

Acid-Base Balance Following Temperature Acclimation in Land Crabs

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ABSTRACT Acid-base responses to change in body temperature have been described for terrestrial ectothermic vertebrates, but not for terrestrial invertebrates. The present study described changes in pH, carbon dioxide contents (C_{CO_2}), and partial pressures (P_{CO_2}) in prebranchial hemolymph of three supralittoral crustaceans acclimated 5 days to three temperatures.

The anomuran *Coenobita brevimanus*, a land hermit crab, and the brachyuran *Cardisoma carnifex*, were acclimated to 25°, 15°, 25°, 35°, 25° in that order. Exposure to 15° caused extreme torpidity in these species, and thus *Birgus latro* were exposed to 25–35–25–20° temperature steps.

All animals tested showed $\Delta pH/\Delta t$ relationships similar to those of other ectotherms (*Birgus* 0.023, *Coenobita* 0.017, *Cardisoma* 0.017 pH units, °C). The manner of acid-base status regulation, however, varied between species. *Birgus* allowed P_{CO_2} levels to rise and maintained a constant C_{CO_2} level as temperature rose, as do many terrestrial ectothermic vertebrates. *Cardisoma* showed a rise in P_{CO_2} without significant change in C_{CO_2} only between 25°C and 35°C. At 15°C no significant fall in P_{CO_2} occurred, whereas C_{CO_2} increased significantly, a situation similar to that seen in many aquatic ectotherms. *Coenobita* also showed responses intermediate between those typical of air-breathing and water-breathing ectotherms. These data suggest that while *Birgus*, reputedly the most "terrestrial" of the three species studied, apparently controls acid-base status in a manner similar to that of most terrestrial ectothermic vertebrates, both *Coenobita*, which has water available in the shell, and *Cardisoma*, which has water available in the burrow, can also utilize mechanisms typical of aquatic ectotherms. Possibly these latter animals are bimodal breathers and can switch from one mechanism of acid-base regulation to the other depending on the availability of water and other physiological needs.

In the majority of ectothermic animals the pH of body and cellular fluids varies predictably with body temperature. This is not purely a passive consequence of temperature change, however. Indeed the relative alkalinity, i.e., $H^+ : OH^-$ ratio (Rahn, '67), or the fractional degree of dissociation of α imidazole groups of protein histidine (Reeves, '72, '77) may be regulated as temperature changes by active physiological processes so as to maintain net protein charge state and thus maintain both protein and metabolic integrity. For the majority of ectothermic vertebrates including reptiles, amphibians, and fishes (see Reeves, '77, for review), the relationship $\Delta pH/\Delta t$ is predictable, approximating the slope of the relationship $\Delta pN/\Delta t$ for water. The relationship $\Delta pH/\Delta t$ is

similar for both water- and air-breathing vertebrates (Rahn and Baumgardner, '72; Randall and Cameron, '73; Reeves, '77), but the mechanisms by which relative alkalinity and/or the dissociation of imidazole groups is regulated are necessarily different, at least in blood.

Control of acid-base balance via the bicarbonate buffer system of the blood may occur through modulation of either the partial pressure of CO_2 (P_{CO_2}) or of the concentration of blood bicarbonate. In water breathers the low O_2 content of water necessitates a relatively high convection of water over the gills in order to satisfy oxygen demand. Under these conditions the more freely diffusible carbon dioxide cannot be retained at high levels in the blood perfusing the gill, and thus acid base

regulation by control of P_{CO_2} is not feasible. Aquatic vertebrates then must control acid-base status by regulation of body fluid bicarbonate levels (Randall and Cameron, '73). Such regulation occurs virtually independently of the ventilation rate at the gills. In air-breathing vertebrates, on the other hand, the much higher O_2 content of air may allow sufficient oxygenation over a range of ventilation flow rates. Under these conditions, control of acid-base status by ventilatory adjustment of blood P_{CO_2} is feasible, and is apparently the method utilised by many less active air-breathing vertebrates (Reeves, '77, for review). High oxygen demand may, however, curtail the use of this route in more active vertebrates (Wood et al., '78).

The concepts above were largely generated from experimental work on vertebrate species, but should be equally applicable to invertebrates (Mangum and Schick, '72; Howell et al., '73; Toulmond, '77a,b). Responses of aquatic crustaceans (Truchot, '73, '78; McMahon et al., '78; Cameron and Batterton, '78) support this contention, but little is known of the responses of either terrestrial or bimodal (i.e., animals able to breathe both water and air) decapod crustaceans (Howell et al., '73).

