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Oxygen and Carbon Dioxide Exchange During Exercise in the Land Crab (*Cardisoma carnifex*)

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ABSTRACT In *Cardisoma carnifex* exercised on a treadmill, there is an inverse relationship between velocity and log fatigue time; crabs run indefinitely at 0.2 body lengths/second, for ≃5 minutes at 0.5 BL/second, and for only ≃30 seconds at burst speeds of 2.2 BL/second. Respiration was studied at rest and after 10 minutes of either mild (0.2 BL/second) or severe (exhausting, 0.5 BL/second) exercise. Gas exchange occurs in large branchial chambers that contain gills and are lined with a respiratory epithelium. The chambers are partially filled with water, and are ventilated with air by forward scaphognathite pumping. Motions of the flabellae, gills, and branchial chamber wall mix the air and water phases. CO_2, but not O_2, equilibrates between the phases, so the water represents a significant CO_2 sink. At rest, the scaphognathites beat in short, often unilateral bursts, and air flow is intermittent. O_2 utilization is >11.4%, the ventilatory convection requirement is ≃1.3 L air/mMole O_2, the gas exchange ratio (R) is ≃0.6, the O_2 diffusing capacity is ≃0.4 μmole $O_2 \cdot kg^{-1}\ min^{-1} \cdot torr^{-1}$, or about 10% of the CO_2 diffusing capacity, and P_{O_2} and P_{CO_2} gradients across the respiratory surface are comparable to those in air-breathing ectothermic vertebrates. During exercise, scaphognathite activity becomes bilateral and continuous, ventilation rises, utilization falls, and gas tensions in the branchial chamber approach those in the inspired air. Heart rate rises slightly. $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ increase 2–5×, the latter to a greater extent, and a considerable O_2 debt is incurred. R rises above 1.0 as metabolic acidosis converts bicarbonate stores to CO_2. The increases in $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ reflect both elevations of the diffusion gradients and approximate doublings of the O_2 and CO_2 diffusing capacities. All changes are more marked during severe than during mild exercise, but the patterns are similar.

The decapod crustaceans are the largest arthropods to invade land, but this evolutionary line toward terrestriality has been much less successful overall than the vertebrate line. The comparative physiology of terrestrial adaptation and air breathing in the two groups may reveal some important principles. Over the past 50 years, an extensive literature on the biology of land crabs has accumulated (for reviews see Edney, '60; Bliss, '68; Bliss and Mantel, '68; Warner, '77; Bliss et al., '78). Most of the early studies dealt with general biology, morphometrics, and reproduction (e.g., Pearse, '29; Gray, '57; Gifford, '62; Herreid and Gifford, '63). More recent work has focused on ion and water balance (e.g., Gross, '63; Skinner, '65; Gross et al., '66; Gifford, '68; Herreid, '69a, b; Harris, '77) and cardiorespiratory function (eg., Redmond, '62, '68a, b; Young, '73; Cameron and Mecklenburg, '73; Cameron, '75; Diaz and Rodriguez, '77; Shah and Herreid, '78; Herreid et al., '79a, b; Smatresk et al., '79; McMahon and Burggren, '79). The brachyuran family Gecarcinidae has received by far the largest attention with approximately equal emphasis on the genera *Gecarcinus* and *Cardisoma*.

The cardiorespiratory studies on the *Gecarcinidae* have each dealt with isolated features of the overall gas transport system, rather than its integrated function. Nevertheless, there have been some surprising and intriguing findings. For example, there are reports of extremely high haemocyanin O_2 affinity and low in vivo P_{O_2}'s (Redmond, '62, '68a), massive ventilation volumes with minimal O_2 extrac-

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tions (Cameron and Mecklenburg, '73; Cameron, '75; Herreid, et al., '79b), unusually low respiratory quotients in resting animals and unusually high values in exercising animals (Herreid et al., '79a), a decrease in heart rate during exercise (Herreid et al., '79a), and a postexercise acid-base disturbance of unknown origin (Smatresk et al., '79). The Alpha Helix Expedition to Palau offered us an opportunity to check some of these findings and to attempt a detailed analysis of the respiratory gas transport system in *Cardisoma carnifex*. To our knowledge, the respiratory physiology of this species has not previously been examined.

We have concentrated on the responses to exercise because the problems of gas exchange and transport should become most acute at this time. Furthermore, the recent studies of McDonald et al. ('79) and McMahon *et al.* ('79) on exercise responses in the aquatic brachyuran *Cancer magister* provide a useful point of reference for the water-breathing situation. We have devoted particular attention to CO_2 excretion and associated acid-base balance because this process must change markedly during the transition from water to air breathing. In water, the CO_2 capacitance is about 30 times the O_2 capacitance, so CO_2 is easily washed out at the gills in the process of O_2 acquisition. However, in air, CO_2 and O_2 capacitances are equal, so CO_2 excretion must become more efficient if in vivo P_{CO_2}'s are to be kept low.

This first in a series of three papers deals with general observations on the animal, an assessment of its exercise performance, a description of its respiratory system, and an analysis of ventilation, heart rate, and gas exchange between air and haemolymph at rest and after forced running activity on a treadmill. Subsequent papers will deal with haemolymph gas transport and acid-base regulation (Wood and Randall, '81) and the mechanism of CO_2 excretion (Randall and Wood, '81) during rest and exercise.

Symbols employed for respiratory parameters in this and the following papers (Wood and Randall, '81; Randall and Wood, '81) follow the system of Dejours ('75), and are defined in the text when first employed.

MATERIALS AND METHODS

Common land crabs, *Cardisoma carnifex*, were collected by hand from the shores of Palau in the Western Caroline Islands during August 1979. On board the R.V. Alpha Helix, they were held in 1–2 cm of 50% seawater at 25 ± 1°C for several days prior to use. All experiments were performed at the holding temperature.

Operative procedures

Prior to operation, the chelipeds were taped shut permanently with no apparent ill effects. Operations were performed while the crab was restrained on a board with rubber bands. For the standard exercise experiments, crabs (N = 14; 250–500 g) were fitted with bilateral branchial and expired cannulae, bilateral scaphognathite rate electrodes, a set of heart rate electrodes, and an arterial sampling membrane. Two additional animals were fitted with branchial chamber windows, and one crab received a ventilation collection mask. A separate group of crabs (N = 16, 100–350 g) were used for the O_2 consumption, CO_2 production, and Diamox experiments. These animals were fitted with only arterial sampling membranes or with nothing at all.

A dental drill was used to pierce 2-mm diameter holes through the carapace to the underlying epithelium on either side of each scaphognathite (anterio ventral surface of the crab) and the heart (dorsal surface). Insulated wires were anchored into the epithelium in each set of holes to detect heart and scaphognathite activity. Each pair of wires was threaded through an 80-cm length of Clay-Adams PE 60 polyethylene tubing in order to avoid tangling. Similar holes were drilled through the dorsolateral margins of the carapace and epithelium into each branchial chamber. A catheter consisting of 1 cm of PE 60 was inserted through each hole. A much larger length of PE 160 (80 cm) was heat-flattened at its distal end, fitted over the PE 60, and sealed flush to the carapace over the hole with latex dental dam and cyanoacrylate glue. Bilateral expired cannulae (80 cm) were constructed by heat moulding PE 60 so as to lie along the anterioventral surface of the carapace and curve into the exhalent channels behind the third maxillipeds. All these leads were firmly anchored to the carapace with strips of dental dam and cyanoacrylate glue and tied together dorsally to prevent any interference with locomotion. Another hole was drilled over the anterior margin of the pericardium, care being taken not to pierce the epithelium. The hole was sealed with several layers of dam and served as an arterial sampling site (McDonald et al., '79). After the operation, the crab was placed in a darkened individual chamber (20 × 30 × 50 cm high) filled with 1–2 cm of 50% seawater and allowed to recover for at least 24 hours.

Branchial chamber windows (cf. Hughes et al., '69) were installed by removing an oval section (approximately 4 × 6 cm) of carapace and underlying epithelium from the lateral

border of the right branchial chamber. The bleeding epithelium was cauterized. A clear Butyrex sheet was cut to size and sealed airtight over the hole with dam and cyanoacrylate glue. A ventilation mask constructed of Butyrex and dental dam almost identical in design to that of McMahon et al., ('79) was fitted to the anterior surface of one animal. This isolated the exhalent apertures from the inhalent channels over the legs so that all expired air passed out through a hole in the anterior surface of the mask.

