activity. In *Biology of Reptilia*, vol. 13 (ed. C. Gans & F. H. Pough), pp. 155–199. New York: Academic Press.

- BENNETT, A. F. & JOHN-ALDER, H. B. (1984). The effect of body temperature on the locomotor energetics of lizards. *J. comp. Physiol.* **155**, 21–27.
- BENNETT, A. F. & RUBEN, J. A. (1979). Endothermy and activity in vertebrates. *Science* **206**, 649–654.
- BLICKHAN, R. & FULL, R. J. (1987). Locomotion energetics of the ghost crab. II. Mechanics of the centre of mass during walking and running. *J. exp. Biol.* **130**, 155–174.
- BURKE, E. M. (1979). Aerobic and anaerobic metabolism during activity and hypoxia in two species of intertidal crabs. *Biol. Bull. mar. biol. Lab., Woods Hole* **156**, 157–168.
- CERRETELLI, P., PENDERGAST, D., PAGANELLI, W. C. & RENNIE, D. W. (1979). Effects of specific training on \dot{V}_{O_2} on-response and early blood lactate. *J. appl. Physiol.* **47**, 761–769.
- CERRETELLI, P., SHINDELL, D., PENDERGAST, D. P., DI PRAMPERO, P. E. & RENNIE, D. W. (1977). Oxygen uptake transients at the onset and offset of arm and leg work. *Respir. Physiol.* **30**, 81–97.
- DAVIS, J. A. (1985). Anaerobic threshold: review of the concept and directions for future research. *Med. Sci. Sports Exerc.* **17**, 6–18.
- FEDAK, M. A., PINSHOW, B. & SCHMIDT-NIELSEN, K. (1974). Energy cost of bipedal running. *Am. J. Physiol.* **227**, 1038–1044.
- FEDAK, M. A. & SEEHERMAN, H. J. (1979). Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature, Lond.* **282**, 713–716.
- FEDER, M. E. (1976). Lunglessness, body size, and metabolic rate in salamanders. *Physiol. Zool.* **49**, 398–406.
- FULL, R. J. (1986). Locomotion without lungs: energetics and performance of a lungless salamander, *Plethodon jordani*. *Am. J. Physiol.* **251**, R775–R780.
- FULL, R. J. & HERREID, C. F. (1983). The aerobic response to exercise of the fastest land crab. *Am. J. Physiol.* **244**, R530–R536.
- FULL, R. J. & HERREID, C. F. (1984). Fiddler crab exercise: the energetic cost of running sideways. *J. exp. Biol.* **109**, 141–161.
- FULL, R. J. & PRESTWICH, K. N. (1986). Anaerobic metabolism of walking and bouncing gaits in ghost crabs. *Am. Zool.* **26**, 88A.
- GARLAND, T. (1982). Scaling maximal running speed and maximal aerobic speed to body mass in mammals and lizards. *Physiologist* **25**, 388.
- GARLAND, T. (1983). The relationship between maximal running speed and body mass in terrestrial mammals. *J. Zool., Lond.* **199**, 157–170.
- GLEESON, T. T. & BENNETT, A. F. (1982). Acid–base imbalance in lizards during activity and recovery. *J. exp. Biol.* **98**, 439–453.
- HAFEMANN, D. R. & HUBBARD, J. I. (1969). On the rapid running of ghost crabs (*Ocypode ceratophthalma*). *J. exp. Zool.* **170**, 25–32.
- HERREID, C. F. (1981). Energetics of pedestrian arthropods. In *Locomotion and Energetics in Arthropods* (ed. C. F. Herreid & C. R. Fournier), pp. 491–526. New York: Plenum Press.
- HERREID, C. F. & FOURTNER, C. R. (1981). *Locomotion and Energetics in Arthropods*. New York: Plenum Press.
- HERREID, C. F. & FULL, R. J. (1984). Cockroaches on a treadmill: aerobic running. *J. Insect Physiol.* **30**, 395–403.
- HERREID, C. F. & FULL, R. J. (1985). Energetics of hermit crabs during locomotion: the cost of carrying a shell. *J. exp. Biol.* **120**, 297–308.
- HERREID, C. F., FULL, R. J. & PRAWEL, D. A. (1981a). Energetics of cockroach locomotion. *J. exp. Biol.* **94**, 189–202.
- HERREID, C. F., LEE, L. W. & SHAH, G. M. (1979). Respiration and heart in exercising land crabs. *Respir. Physiol.* **36**, 109–120.