Some tendencies toward the terrestrial mode of regulation may be ascertained in the responses of intertidal crabs such as *Carcinus maenas* (Truchot, '73, '78) and in this species, as well as *Uca pugilator* (Howell et al., '73). The presence of elevated P_{CO_2} levels in supralittoral crabs (Cameron and Mecklenburg, '73; McMahon and Burggren, '79) indicates a potential for regulation by control of P_{CO_2} , but no data on the effects of temperature change are available. The responses of these semiterrestrial and terrestrial forms are of particular interest in that these animals may be commonly exposed to rapid and marked temperature change in their natural environment. Consequently the present study seeks to determine the responses of three supralittoral decapod crustaceans: the anomurans *Birgus latro* (coconut or robber crab) and *Coenobita brevipanus*, (the land hermit crab) as well as the brachyuran *Cardisoma carnifex*. All animals are found within facets of the same supralittoral habitat but are differently adapted to terrestrial life. *Birgus* is virtually fully terrestrial, *Coenobita* sp. are found considerable distances from the sea (de Wilde, '73) but retain water in their molluscan "mobile homes" and may retain some aquatic regulatory abilities (McMahon and Burggren, '79), whilst

Cardisoma carnifex appears not to move far from a burrow in which water is at least periodically available. These animals were selected because they exhibit varying degrees of adaptation to supralittoral habitats.

MATERIALS AND METHODS

Nine *Birgus latro* of 44 ± 14 g, 9 *Coenobita brevipanus* of 44 ± 18 g, and 9 *Cardisoma carnifex* of 236 ± 88 g were collected from above the tideline of several small islets in the Palau Island group of the Western Carolines. On board the R.V. Alpha Helix, the animals were maintained in plastic containers, singly in the case of *Birgus*, singly or in pairs in the case of *Cardisoma* and in groups of 5–10 in the case of *Coenobita*. Initially a choice of both fresh and seawater was provided daily. *Coenobita* and *Birgus* preferred freshwater, which was subsequently provided daily. Animals fed on coconut meat. Green plant material was also presented and may have provided additional food as well as shelter.

All animals and equipment used in this study were maintained in a temperature-controlled room throughout the course of the experiments. *Cardisoma* and *Coenobita* were acclimated for 5 days to each of three temperatures in the following sequence 25° , 15° , 25° , 35° , 25° . Hemolymph was sampled on the fifth day of each acclimation period. *Birgus* were not available at the start of the study but joined the series at the 25° midpoint and were thus exposed to 25° , 35° , 25° for 5-day periods. At 15° *Cardisoma* and *Coenobita* became torpid, and a few animals died. Thus, to conserve the limited supply of *Birgus*, these animals were acclimated to 20° rather than 15° . Set temperatures did not normally vary more than $\pm 1^\circ$. To minimize the risk of damage induced by temperature change, transitions were allowed to occur slowly, approximately $1^\circ h^{-1}$ in two 5° steps, separated by a 12-hour period at the intermediate temperature. No mortality occurred in these temperature transitions. Animal temperatures could not be measured directly but were assumed to follow very closely behind ambient temperature in these fairly small animals. Daily variation in deck temperature and humidity, measured at 4-hour intervals are presented (Fig. 1). Although these data were collected for only a 3-week period in August 1979, little seasonal variation occurs in this region; thus these ranges may be taken as an indication of the normal environmental range in the collecting sites close by.

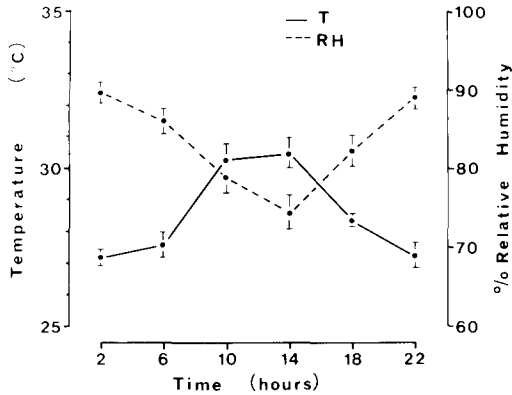


Fig. 1. Mean temperature and relative humidity profiles recorded at deck level on board R.H. Alpha-Helix for the duration of the experimental period.