Exercise procedure

Crabs were exercised on a canvas treadmill 30 cm wide × 45 cm long enclosed in a Perspex chamber. The anterior half of the chamber was shielded with black plastic, and the posterior half was patterned with vertical black stripes and bathed in strong light. Crabs generally ran so as to maintain their position in the anterior darkened "refuge," falling back into the light only when close to fatigue. The speed of the treadmill was continuously variable from 0 to 35 cm/second. The velocity-versus-fatigue time relationship (Fig. 1) was defined with 15 unoperated crabs, most exercised at only one speed. A few were retested at a different speed after 24 hours' recovery. Two experimental velocities were selected on the basis of this relationship: 0.2 body lengths/second (≈4.5 cm/second; mild, sustainable exercise) and 0.5 body lengths/second (≈11.0 cm/second; severe, exhausting exercise), each imposed for 10 minutes. At the higher speed, crabs invariably fatigued before the end of the period, but were forced to continue activity by manual prodding for the whole 10 minutes to ensure complete exhaustion. Some of the experimental crabs were tested at both speeds, but at least 24 hours intervened between the two runs.

Experimental procedures

Standard Exercise Experiments. Prior to an experiment, the holding chamber was drained, the catheters were led outside, and the electrodes were connected to recording devices. The crab was then allowed to recover from this disturbance for about 1 hour. After control measurements at rest, the crab was transferred to the treadmill and immediately exercised for 10 minutes. Subsequent measurements were taken at 0, 0.5, 1, 2, 4, 6, and 24 hours postexercise. The animal was returned to its holding chamber between the 0 and 0.5 hour samples. At each time, heart (f_H) and scaphognathite rates (f_S) were recorded, gas samples were taken from the holding chamber (inspired air), left and right exhalent cannulae, and left and right branchial cannulae, and venous and arterial haemolymph samples were withdrawn in the order stated. The branchial catheters were plugged between samples. Gas samples (≈3 ml) were taken in plastic syringes, and haemolymph samples (generally 500 μl) were drawn anaerobically into ice-cold glass syringes from the pericardial sampling site (arterial blood) and from the arthrodial membrane over the infrabranchial sinus at the base of a walking leg (venous blood). Rapid processing was essential to prevent clotting as no anticoagulant was used.

O_2 Consumption and CO_2 Production Experiments. Respirometers (1 L beakers) were shielded with black plastic and sealed with rubber bungs fitted with gas sampling ports. O_2 consumption ($\dot{M}_{O_2}$) and CO_2 production ($\dot{M}_{CO_2}$) were calculated from changes in P_{O_2} and P_{CO_2} over time and the known volume of the system. Animals were placed in the respiromters at least 6 hours before the start of an experiment. Control resting values were recorded over two successive 1-hour periods. The crab was then transferred to the treadmill, exercised as described above, and immediately returned to its respirometer. $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ were measured over the following postexercise periods: 0–0.25, 0.05–0.8, 1.0–1.5, 2.0–2.75, 4–5, and 6–7 hours.

Analytical and recording techniques

Heart and scaphognathite activities were recorded from electrodes attached to Biocom 2991 impedance converters. Branchial chamber pressures were measured by connecting a branchial catheter to one side of a Hewlett Packard 270 differential air pressure transducer. In the crab fitted with a mask, ventilatory air flow ($\dot{V}_a$) was recorded by sealing a hot-wire anemometer probe (Thermonetics) into the mask outflow. The anemometer was custom built and very similar to that described by Cameron and Mecklenburg ('73). Instantaneous velocity (calibrated to flow) and integrated mean flow could be recorded simultaneously; the outputs were linear over the range of flows measured here. All signals were displayed on a Gilson 1CT-5H four-channel recorder writing on rectilinear coordinates.

Gas samples were analyzed for P_{O_2} and P_{CO_2}. All haemolymph samples were analyzed for P_{O_2}, P_{CO_2}, total CO_2 (C_{CO_2}), pH, lactate, and pyruvate levels in the standard exercise experiments, and for P_{CO_2}, C_{CO_2}, and pH in the Diamox experiments. [HCO_3^-] was calculated

as $C_{CO_2} - \alpha_{CO_2} \cdot P_{CO_2}$ using a value of α_{CO_2} at 25°C from Truchot ('76). Oxygen capacities ($C_{O_2}^{max}$) were determined on the control and 24-hour samples, and haemolymph nonbicarbonate buffer capacity (β) on most 24-hour samples. Some samples were also assayed for ammonia, Na^+, Cl^-, and Ca^{++} concentrations.

P_{O_2}, P_{CO_2}, and pH were measured with Radiometer microelectrodes at experimental temperature connected to a Radiometer PHM 71 MK 2 acid-base analyzer. The pH electrodes were calibrated with Radiometer precision buffers, the P_{O_2} electrode with humidified air and N_2, and the P_{CO_2} electrode with humidified gas mixtures from Wösthoff gas mixing pumps. Sample replacement was employed as recommended by Boutilier et al. ('78). C_{CO_2} was determined by the method of Cameron ('71). Enzymatic assays were employed for lactate (lactic dehydrogenase/NADH), pyruvate (lactic dehydrogenase/NAD), and ammonia (l-glutamate dehydrogenase/NAD) with Sigma reagents and micromodifications of the recommended protocols (Sigma, '77a, b). Haemolymph $[Na^+]$ and $[Ca^{++}]$ were determined by flame photometry (EEL Mark II and Coleman 20, respectively), appropriate swamping being used to remove the interference of Na^+ on Ca^{++} emission. Cl^- was determined by coulometric titration (Radiometer CMT 10).

Haemolymph used for O_2 and buffer capacity measurements was allowed to clot, disrupted by vigorous shaking, and then centrifuged at 10,000g for 5 minutes to remove the clot. $C_{O_2}^{max}$ was determined by equilibrating the sample with air and analyzing for total O_2 content with a "Lex-O_2-Con" analyzer (Lexington Instruments) calibrated according to the corrective procedure of Wood et al. ('79). Oxygen contents of haemolymph in vivo (C_{O_2}) and percentage saturation of the haemocyanin (S_{O_2}) were estimated from the measured values for $C_{O_2}^{max}$, P_{O_2}, and pH, and a family of haemolymph O_2 dissociation curves at different pH's supplied by W.W. Burggren and B.R. McMahon (personal communication). O_2 physically dissolved in the haemolymph was taken into account in these calculations with a value of α_{O_2} equal to that of 75% seawater at 25°C (Dejours, '75) as the osmotic concentration of *Cardisoma carnifex* haemolymph is 600–1,000 mOsm/L (R.R. Harris and G. Kormanik, personal communication). Nonbicarbonate buffer capacities (β) and CO_2 content curves were determined by in vitro tonometry (cf. McDonald et al., '79) with gas mixtures of P_{CO_2} = 7.3, 14.6, 29.2 and 58.4 torr. β was calculated as the slope of the $[HCO_3^-]$ vs. pH line ($\Delta HCO_3^-/\Delta pH$).

Branchial chamber volume was determined in nine crabs at autopsy by weighing the animals before and after filling their branchial chambers with Branch-o-fil (identical to batch 7908 of Hunt's Tomato Ketchup produced by Hunt-Wesson Foods, Inc., Fullerton, California). One gram of Branch-o-fil had a volume of 0.8691 ml at 25°C.

Data analysis

All data are reported as means ± 1 standard error (N) where N represents the number of different animals contributing to the mean. The significance ($P \leq 0.05$) of changes within an experimental group was determined by the Student's paired two-tailed t-test, with each crab as its own control. Differences between groups ($P \leq 0.05$) were assessed by Student's unpaired two-tailed t-test. Where linear regression relationships are employed, the significance level of the correlation coefficient is given.

RESULTS

Exercise performance

On the treadmill, crabs ran with their bodies raised high above the surface. They normally ran sideways, with one side leading, then reversed their body position so the other side led. As time went on, they ran backward and then finally forward before collapsing. Exhaustion was preceded by an inability to keep the abdomen elevated; when fatigued, they literally dragged their bodies on the ground. The alterations of position probably help to extend running time by switching from one set of muscles to another. As locomotion was predominantly sideways, velocity has been expressed in body lengths/second, the operative length being the lateral distance between the tips of the walking legs when the crab was in a normal standing position. Body length ranged from ≈ 18 cm for a 100-g crab to ≈ 27 cm for a 500-g crab. There was an inverse relationship between log fatigue time and velocity (Fig. 1). At 0.2 BL/second, exercise could be maintained for at least 2 hours, at 0.5 BL/second, for about 5 minutes, whereas burst speeds of 2.2 BL/second were only sustained for about 30 seconds. The operative procedures had negligible influence on exercise performance. Mean fatigue time at 0.5 BL/second was 3.73 ± 0.40 minute in 8 operated crabs versus 4.62 ± 0.68 minutes in 8 unoperated ones.