- HERREID, C. F., II, O'MAHONEY, P. J. & FULL, R. J. (1983). Locomotion in land crabs: respiratory and cardiac response of *Gecarcinus lateralis*. *Comp. Biochem. Physiol.* **74A**, 117–124.
- HERREID, C. F., PRAWEL, D. A. & FULL, R. J. (1981b). Energetics of running cockroaches. *Science* **212**, 331–333.
- HOYT, D. F. & TAYLOR, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature, Lond.* **292**, 239–240.
- JOHN-ALDER, H. B. & BENNETT, A. F. (1981). Thermal dependence of endurance and locomotory energetics in a lizard. *Am. J. Physiol.* **241**, R342–R349.

- LIGHTON, J. R. B. (1985). Minimum cost of transport and ventilatory patterns in three African beetles. *Physiol. Zool.* **58**, 390–399.
- MCDONALD, D. G., MCMAHON, B. R. & WOOD, C. M. (1979). Analysis of acid–base disturbances in the haemolymph following strenuous activity in the Dungeness crab, *Cancer magister*. *J. exp. Biol.* **79**, 47–58.
- MCMAHON, B. R. (1981). Oxygen uptake and acid–base balance in decapod crustaceans. In *Locomotion and Energetics in Arthropods* (ed. C. F. Herreid & C. R. Fournier), pp. 299–335. New York: Plenum Press.
- MARCONI, C., PENDERGAST, D., SELYK, P., RENNIE, D. W. & CERRETELLI, P. (1982). Dynamical and steady-state metabolic changes in running dogs. *Respir. Physiol.* **50**, 93–110.
- MARGARIA, R., CERRETELLI, P., AGHEMO, P. & SASSI, G. (1963). Energy cost of running. *J. appl. Physiol.* **18**, 367–370.
- MANTON, S. M. (1977). *The Arthropods*. London: Clarendon Press.
- SEEHERMAN, H. J., DMI'EL, R. & GLEESON, T. T. (1983). Oxygen consumption and lactate production in varanid and iguanid lizards: a mammalian relationship. *Int. Ser. Sports Sci.* **13**, 421–427.
- SEEHERMAN, H. J., TAYLOR, C. R., MALOIY, G. M. O. & ARMSTRONG, R. B. (1981). Design of the mammalian respiratory system: measuring maximum aerobic capacity. *Respir. Physiol.* **44**, 11–24.
- STAINSBY, W. N., GLADDEN, L. B., BARCLAY, J. K. & WILSON, B. A. (1980). Exercise efficiency; validity of base-line subtractions. *J. appl. Physiol.* **48**, 518–522.
- TAIGEN, T. L. & BEUCHAT, C. A. (1984). Anaerobic threshold of anuran amphibians. *Physiol. Zool.* **57**, 641–647.
- TAYLOR, C. R. (1985). Force development during sustained locomotion: a determinant of gait, speed and metabolic power. *J. exp. Biol.* **115**, 253–262.
- TAYLOR, C. R., HEGLUND, N. C. & MALOIY, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 1–21.
- TAYLOR, C. R., MALOIY, G. M. O., WEIBEL, E. R., LANGMAN, V. A., KAMAU, J. M. Z., SEEHERMAN, H. J. & HEGLUND, N. C. (1980). Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respir. Physiol.* **44**, 25–37.
- TAYLOR, C. R., SCHMIDT-NIELSEN, K. & RAAB, J. L. (1970). Scaling of energetic cost to body size in mammals. *Am. J. Physiol.* **210**, 1104–1107.
- TAYLOR, E. W. (1982). Control and co-ordination of ventilation and circulation in crustaceans; responses to hypoxia and exercise. *J. exp. Biol.* **100**, 289–319.
- WARNER, G. F. (1977). *The Biology of Crabs*. New York: Van Nostrand Reinhold. 202 pp.
- WASSERMAN, K., VANKESSEL, A. L. & BURTON, G. G. (1967). Interaction of physiological mechanisms during exercise. *J. appl. Physiol.* **22**, 71–85.
- WOOD, C. M. & RANDALL, D. J. (1981a). Oxygen consumption and carbon dioxide exchange during exercise in the land crab (*Cardisoma carnifex*). *J. exp. Zool.* **218**, 7–16.
- WOOD, C. M. & RANDALL, D. J. (1981b). Haemolymph gas transport, acid–base regulation, and anaerobic metabolism during exercise in the land crab (*Cardisoma carnifex*). *J. exp. Zool.* **218**, 23–35.