Hemolymph sampling was usually restricted to a single prebranchial sample taken on the fifth day at each temperature so as to minimize blood loss and sampling disturbance. Frequent sampling has been associated with acidosis in other crustacean species (Truchot, '73; McMahon et al., '78). Prebranchial sampling was selected to minimize the effects of the ventilatory and other changes accompanying the sampling process. Two hundred to three hundred μ l samples were taken into a 250- μ l Hamilton gas-tight syringe, with a 22-gauge needle inserted through the arthroal membrane between the meropodite and coxopodite of the (larger in the case of *Coenobita*) cheliped. This was the only rapidly accessible sampling site for the small coenobitids and thus was used for all. These samples were expected to show some variability resulting from differential cheliped activity in the moments preceding sampling, but occasional samples from the infrabranchial sinus—usually penetrated via autotomised cheliped limb bases, and taken as more representative of mixed venous blood—exhibited a similar range to the cheliped samples. Two hundred to three hundred μ l hemolymph samples yielded measurements of oxygen and carbon dioxide partial pressures (P_{vO_2} , P_{vCO_2}) and pH_v (single 100- μ l sample) oxygen and carbon dioxide contents (C_{vO_2} , C_{vCO_2} , separate 40- μ l samples). Oxygen contents and partial pressures are not reported in this study. Each sample represents < 5% hemolymph volume of the smallest animals used, < 2.5% of the mean hemolymph volume of *Coenobita* and *Birgus*, and < 0.5% of the

mean hemolymph volume of *Cardisoma*. However, samples were taken on five occasions, and thus a small loss of protein and ionic components of hemolymph may have resulted in some animals. No significant differences were observed however between measured variables on samples taken at 25° at the beginning and end of the experimental period.

Carbon dioxide tensions and pH were measured simultaneously using a blood gas analyser (Instrumentation Laboratories μ 13) with its cuvette modified to decrease sample volume. The CO_2 electrode was calibrated using humidified gas mixtures (1–2%) approximating the natural in vivo range (McMahon and Burggren, '79) and produced by Wösthoff gas mixing pumps. Carbon dioxide content (C_{CO_2}) was analysed by the micro-method of Cameron ('71). HCO_3^- concentration was calculated using the relationship $HCO_3^- = C_{CO_2} - (\alpha_{CO_2} \cdot P_{CO_2})$. α_{CO_2} was obtained from nomographs for crustacean hemolymph published by Truchot ('76).

All differences between mean values were tested for significance using a two-tailed Student's t-test for independent means and significance level of $P = < 0.01$.

RESULTS AND DISCUSSION

Experimental regime and rationale

A 2-decade experimental temperature regime was envisaged initially so as to provide comparison with studies on terrestrial vertebrates, to provide overlap with previous work on aquatic crustaceans (McMahon et al., '78; Cameron and Batterton, '78; Truchot, '73, '78), and also to provide a wide basis over which to test for hysteresis effects. On-site measurements of the local temperature regime, however (Fig. 1), suggest that 15°C, the lower temperature used, lies below the normal environmental range for these species, at least in Palau. At 15° the animals became torpid, and some mortality (< 10%) occurred. The results obtained at this temperature should thus be treated with caution.

Acid-base status

At equivalent temperatures, pH values recorded here are closely similar for each species and are generally similar to the published values for other ectothermic animals, terrestrial or aquatic, listed by Dejours ('75) and Reeves ('77). The relative alkalinity, i.e., displacement of pH above pN (Rahn, '67) is similar to that

TABLE 1. Variation in acid-base status in three supralittoral crab species acclimated to three temperatures