The velocity-vs.-fatigue time relationship agreed with our field observations. *Cardisoma* live in burrows at the base of limestone cliffs, and roam the shores of the Palau islands. They

normally amble at rather slow speed (< 0.2 BL/second) with frequent stops, but when danger appears they rapidly retreat to their burrows at close to burst velocity. A large crab (400 g) with a body length of ≈25 cm could cover about 15 m at burst speed. This was about the maximum distance we ever observed the crabs to run to their burrows when chased. As velocity is size related, large crabs presumably wander farther from home than do small animals. This may be one factor limiting the normal foraging range.

Another factor influencing velocity is the presence or absence of legs. The majority of crabs which we collected were missing one or more walking legs or chelipeds, presumably a result of natural aggression. The absence of chelipeds greatly enhanced exercise ability because of the reduction in load; in a large crab, the chelipeds can account for 25% of the body weight. Herein may lie a trade-off between fight or flight as a defense strategy. The loss of one walking leg had little influence, but the absence of more than one, especially on the same side, obviously impaired performance.

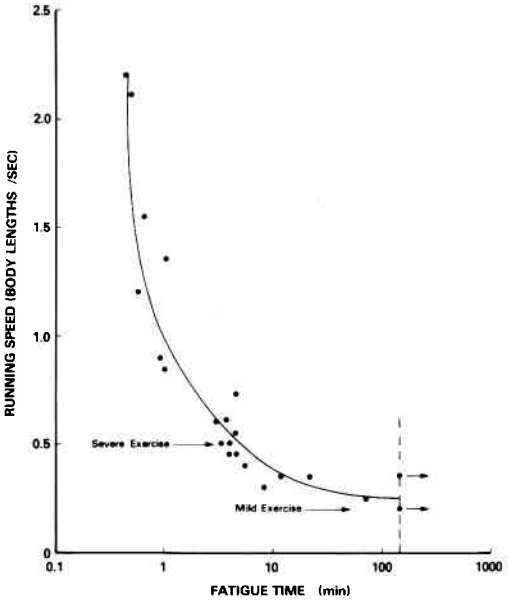

Fig. 1. The relationship between running speed on a treadmill and fatigue time in *Cardisoma* at 25°C.

The respiratory system

Cardisoma respires by ventilating its large bilateral branchial chambers with air via the paddle-like action of the large scaphognathite on each side (Fig. 2). This could be clearly observed through the branchial window. The scaphognathites force air out of the chambers through the exhalent channels behind the third maxillipeds. This action reduces pressure within the cavity, thereby drawing air into the chamber around its base where the branchiostegite touches the walking legs. The Milne-Edwards opening over the cheliped is the main inhalent channel. Scaphognathite activity invariably caused negative pressures within the

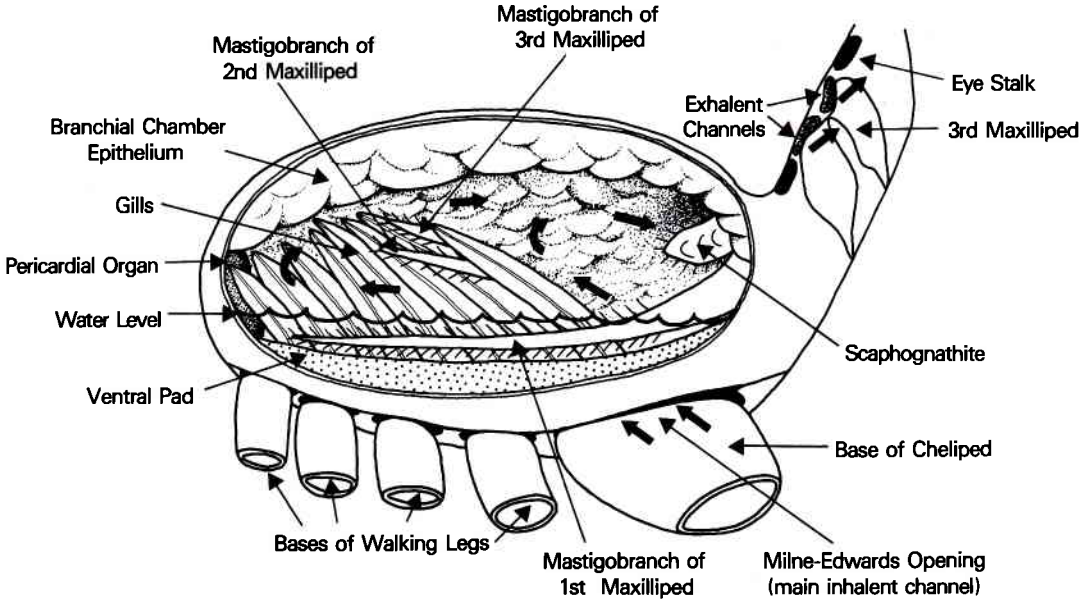

Fig. 2. A semidiagrammatic view of the respiratory system as seen through a Butyrex window implanted in the right branchial chamber of a living *Cardisoma*. See text for details.

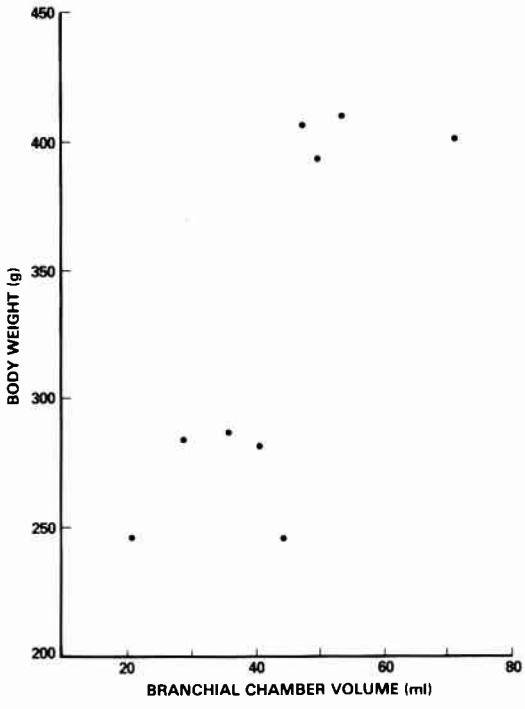

Fig. 3. The relationship between the volume of the two branchial chambers and the total body weight in *Cardisoma*. The mean volume was 133.5 ± 10.6 ml/kg.

branchial chamber (Fig. 4), and ventilatory reversals were never observed. The branchial chamber can be sealed and its volume altered, because we observed sharp reductions in branchial pressures in the absence of scaphognathite activity. This presumably results from the actions of prominent muscle bands (epimeral retractors?) which can be seen upon dissection to run along the dorsal surface of the chamber wall. A spongy white pad runs along the entire lower edge of the inhalent margin and is capable of an effective seal, as is the scaphognathite. The total branchial chamber volume is high, on average 131.5 ± 10.6(9) ml/kg. There is considerable variability between individuals, because animals with similar body size can have small, large or no chelipeds, and therefore very different body weights (Fig. 3).

The gills of *Cardisoma* are small (Fig. 2), about 1/3 to 1/4 the size of those in *Cancer*. Gas transfer across the gills is undoubtedly augmented by transfer across the extensive folded epithelium, which covers the surface of the branchial cavity. This epithelium is well vascularized and is much more spongy in live animals than dead, indicating that it may be supported by the blood pressure. The epithelium is streaked with white deposits, which are probably uric acid (Gifford, '68). The branchial chamber is normally partly filled with water (Fig. 2), which the crab obtains by lowering the posterior margin of its branchiostegite into a puddle and generating negative pressure