| Prebranchial hemolymph | 25 | Δ/t | 15 | Δ/t | 25 | Δ/t |
|----------------------------------|------------------|------------|--------------------|------------|------------------|------------|
| <i>Birgus</i> | | | | | | |
| n | | | | | (9) | |
| pH | | | | | 7.569 ± 0.09 | 0.015 |
| P_{CO_2} torr | | | | | 8.41 ± 1.7 | +0.50 |
| C_{CO_2} m mol.l ⁻¹ | | | | | 12.5 ± 4.6 | 0 |
| HCO_3^- m mol.l ⁻¹ | | | | | 12.16 | |
| CO_2 m mol.l ⁻¹ | | | | | 0.34 | |
| <i>Coenobita</i> | | | | | | |
| n | (9) | | (10) | | (9) | |
| pH | 7.581 ± 0.16 | 0.021 | $7.789 \pm 0.07^*$ | 0.017 | 7.623 ± 0.07 | 0.013 |
| P_{CO_2} torr | 8.3 ± 0.2 | -0.26 | $5.7 \pm 0.6^*$ | 0.37 | 9.4 ± 2.1 | +0.10 |
| C_{CO_2} m mol.l ⁻¹ | 22.1 ± 6.6 | -0.81 | $14 \pm 5.2^*$ | +0.61 | 20.1 ± 4.8 | -0.01 |
| HCO_3^- m mol.l ⁻¹ | 21.78 | | 13.71 | | 19.73 | |
| CO_2 m mol.l ⁻¹ | 0.32 | | 0.29 | | 0.37 | |
| <i>Cardisoma</i> | | | | | | |
| n | (8) | | (9) | | (8) | |
| pH | 7.461 ± 0.15 | 0.025 | $7.771 \pm 0.12^*$ | 0.020 | 7.572 ± 0.09 | 0.012 |
| P_{CO_2} torr | 9.2 ± 2.8 | +0.09 | 10.1 ± 8.5 | -0.11 | 9.0 ± 1.4 | +0.40 |
| C_{CO_2} m mol.l ⁻¹ | 15.7 ± 4.7 | +1.53 | $31 \pm 8^*$ | -1.6 | 19.4 ± 5.7 | -0.22 |
| HCO_3^- m mol.l ⁻¹ | 15.33 | | 30.47 | | 19.04 | |
| CO_2 m mol.l ⁻¹ | 0.37 | | 0.53 | | 0.36 | |

* Significant difference ($P < .01$) \bar{X} values at 25°C.
 $\bar{x} \pm S.D.$

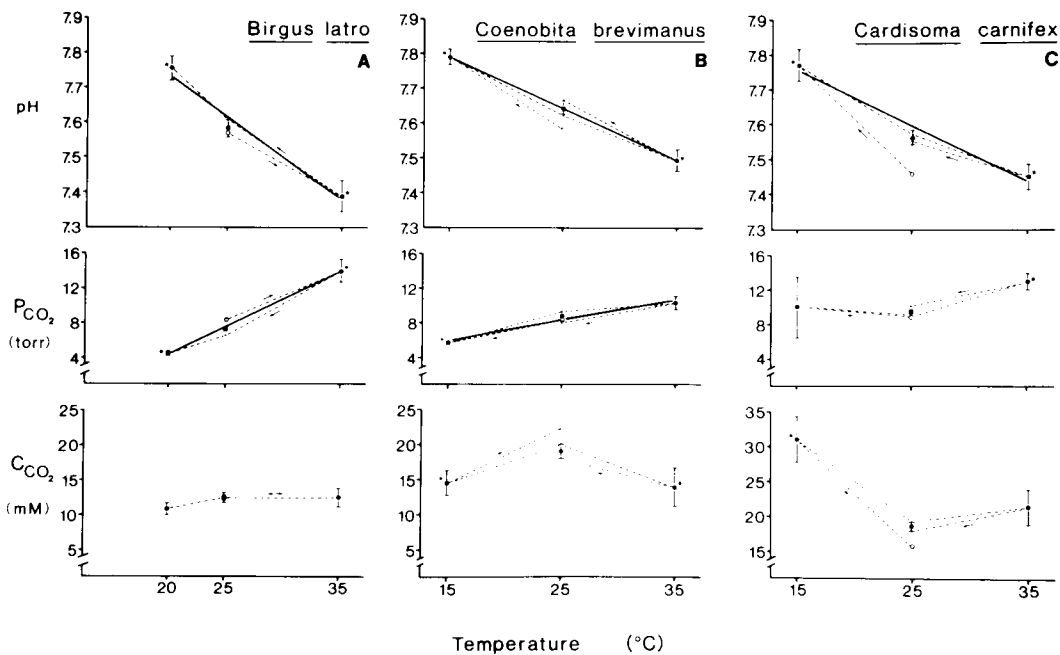


Fig. 2. Variation in pH, C_{CO_2} , and P_{CO_2} levels in *Birgus*, *Coenobita*, and *Cardisoma* following acclimation, and after cooling and warming to 25°C. Several measurements were taken at 25°C. The initial measurement is denoted by the open circles. The broken line connect means of samples at each temperature; arrows denote the direction of tempera-

ture change. Solid circles denote the means of measurements at each temperature (repeated measurements at 25°C). Regression lines (unbroken), calculated by method of least squares from mean values at each temperature, are drawn where relevant. Asterisks show values which are significantly different ($P = < 0.01$) from mean values at 25°C.

| 35 | Δ/t | 25 | Δ/t | 20 | \bar{x} 25 | \bar{x} Δ/t |
|-------------------|------------|------------------|------------|-------------------|------------------|----------------------|
| (9) | | (9) | | (9) | | |
| 7.391 \pm 0.13 | 0.022 | 7.608 \pm 0.07 | 0.03 | 7.756 \pm 0.01* | 7.582 \pm 0.11 | 0.023 |
| 14.0 \pm 3.7* | -0.74 | 6.6 \pm 0.7 | -0.42 | 4.5 \pm 0.7* | 7.3 \pm 1.2 | 0.57 |
| 12.6 \pm 4.0 | 0 | 12.6 \pm 4.0 | -0.34 | 10.9 \pm 2.4 | 12.5 \pm 2.7 | 0 |
| 12.17 | | 12.34 | | | | |
| 0.43 | | 0.26 | | 10.70 | 12.21 | |
| | | | | 0.20 | 0.29 | |
| (10) | | (8) | | | | |
| 7.495 \pm 0.10* | 0.017 | 7.668 \pm 0.07 | | | 7.642 \pm 0.07 | 0.017 |
| 10.4 \pm 2.2 | -0.23 | 8.1 \pm 2.0 | | | 8.8 \pm 1.3 | 0.24 |
| 14.0 \pm 8.1* | 0.41 | 18.1 \pm 4.5 | | | 19.1 \pm 4.5 | |
| 13.68 | | 17.78 | | | 18.77 | |
| 0.32 | | 0.32 | | | 0.34 | |
| (7) | | | | | | |
| 7.451 \pm 0.13* | 0.011 | 7.554 \pm 0.09 | | | 7.563 \pm 0.09 | 0.017 |
| 13 \pm 2* | -0.28 | 10.23 \pm 1.6 | | | 9.5 \pm 0.6 | 0.22 |
| 21.6 \pm 6 | -0.33 | 18.1 \pm 1.4 | | | 17.73 \pm 1.9 | 0.81 |
| 21.19 | | 17.69 | | | 17.35 | |
| 0.41 | | | | | 0.38 | |

recorded for *Carcinus maenas* by Truchot ('73).

Dejours ('75) states that "compared to water breathers, air breathers are in a state of compensated hypercapnic acidosis." The primary cause of the hypercapnia is the higher oxygen capacity of air, which allows marked hypoventilation. Compensation for this acidosis at the level of body fluids is normally by accumulation of bicarbonate, as was first shown over a range of crabs by Fontaine ('33). In general, the present study supports these views. At equivalent temperature and pH levels of both P_{CO_2} and HCO_3^- measured in hemolymph, all three species exceed both literature values for subtidal marine species (Truchot, '73) and the somewhat higher values reported for freshwater species (Hassall, '79). However, the values reported for *Birgus*, supposedly the most terrestrial of the species used in the present study, showed the lowest P_{vCO_2} values at all temperatures except 35°, and the lowest bicarbonate levels at any temperature. In fact, at the lower temperature the levels recorded for *Birgus latro* are not markedly different from those recorded for air-exposed *Carcinus maenas* at similar temperature (Truchot, '73; Taylor and Butler, '78; Wheatly and Taylor, '79), suggesting that no special acid-base status modification occurs in this species. That the lowest values for P_{CO_2} and C_{CO_2} should occur

in *Birgus*, perhaps the most terrestrial decapod studied, is a surprising finding that is somewhat contrary to the general view outlined above. Circulating oxygen tensions are higher in this species than in most terrestrial decapods (Redmond, '68; Burggren and McMahon, '81; McMahon and Burggren, '79), and it is possible that some special properties of the complex air-breathing organ (lung), or of the gills, or of a combination of these structures, may allow enhanced gaseous exchange. In fact, both P_{CO_2} and C_{CO_2} levels are generally somewhat lower in air breathing crustaceans than in tidal air breathers, and it is possible that the scaphognathite system allows a unidirectional flow of air past the complex branchial apparatus of *Birgus* which allows the enhanced gaseous exchange (McMahon and Burggren, unpublished observations).