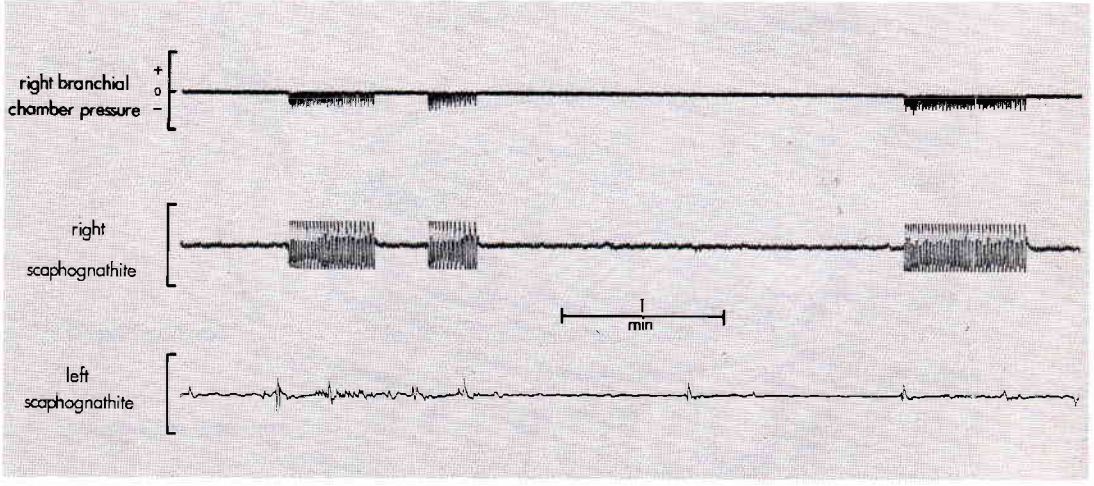

Fig. 4. Simultaneous records of right branchial chamber pressure and the activities of the right and left scaphognathites in a resting *Cardisoma* at 25°C. Note the unilateral and intermittent nature of ventilation (lack of activity in left scaphognathite) and the production of negative pressures by right scaphognathite activity. Activity was detected by impedance conversion. The pressure record was not accurately calibrated, but the maximum deflections during scaphognathite activity were less than 3 mm H_2O.

with the scaphognathite and possibly the epimeral retractors. This water is changed over every few minutes when the crab has access to water, but is held in place when the crab is removed from the water. The seal created by the ventral pad facilitates this. The water is not released even during violent exercise. The water generally collects around the base of the gills. However, a large flabella, the mastigobranch of the first maxilliped, is in almost constant motion, flicking the water up over the gills and mixing it with the air. Two smaller mastigobranchs of the second and third maxillipeds perform a similar though less vigorous activity behind the gills. In addition, the gills move as the crab runs, for they are attached to the bases of the walking legs. Further mixing is effected by the epithelium of the branchial chamber, which pulsates markedly in time with the heart beat.

Ventilation

At rest, the scaphognathites beat periodically in high frequency bursts separated by anywhere from 15 seconds to 15 minutes (Figs. 4, 5, 7). The usual interval is 1–4 minutes. Typically, ventilation is unilateral with one scaphognathite either completely inactive or much less active than the other one (Fig. 4). The animal alternates the active side periodically, with intermittent bilateral ventilation during the transitional phase. In a few crabs, intermittent bilateral ventilation was the common resting pattern, but even here, synchronization between the two sides was only partial (Fig. 5A). Direct measurements of ventilatory air flow ($\dot{V}_A$) in the masked crab showed that an intermittent $\dot{V}_A$ resulted (Fig. 6A). During exercise, scaphognathite activity always becomes bilateral and more or less continuous (Fig. 5B). A continuous, though irregular, pattern of $\dot{V}_A$ resulted (Fig. 6B).

Within 2 minutes, mean f_s (two sides averaged) increased about 4-fold with mild and 5-fold with severe exercise (Fig. 8). During recovery f_s remained elevated until 2 and 4 hours postexercise, respectively. Indirect estimates of total $\dot{V}_A$ were obtained with the Fick equation from the $\dot{M}_{O_2}$ data of Figure 10 and the branchial chamber P_{O_2} data ($P_{B_{O_2}}$) of Figure 9. The resulting values were probably overestimates as $P_{B_{O_2}}$ will overestimate true $P_{E_{O_2}}$ (see *Gas exchange*, below). Nevertheless, the basic patterns agreed with those seen in f_s, $\dot{V}_A$ rising from about 70 ml · $kg^{-1}min^{-1}$ at rest to 300 and 500 ml · $kg^{-1}min^{-1}$ during mild and severe exercise, respectively, and then declining with a similar time course to f_s. Direct measurements of V_A in the single masked crab showed an increase from ≈25 ml · $kg^{-1}min^{-1}$ at rest to ≈120 ml · $kg^{-1}min^{-1}$ during mild exercise (Fig. 6). However it should be noted the O_2 utilizations were exceptionally high in this animal, and therefore $\dot{V}_A$ probably unusually low (compare $P_{B_{O_2}}$s in Fig. 6 with the mean values in Fig. 9). In summary, while the absolute values of $\dot{V}_A$ are in some doubt, changes in f_s appear to provide a reliable index of their relative changes.

Heart rate

At rest, the heartbeat was generally regular but periodically interrupted by short pauses that were sometimes loosely correlated with periods of scaphognathite activity (e.g., Fig. 5A). During exercise, f_H increased, reflecting both a greater intrinsic frequency and an elimination of the pausing periods (Fig. 5B). Mean f_H rose by about 15% during mild and 30% during severe exercise and remained elevated until 2 and 6 hours, respectively (Fig. 8). Estimates of total cardiac output ($\dot{V}_b$) were obtained from the Fick principle from the $\dot{M}_{O_2}$ data of Figure 10 and the haemolymph $C_{a_{O_2}}$ and $C_{v_{O_2}}$ data in Wood and Randall ('81). The resulting values were probably subject to even greater inaccuracies than those for $\dot{V}_A$, but did indicate that changes in f_H were not representative of changes in total $\dot{V}_b$. Estimated $\dot{V}_b$ rose from ≈100 ml · $kg^{-1}min^{-1}$ at rest to 200–300 ml · $kg^{-1}min^{-1}$ at both exercise levels. Therefore cardiac stroke volume must have increased to a much greater extent than f_H during activity.

Gas exchange

$P_{B_{O_2}}$ (branchial chamber P_{O_2}) steadily decreased and $P_{B_{CO_2}}$ increased during the pauses between bursts of scaphognathite activity (e.g., Fig. 7). The longer the pause, the greater the changes. Each ventilatory burst brought in new air, thereby raising $P_{B_{O_2}}$ and lowering $P_{B_{CO_2}}$. The longer the ventilatory burst, the greater the changeover of air, and the closer $P_{B_{O_2}}$ and $P_{B_{CO_2}}$ approached inspired values ($P_{I_{O_2}}$ = 153 torr; $P_{I_{CO_2}}$ = torr). On an intermittently ventilated side, $P_{B_{O_2}}$ was generally held in the range of 130–150 torr by this strategy, and $P_{B_{CO_2}}$ in the range 2–12 torr. However on a nonventilated or poorly ventilated side, $P_{B_{O_2}}$ sometimes fell below 100 torr while $P_{B_{CO_2}}$ rose above 20 torr.