Changes in pH in crabs acclimated to a range of temperatures ($\Delta pH/\Delta t$) (Table 1, Fig. 2) are similar for all three species tested, and to results from other ectothermic animals, aquatic or terrestrial, vertebrate or invertebrate, which have been examined (Reeves, '77; McMahon et al., '78; Truchot, '78; Cameron and Batterton, '78). Constant relative alkalinity (Rahn, '67) or constant fractional dissociation of histidine imidazole groups and hence protein net charge state (Reeves, '72, '77) is

thus maintained. The manner of acid-base regulation differs somewhat between species, however, as discussed in the introduction.

Birgus latro exhibited a pH change of -0.023 pH unit per degree rise in temperature over the full range $20-35^\circ$ but a somewhat lower value 0.019° per pH unit over the range of $25-35^\circ$. The latter value should perhaps be regarded as more representative considering the torpor resulting from exposure to 20° in this species. A considerable rise in P_{vCO_2} accompanied the increased temperature (Fig. 2A, Table 1), whereas total CO_2 (Fig. 2A) and bicarbonate levels (Table 1) remained very constant. It is thus clear that this animal is able to duplicate the abilities of terrestrial vertebrates and closely regulate acid-base status by ventilatory regulation of body fluid P_{CO_2} . Venous hemolymph PO_2 levels increase following acclimation to higher temperature in this species (McMahon and Burggren, unpublished observations), and thus sufficient oxygenation for at least routine activity can apparently be supplied despite an apparent relative reduction in ventilation.

The situation in *Cardiosoma* is somewhat different. Changes in pH are within the predictable range (Table 1, Fig. 2) over the entire temperature study, but the mechanism of acid-base control apparently varies with temperature on either side of 25° . Over the interval $15-25^\circ$, there is no significant change in mean P_{CO_2} , but a very substantial (significant at $P < 0.001$) decrease in hemolymph bicarbonate concentration occurs. Under these conditions *Cardiosoma* is clearly able to regulate its acid-base status but utilises a method very similar to that of aquatic ectotherms. Over the interval $25-35^\circ$, which is probably much more frequently encountered in the natural habitat, a radically different pattern is seen (Table 1, Fig. 2). No significant change in bicarbonate occurs, but P_{CO_2} increases significantly. Thus acid-base status over this higher temperature range appears to be regulated by carbon dioxide retention, in much the same manner as in terrestrial ectotherms. Venous PO_2 levels again increase with increasing temperature (McMahon and Burggren, unpublished observations), suggesting that adequate oxygenation occurs at each temperature step. The radical difference between responses between the two temperature intervals should be regarded not only in purely physiological terms but also in terms of behavioral responses to environmental change. The temperature interval $15-25^\circ$ represents strongly adverse conditions for

these animals. They become torpid at 15° , and under these conditions would thus remain in the burrows, where water is available. Under these conditions it is not surprising that an "aquatic" mode of temperature control, i.e., variation of hemolymph HCO_3^- , could be entertained. Over the temperature interval $25-35^\circ$ the animal is normally active, out of the burrow, and exposed to the terrestrial environment, conditions in which the "terrestrial" mode of regulation by variation in P_{CO_2} would be favoured. A somewhat similar dichotomy in acid-base regulatory mechanism above and below 25° is reported for the marine iguana *Amblyrhynchus cristatus* by Ackerman and White ('80); in contrast with the crustacean, however, *Amblyrhynchus* also displays a marked reduction in $\Delta\text{pH}/\Delta t$ at cooler temperatures at least in the short term. In this, purely lung breathing form Ackerman and White ('80) relate the dichotomy to respiratory disturbance resulting from exposure to abnormally low temperature.

The situation in the land hermit crab *Coenobita brevimanus* is likewise complex. The relationship $\Delta\text{pH}/\Delta t$ is most constant in this species (Table 1, Fig. 2) being -0.018 pH units per degree rise in temperature over the whole 2-decade temperature range, but the other results are difficult to interpret. Mean P_{CO_2} increases with rise in body temperature throughout the test range, but the increase is rather less (0.24 torr per degree) than *Birgus* (0.7 torr per degree). Mean bicarbonate concentration in hemolymph is precisely similar at both 15° and 35° , but is significantly ($P < 0.05$) elevated (Fig. 2c, Table 1) in three distinct series of measurements at 25° . The measured levels at 15° are perplexing, but may possibly be attributed to the fact that *Coenobita* at this temperature were exceptionally torpid, and may not have been able to regulate bicarbonate and CO_2 levels satisfactorily owing to greatly reduced metabolic capacity. Two animals actually died at this temperature, perhaps as a result. Over the interval $25-35^\circ$, both increase in P_{CO_2} and decrease in hemolymph bicarbonate are observed, suggesting that in this animal the possession of the shell water stores allows the retention of either mode of acid-base regulatory capability. Animals thus could utilize both systems simultaneously or could perhaps use either, depending upon water availability.