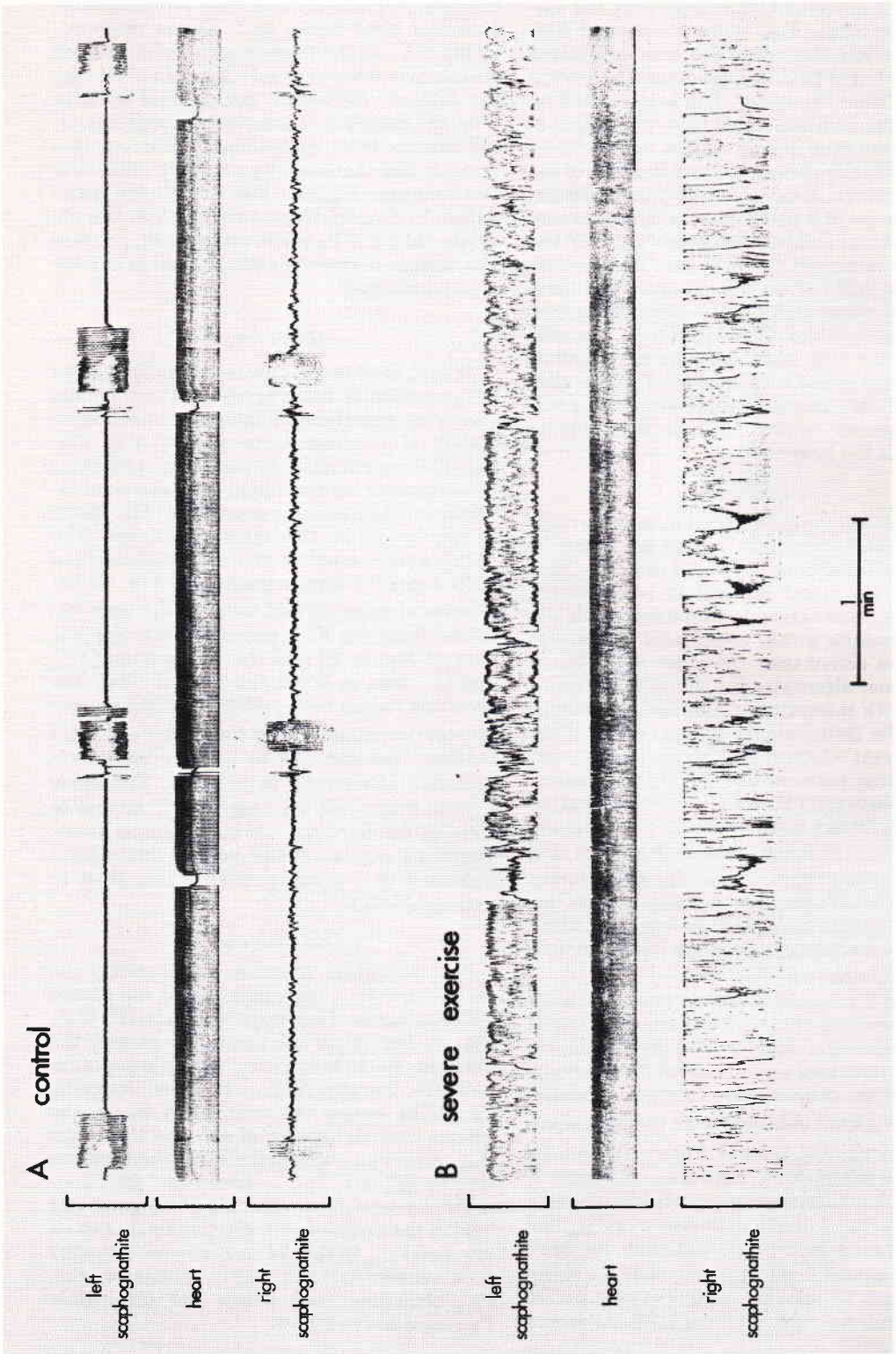

Fig. 5. Simultaneous impedance records of the activities of the heart and the left and right scaphognathites in a *Cardisoma* at rest (A) and during severe exercise (B) at 25°C. Ventilation was typically bilateral in this animal, but note the lack of complete correlation between scaphognathite activities on the two sides in (A). Note also the occasional pauses in heart rate in (A). During exercise (B), heart and scaphognathite activity became more or less continuous.

Because of this intermittent ventilation at rest, values of $P_{E_{O_2}}$ (expired P_{O_2}) and $P_{E_{CO_2}}$ (expired P_{CO_2}) taken from the exhalent cannulae were meaningless; indeed, as might be expected, they were very close to the inspired values during periods of nonventilation. Only during continuous bilateral ventilation were values of $P_{E_{O_2}}$ and $P_{E_{CO_2}}$ similar to those of $P_{B_{O_2}}$ and $P_{B_{CO_2}}$. Therefore the true values of $P_{E_{O_2}}$ and $P_{E_{CO_2}}$ are unknown. Obviously they must be equal to or lower than those for $P_{B_{O_2}}$ and equal to or higher than those for $P_{B_{CO_2}}$. P_B values would equal P_E values only if the gas samples were drawn at the exact time of a burst of scaphognathite activity, an event that was impossible to predict. Therefore our randomly sampled and bilaterally averaged values of $P_{B_{O_2}}$ and $P_{B_{CO_2}}$ (e.g., Figs. 6, 9) are valid representations of mean gas tensions in the chambers but must systematically overestimate $P_{E_{O_2}}$ and underestimate $P_{E_{CO_2}}$. Resting percentage utilization of O_2 from the inspired air as underestimated from $P_{B_{O_2}}$ was 11.4 ± 1.8(15)%.

The position of the crab occasionally allowed us to draw samples of branchial chamber water through the exhalent cannulae. The P_{O_2} of this water was much lower than that of branchial chamber air but rather similar to that of arterial haemolymph (Table 1). On the other hand, P_{CO_2} levels in the water were similar to those in the gas phase but lower than those in the haemolymph (Table 1).

With the onset of exercise, the increase in $\dot{V}_A$ resulted in a marked rise in $P_{B_{O_2}}$ and a fall in $P_{B_{CO_2}}$ to close to inspired values (Fig. 9). Utilization fell to 2.8 ± 0.6(15)%, as estimated from either $P_{B_{O_2}}$ or $P_{E_{O_2}}$. Gas tensions quickly returned to normal after mild activity, but were disturbed for at least 2 hours after severe exercise (Fig. 9). The gas exchange ratio R calculated from simultaneous measurements of $P_{B_{O_2}}$ and $P_{B_{CO_2}}$, i.e.,

$$R = \frac{P_{B_{CO_2}} - P_{I_{CO_2}}}{P_{I_{O_2}} - P_{B_{O_2}}}$$

was consistently low at rest, generally below 0.5, and occasionally below 0.2 (e.g., Figs. 6, 7, 9). Immediately after exercise, branchial chamber R tended to rise, but the values of $P_{B_{CO_2}} - P_{I_{CO_2}}$ and $P_{I_{O_2}} - P_{B_{O_2}}$ became so small (Fig. 9) as to introduce some uncertainty.

Both $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ approximately doubled following mild exercise (Fig. 10A). Severe exercise increased $\dot{M}_{O_2}$ by a factor of 3 and $\dot{M}_{CO_2}$ by a factor of 5 (Fig. 10B). This was reflected in a large change in the value of R for the whole animal, which increased from 0.60 to 1.17 after severe exercise and remained significantly elevated for at least 30 minutes (Fig. 11B). There was also a slight but nonsignificant rise in whole animal R after mild activity (Fig. 11A). It seems unlikely that the animals came into any sort of steady state in the 10-minute exercise periods. Substantial O_2 debts were accumulated, as shown by high haemolymph lactate levels (Wood and Randall, '81) and significant elevations of $\dot{M}_{O_2}$ for up to 3 and 5 hours after mild and severe exercise respectively (Fig. 10). $\dot{M}_{CO_2}$ returned to normal more quickly than did $\dot{M}_{O_2}$ (Fig. 10), and R fell slightly below resting levels at this time (Fig. 11), which may indicate repayment of a CO_2 debt.

DISCUSSION

Exercise performance

The only comparable data are those of Herreid et al. ('79a), who reported that *Cardisoma guanhami* fatigued after 10 minutes at ≈0.2 BL/second but not at ≈0.1 BL/second. This is inferior to our animals who maintained 0.2 BL/second for at least 2 hours (Fig. 1). Indeed, in terms of endurance at different speeds, the present data compare quite favourably with those for a tropical ecothermic vertebrate, the iguana (Moberly, '68). The maximum speed of *Cardisoma carnifex* was about 2.5 BL/second, and two unidentified Palauan grapsid crabs we tested showed similar capacity. However, the ghost crab *Ocypode* is reported to run at up to 10 BL/second, so we are by no means dealing with the fastest land crabs. *Ocypode* periodically reverses its orientation during running in the same manner as *Cardisoma* so as to stave off fatigue (Lochead, '60).

The respiratory system

Our observations are in basic agreement with those of Bliss ('68), Cameron ('75), and Diaz and Rodriguez ('77) on *Cardisoma guanhami*. However, an important difference is the presence of branchial water in *Cardisoma carnifex* and its apparent absence in *Cardisoma guanhami*. While the latter is reported to frequently flush the gills with water, it apparently does not retain the water. In *Cardisoma carnifex*, the water retention may be associated with the presence of the spongy white pad along the inhalent margin over the legs, about which we can find no mention in *Cardisoma*