Both Jackson and Kagen ('76) and Ackerman and White ('80) have studied differential effects of warming and cooling on acid-base

balance in reptiles but to our knowledge no previous study has investigated these hysteresis effects in invertebrates. The present study includes sufficient measurements to assess the degree of hysteresis in pH, P_{CO_2} , and C_{CO_2} measured over the range 15–25° and 25–35° for *Coenobita* and *Cardisoma*, and 25–35° for *Birgus*. Although small differences between the means of measurements repeated at 25°C throughout the experimental period can be ascertained in the data presented in Table 1 and Figure 2, no predictable hysteresis effect such as that demonstrated for the marine iguana by Ackerman and White ('80) could be observed. With the exceptions of pH and C_{CO_2} for the first sampling period in *Cardisoma* ($P = < 0.05$) repeated measurements at 25° are never significantly different. There is, however, a tendency for pH measurements to be lower at the first measurement period in all species. This suggests that a slight acidosis may result from initial handling and acclimation to the experimental holding conditions. Previous studies (McMahon et al., '78; Truchot, '73) have suggested that repeated sampling disturbance causes progressive acidosis in crustaceans. The present study suggests that a 4-day recovery period between samples is sufficient to prevent this occurrence, at least in these terrestrial forms. Control of all variables tested is thus quite precise in these animals, at least as evidenced by multiple measurements at 25°. The close correspondence of these repeat measurements also provides good evidence against any deterioration of health in the animal stocks occurring during the experiment.

In conclusion it is evident that *Birgus latro*, a virtually fully terrestrial crab with a well-developed accessory air-breathing organ, is able to maintain acid-base status as temperature varies by ventilatory adjustment of P_{CO_2} at constant hemolymph bicarbonate. In this regard its responses are essentially similar to those of terrestrial ectothermic vertebrates. Both *Cardisoma*, which has access to water in the burrow, and *Coenobita*, which has access to water in the shell, can apparently regulate acid-base status either by control of P_{CO_2} or by control of bicarbonate at the gills and may be able to use either mechanism or a blend, depending on the availability of water and on other physiological or environmental requirements. These animals thus may be doubly bimodal, using the gills not only for O_2 acquisition (O'Mahoney, '77; McMahon and Burggren, '79) but also in acid-base regulation. Such a condition is clearly of survival benefit

for animals in an environment in which temperature and water availability varies.