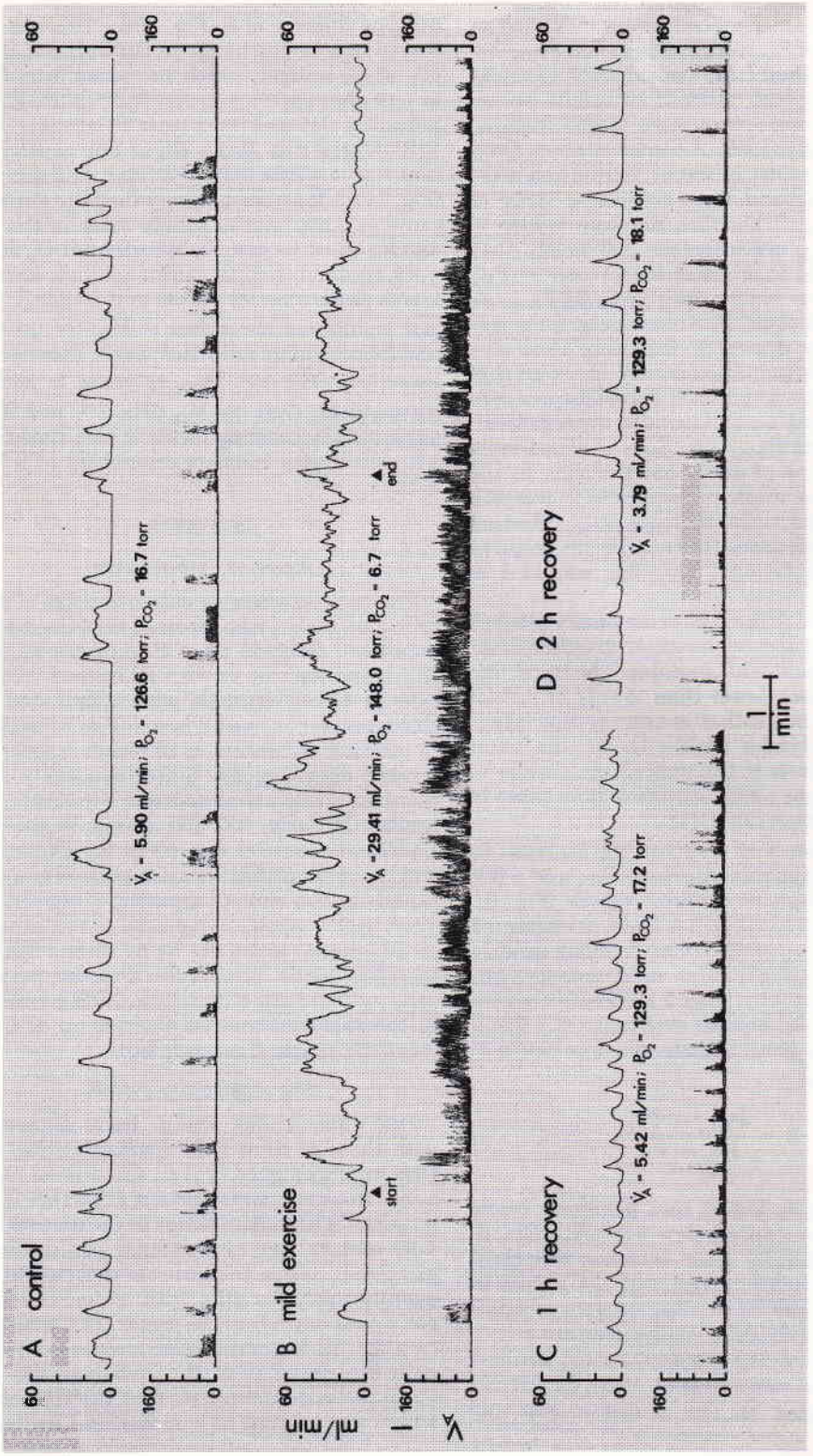

Fig. 6. Simultaneous records of instantaneous and integrated mean air flow ($\dot{V}_A$) in a crab fitted with a ventilation mask and anemometer probe during (A) rest, (B) mild exercise, and at (C) 1 hour and (D) 2 hours' recovery at 25°C. The upper panel in each section is mean flow and the lower panel is instantaneous flow. The average $\dot{V}_A$, branchial chamber P_{O_2}, and branchial chamber P_{CO_2} are shown under each treatment. Crab weight = 240 g.

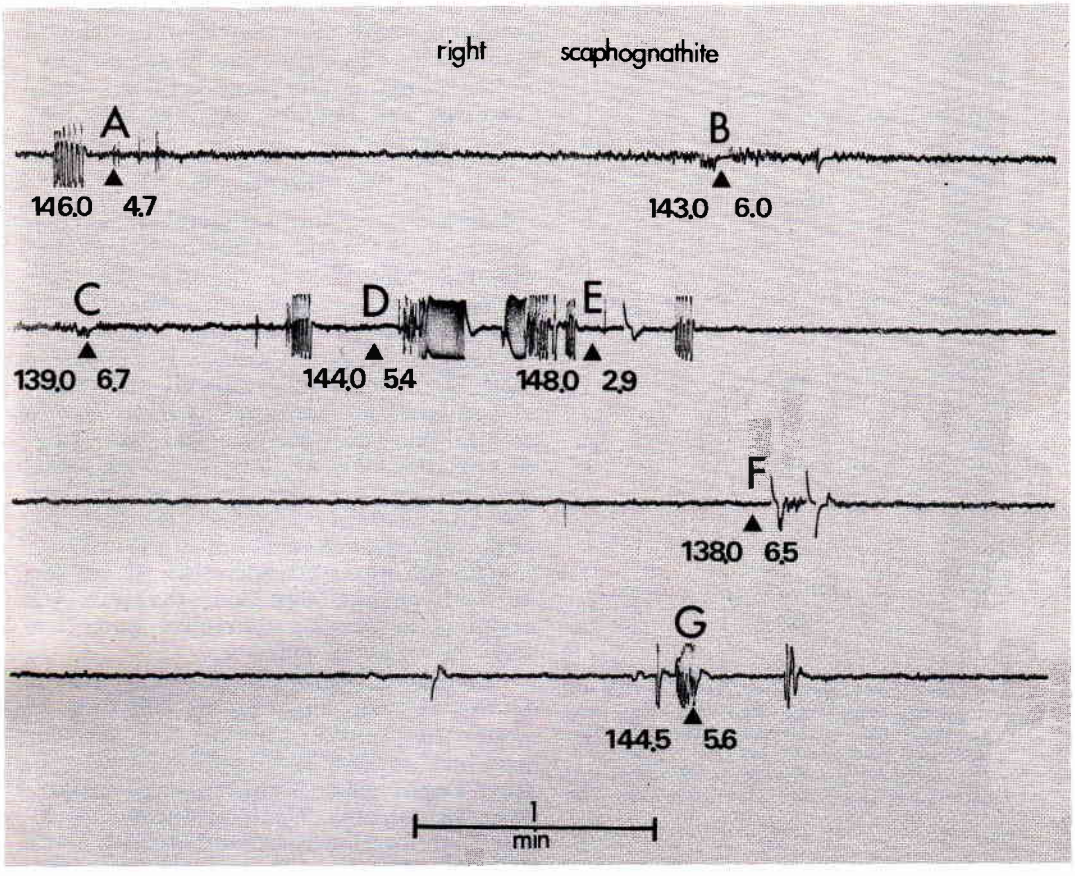

Fig. 7. Simultaneous records of right scaphognathite activity and gas tensions in the right branchial chamber during intermittent ventilation in a resting *Cardisoma* at 25°C. Gas samples were drawn at A, B, C, D, E, F, and G. The first value in each pair represents P_{BO_2}, the second value P_{BCO_2}, in torr. The four sections of the record were continuous. Note the progressive drop in P_{BO_2} and rise in P_{BCO_2} during a pause (e.g., ABC), the rise in P_{BO_2} and fall in P_{BCO_2} after a bout of scaphognathite activity (e.g., G), the changes being proportional to the length of the ventilatory burst (e.g., D, E). Note also the much larger changes in P_{BO_2} than in P_{BCO_2} after a pause (e.g., EF) or a ventilatory bout (e.g., CE).

*TABLE 1. A comparison of O_2 and CO_2 tensions in branchial chamber water with those determined simultaneously in branchial chamber air and arterial and venous haemolymph**

	Branchial chamber water		Branchial chamber air		Arterial haemolymph		Venous haemolymph	
Crab	P_{O_2}	P_{CO_2}	P_{O_2}	P_{CO_2}	P_{O_2}	P_{CO_2}	P_{O_2}	P_{CO_2}
2	77.0	6.9	151.5	3.4	67.0	11.0	11.0	13.5
3	82.0	4.1	152.0	2.7	72.0	9.0	7.3	11.3
3	69.0	4.6	124.0	5.5	72.0	9.0	7.3	11.3
11	93.0	6.9	135.0	8.2	63.0	7.6	10.5	10.2
$\bar{X}$	80.3	5.6	140.6	5.0	68.5	9.2	9.0	11.6

* The branchial chamber air values are unilateral, taken from the same side as the branchial chamber water values. The two data sets from crab 3 were taken separately from the two branchial chambers.