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LITERATURE CITED

- Ackerman, R.A., and F.N. White (1980) The effects of temperature on acid-base balance and ventilation of the marine iguana. *Resp. Physiol.* 40:133–147.
- Burggren, W.W., and B.R. McMahon (1981) Hemolymph oxygen transport, acid-base status, and hydromineral regulation during dehydration in three terrestrial crabs, *Cardisoma*, *Birgus* and *Coenobita*. *J. Exp. Zool.* 218:53–64.
- Cameron, J.N. (1971) Rapid method for determination of total carbon dioxide in small blood samples. *J. Appl. Physiol.* 31:632–634.
- Cameron, J.N., and C.V. Batterton, Temperature and blood acid-base status in the blue crab, *Callinectes sapidus*. *Resp. Physiol.* 35:101–110.
- Cameron, J.N., and T.A. Mecklenburg (1973) Aerial gas exchange in the coconut crab, *Birgus latro*, with some notes on *Geocarcoidea lalandii*. *Resp. Physiol.* 19:245–261.
- Dejours, P. (1975) Principles of Comparative Respiratory Physiology. North Holland, American Elsevier.
- de Wilde, P.A.W.J. (1973) On the ecology of *Coenobita clypeatus* in Curacao. With reference to reproduction, water economy and osmoregulation in terrestrial hermit crabs. In Studies on the Fauna of Curacao and Other Caribbean Islands, vol. 44. The Hague, Martinus Nijhoff.
- Fontaine, M. (1933) Sur un relation entre le teneur en gaz carbonique libre et combiné du milieu intérieur et le niveau moyen de l'habitat chez quelques décapodes brachyryhnes. *Bull. Inst. Oceanogr.* 639:1–4.
- Hassall, C.D.H. (1979) Respiratory physiology of the crayfish *Procambarus clarki*. M.Sc. Thesis, University of Calgary, Calgary, Alberta, Canada.
- Howell, B.J., H. Rahn, D. Goodfellow, and C. Herreid (1973) Acid-base regulation and temperature in selected invertebrates as a function of temperature. *Am. Zool.* 13:557–563.
- Jackson, D.C., and R.D. Kagen (1976) Effects of temperature transients on gas exchange and acid-base status of turtles. *Am. J. Physiol.* 230:1389–1393.
- Magnum, C.P. (1973) Evaluation of the functional properties of invertebrate hemoglobins. *Neth. J. Sea Res.* 7:303–315.
- Mangum, C.P., and J.M. Schick (1972) The pH of body fluids of marine invertebrates. *Comp. Biochem. Physiol.* 42A:693–697.
- McMahon, B.R., F. Sinclair, C. Hassall, P.L. deFur, and P. Wilkes (1978) Ventilation and control of acid-base status during temperature acclimation in the crab *Cancer magister*. *J. Comp. Physiol.* 128:109–116.
- McMahon, B.R., and W.W. Burggren (1979) Respiration and adaptation to the terrestrial habitat in the land hermit crab *Coenobita clypeatus*. *J. Exp. Biol.* 79:265–282.

- O'Mahoney, P.M. (1977) Respiration and acid-base balance in brachyuran decapod crustaceans: The transition from water to land. Ph.D. Thesis, State University of New York at Buffalo.
- Rahn, H. (1967) Gas transport from the external environment to the cell. Ciba Foundation Symposium: Development of the Lung. London, Churchill.
- Rahn, H., and F.W. Baumgardner (1972) Temperature and acid-base regulation in fish. *Resp. Physiol.* *14*:171-182.
- Randall, D.J., and J.N. Cameron (1973) Respiration and control of arterial pH as temperature changes in rainbow trout, *Salmo gairdneri*. *Am. J. Physiol.* *225*:997-1002.
- Redmond, J. (1968) Transport of oxygen by the blood of the land crab *Gecarcinus lateralis*. *Am. Zool.* *8*:471-479.
- Reeves, R.B. (1972) An imidazole alphastat hypothesis for vertebrate acid-base regulation: Tissue carbon dioxide content and body temperature in bullfrogs. *Resp. Physiol.* *14*:219-236.
- Reeves, R.B. (1977) The interaction of body temperature and acid-base balance in ectothermic vertebrates. *Ann. Rev. Physiol.* *39*:559-586.
- Taylor, E.W., and P.J. Butler (1978) Aquatic and aerial respiration in the shore crab *Carcinus maenas* (L.) acclimated to 15°. *J. Comp. Physiol.* *127(B)*:315-323.
- Toulmond, A. (1977a) Temperature-induced variations of blood acid-base status in the lugworm, *Arenicola marina*. I: In vitro study. *Resp. Physiol.* *31*:139-149.
- Toulmond, A. (1977b) Temperature-induced variations of blood acid-base status in the lugworm, *Arenicola marina*. II: In vivo study. *Resp. Physiol.* *31*:151-160.
- Truchot, J.P. (1973) Temperature and acid-base regulation in the shore crab *Carcinus maenas* (L.). *Resp. Physiol.* *17*:11-20.
- Truchot, J.P. (1976) Carbon dioxide combining properties of the blood of the shore crab *Carcinus maenas* (L.): Carbon dioxide solubility coefficients and carbonic acid dissociation constants. *J. Exp. Biol.* *64*:45-57.
- Truchot, J.P. (1978) Mechanisms of extracellular acid-base regulation as temperature changes in decapod crustaceans. *Resp. Physiol.* *33*:161-176.
- Wheatly, M.G., and E.W. Taylor (1979) Oxygen levels, acid-base status and heart rate during emersion of the shore crab *Carcinus maenas* (L.) into air. *J. Comp. Physiol.* *132(B)*:305-311.
- Wood, S.C., M. Glass, and K. Johansen (1977) Effects of temperature on respiration and acid-base balance in a monitor lizard. *J. Comp. Physiol.* *116*:287-296.