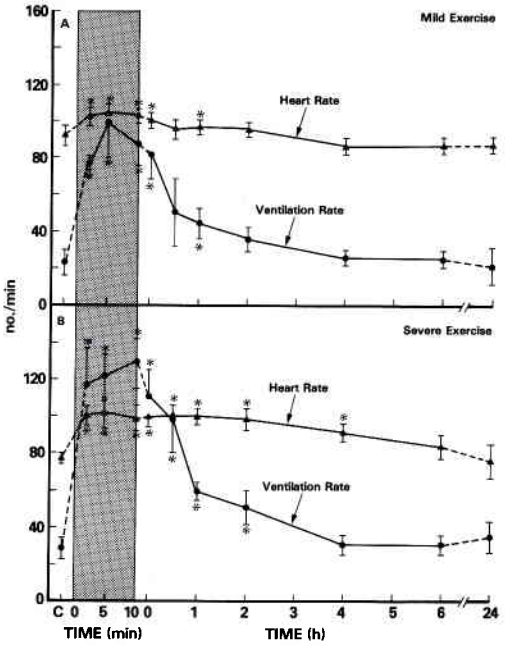

Fig. 8. Changes in heart rate (f_H) and ventilation rate (mean f_s, bilaterally averaged) in *Cardisomia* during and after 10 minutes of either (A) mild or (B) severe exercise at 25°C. The exercise period is indicated by the stippled bar (note the difference in time scale). Means ± 1 S.E. * = significantly different from preexercise control value. In (A), N = 5 for f_H and 4–5 for f_s. In (B), N = 4 for f_H and 5–7 for f_s.

guanhami. The presence of this water offers at least three benefits. First, it helps prevent dehydration of the respiratory membranes. Second, when the water is changed over, it may serve as a significant route of CO_2 excretion. Even in the absence of changeover, the presence of the retained water will reduce fluctuations in P_{BCO_2} and therefore maintain a more constant gradient for CO_2 excretion across the respiratory surface. The capacitances of air and water for CO_2 are about equal. The convective action of the flabellae, gill movements, and pulsation of the branchial chamber wall, combined with the high diffusibility of CO_2, ensures good equilibration of CO_2 between the air and water phases (Table 1). O_2 is much less diffusible, does not equilibrate, and has negligible solubility in water relative to air. As a result, P_{BCO_2} is much more constant than P_{BO_2} during intermittent ventilation (see, for example, Fig. 7). Finally, the retention of branchial water may allow salt, water, ammonia, acid, and base exchanges across the gills to continue while the animal is in air. The latter possibility clearly deserves further experimental attention. The anomurans *Birgus* and *Coenobita* are also said to retain branchial water (Cameron and Mecklenburg, '73; McMahon and Burggren, '79).

Ventilation

Intermittent, often unilateral ventilation appears to be the true resting pattern in *Cardisoma carnifex* (Figs. 4–7). Direct anemometer records of $\dot{V}_A$ suggest that similar ventilatory patterns sometimes occur in *Gecarcoidea lalandii* (Cameron and Mecklenburg, '73), *Cardisoma guanhami,* and *Gecarcinus lateralis* (Cameron, '75). The same is also true in the marine brachyuran *Cancer magister* (McDonald et al., '77, '80). In the dense, viscous, aquatic environment, the strategy may be directed at reducing the energetic cost of ventilatory convection, but this is probably not an important consideration for an air-breathing animal. More likely, the strategy is aimed at minimizing convective water loss from the branchial chamber.

Fick equation-based values for $\dot{V}_A$ in resting *Cardisoma carnifex* (which we believe to be overestimates—see Results *(Ventilation)*) were only about 50% of the $\dot{V}_A$'s reported in other Gecarcinidae (Cameron and Mecklenburg, '73; Cameron, '75; Herreid et al., '79a, b). Our single direct measurement was only about 20% of these values. This must reflect either a real interspecific difference or a lack of truly resting conditions in the other studies. Assuming a resting $\dot{V}_A$ of 50 ml · kg^{-1} · min^{-1}, midway between our Fick estimates and direct measurement, the ventilatory convection requirement ($\dot{V}_A/\dot{M}_{O_2}$) would be about 1.3 L air/mMole O_2, very similar to that in air-breathing vertebrates (Dejours, '75). It would seem to make sense for a terrestrial animal to keep its ventilatory convection as low as possible to minimize respiratory water loss. During exercise, $\dot{V}_A$ increased markedly (Figs. 6,8), but again our estimates were much lower than those of Herreid et al. ('79a) in *Cardisoma guanhami* at the same speed (0.2 BL/second), though the relative changes were similar.

The ventilatory increase at the onset of exercise was almost instantaneous, and essentially complete within 2 minutes (Figs. 6, 8). While there is some evidence that ventilation is CO_2 driven in land crabs (Cameron and Mecklenburg, '73; Cameron, '75), the speed of the response suggests that there may also be

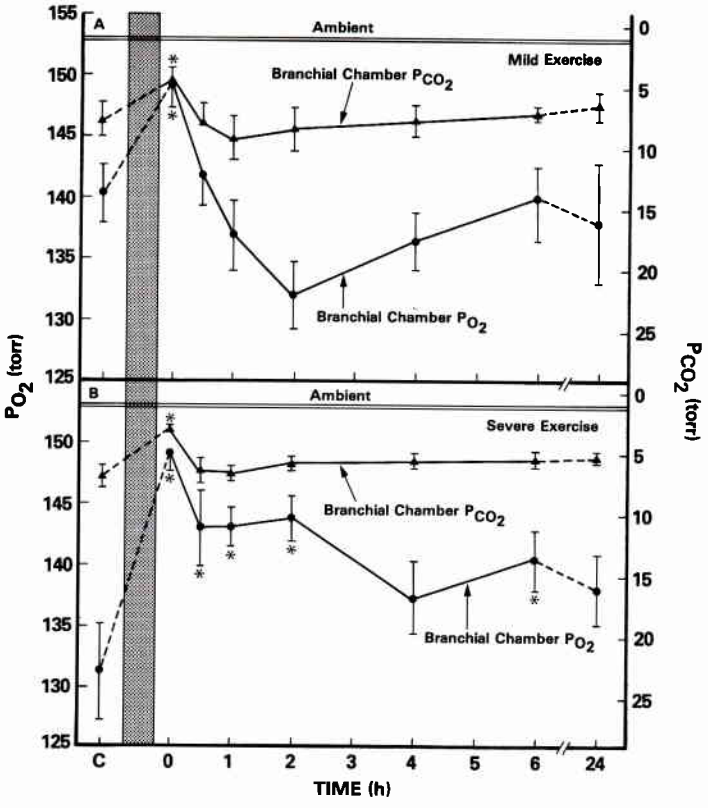

Fig. 9. Changes in the mean oxygen (P_{BO_2}) and carbon dioxide (P_{BCO_2}) tensions (bilaterally averaged) in the branchial chambers of *Cardisoma* after 10 minutes of either (A) mild or (B) severe exercise at 25°C. The ambient levels of P_{O_2} and P_{CO_2} (i.e., inspired values) are indicated by the double horizontal lines. In (A), N = 5–7. In (B), N = 5–8. Other details as in Figure 8.

feedback input from limb proprioreceptors. During the recovery phase, the time course of the ventilatory decrease (Fig. 8) seemed to correlate with changes in haemolymph pH rather than with haemolymph gas tensions (Wood and Randall, '81).

Heart rate

There was a modest but long-lasting increase in f_H in *Cardisoma carnifex* during and after exercise, as in the aquatic *Cancer magister* (McMahon et al., '79), and most air-breathing vertebrates. Herreid et al. ('79a) found exactly the opposite, a bradycardia, during comparable treadmill exercise in *Cardisoma guanhami*. The reason for this difference is unknown. However, the important point is that the Fick equation estimate of $\dot{V}_b$ showed that it increased to a much greater extent than f_H. Mechanical pumping by the activity of the walking legs may have contributed to this effect.

Gas exchange

Resting utilization of O_2 (>11.4%) was at least three times greater than previously reported for other Gecarcinidae (Cameron and Mecklenburg, '73; Cameron, '75; Herreid et al., '79a, b). This difference correlates with the much lower value of $\dot{V}_A$ in the present study, and similar explanations may apply (see *Heart Rate* above). During exercise, $\dot{V}_A$ increased and utilization fell to about 3%, the resting value in other studies. P_{O_2} and P_{CO_2} gradients between haemolymph and air in the branchial chamber (Table 2) were high relative to mammals, but quite close to those in turtles at a similar temperature (Burggren and Shelton, '79), which is probably a fairer comparison. Gas exchange in the land crab may be much more effective than previously believed.

The increase in $\dot{V}_A$ during exercise elevated P_{BO_2} (Figs. 6, 9), but the calculations in Table 2 illustrate that the more important factor in-

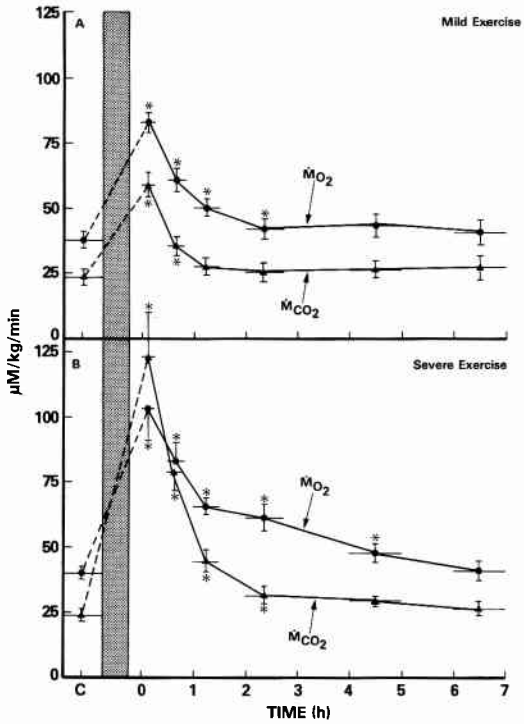

Fig. 10. Changes in oxygen consumption ($\dot{M}_{O_2}$) and carbon dioxide production ($\dot{M}_{CO_2}$) in *Cardisoma* after 10 minutes of either (A) mild or (B) severe exercise at 25°C. In (A), N = 6. In (B), N = 5–6. The horizontal bars indicate the time periods over which determinations were made. Other details as in Figure 8.

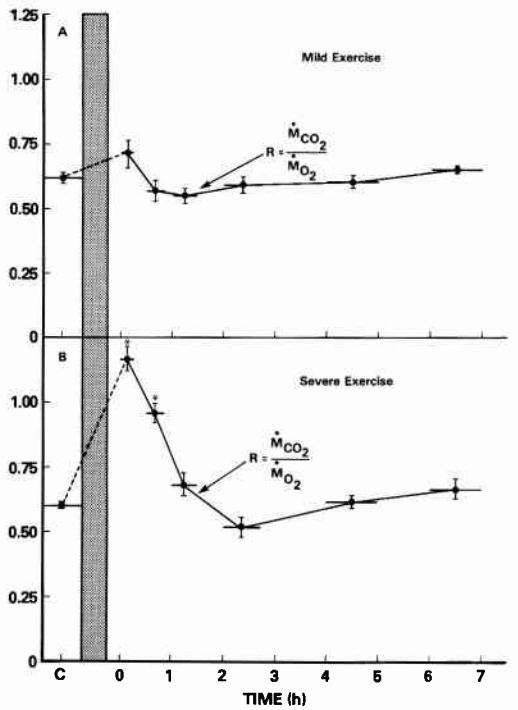

Fig. 11. Changes in the gas exchange ratio (R) for the whole animal in *Cardisoma* after 10 minutes of either (A) mild or (B) severe exercise at 25°C. In (A), N = 6. In (B), N = 5–6. The horizontal bars indicate the time periods over which determinations were made. Other details as in Figure 8.

fluencing the mean P_{O_2} gradient ($P_{BO_2} - \frac{1}{2}(P_{aO_2} + P_{vO_2})$ between haemolymph and air in the branchial chamber was the fall in mean haemolymph P_{O_2}. This in turn resulted largely from the drop in Pa_{O_2}, the cause of which is dealt with in Wood and Randall ('81). Overall, the mean P_{O_2} gradient increased about 30%, whereas $\dot{M}_{O_2}$ rose by a factor of 2 in mild exercise and nearly 3 in severe. Obviously, the increase in $\dot{M}_{O_2}$ was not simply the result of an increased gradient, and there must have been changes in the conditions for gas transfer across the respiratory surface. These changes are reflected in the diffusing capacity for O_2 ($\dot{M}_{O_2}/\Delta P_{O_2}$ = transfer factor, conductance), which is defined as the amount of O_2 taken up per unit P_{O_2} difference across the respiratory surface. $\dot{M}_{O_2}/\Delta P_{O_2}$ approximately doubled after exercise (Table 2). The nature of the changes are unknown, but they could reflect differences in diffusion distance, surface area, permeability, and reaction kinetics. Interestingly, O_2 diffusing capacity and its elevation during exercise were almost identical in the aquatic crab *Cancer magister* (McMahon et al., '79).

The situation is basically similar for CO_2 exchange (Table 2). However, the buffering effect of branchial water on P_{BCO_2} tends to be reduced at high $\dot{V}_A$, so the change in P_{BCO_2} is a relatively more important contributor to the increase in mean CO_2 diffusion gradient. The diffusing capacity for CO_2 increased to a greater extent than that for O_2 after exercise. Overall, the CO_2 diffusing capacity was 9–12-fold the O_2 diffusing capacity of the system. If only differences in the diffusivities of the two gases were involved, the ratio should have been 25 to 30 at this temperature. Clearly other factors are implicated. The mechanism of CO_2 excretion is discussed in greater detail by Randall and Wood ('81).

The whole animal R value at rest was ≈0.60

TABLE 2. Mean O_2 and CO_2 gradients and diffusing capacities between haemolymph and air in the branchial chamber before and immediately after mild and severe exercise

	Control	Mild Exercise	Control	Severe Exercise
P_{vO_2} (torr)	11.7	9.1	13.8	8.0
P_{aO_2} (torr)	57.0	26.3	53.2	37.8
mean haemolymph P_{O_2} (torr)[a]	34.3	17.7	33.5	22.9
P_{BO_2} (torr)	140.3	148.3	131.2	149.1
ΔP_{O_2} (torr) +	106.0	130.6	97.7	126.2
$\dot{M}_{O_2}$ (μM $O_2 \cdot kg^{-1} \cdot min^{-1}$)	37.55	82.75	39.62	102.46
$\frac{\dot{M}_{O_2}}{\Delta P_{O_2}}$ (μM $O_2 \cdot kg^{-1} \cdot min^{-1} \cdot torr^{-1}$)	0.354	0.634	0.406	0.812
P_{vCO_2} (torr)	16.33	16.16	13.40	19.05
P_{aCO_2}	15.43	12.95	12.36	15.09
mean haemolymph P_{CO_2} (torr)[a]	15.88	14.56	12.88	17.07
P_{BCO_2} (torr)	7.70	4.83	6.51	3.03
ΔP_{CO_2} (torr)[b]	8.18	9.73	6.37	14.04
$\dot{M}_{CO_2}$ (μM $CO_2 \cdot kg^{-1} \cdot min^{-1}$)	23.76	58.79	23.95	122.67
$\frac{\dot{M}_{CO_2}}{\Delta P_{CO_2}}$ (μM $CO_2 \cdot kg^{-1} \cdot min^{-1} \cdot torr^{-1}$)	2.905	6.042	3.753	8.737

[a] Average of arterial and venous values.
[b] Difference between mean haemolymph value and branchial chamber value.

(Fig. 11), which represents a respiratory quotient lower than that which would be produced by standard aerobic metabolism of even an all-lipid diet. Herreid et al. ('79a) reported similar values in some resting *Cardisoma guanhami*, though most of their resting values were in the range 0.7–0.9. We believe that this abnormally low R reflects not an abnormal metabolism, but rather the retention of respiratory CO_2 as HCO_3^- or $CO_3^=$ within the animal for formation of the carapace (cf. Wood and Randall, '81; Randall and Wood, '81). R values calculated from branchial chamber gas samples were even lower (0.2–0.5). While we cannot rule out the possibility that there is some other additional site of CO_2 excretion outside the branchial chamber, this again may reflect a buffering effect of the branchial water. Between breaths, a significant proportion of the CO_2 excreted will be in the water phase, whereas virtually all of the O_2 will be in the gas phase, thereby reducing the apparent "branchial R." When the crab ventilates its chambers, CO_2 will be removed from the water as well as from the gas phase, producing the higher (true) whole animal R value.

This R value increased enormously during severe exercise (Fig. 11B) as a result of a large increase in CO_2 excretion (Fig. 10B), in agreement with the findings of Herreid et al. ('79a). This resulted from both an increased production of CO_2 by aerobic metabolism and from conversion of bicarbonate stores to CO_2 by organic acids (principally lactic) produced by anaerobic metabolism (Wood and Randall, '81). The slight depression of R below resting levels during recovery probably represented a restoration of these bicarbonate stores.

Some of the O_2 taken up by the whole animal during exercise was utilized to raise O_2 stores in the large branchial chambers and similarly some of the CO_2 excreted was flushed out from these stores by the increased $\dot{V}_A$. True $\dot{M}_{O_2}$, $\dot{M}_{CO_2}$, and R values across the respiratory surface would therefore be in error by these amounts. However, calculations based on the P_{BO_2} and P_{BCO_2} data (Fig. 9) and the known branchial chamber volume (Fig. 3) indicated that at most the error in $\dot{M}_{O_2}$ or $\dot{M}_{CO_2}$ was about 5%, and the influence of this on R was negligible.

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