

## **EFFECTS OF TEMPERATURE ON GAS EXCHANGE AND ACID–BASE BALANCE IN THE SEA TURTLE *CARETTA CARETTA* AT REST AND DURING ROUTINE ACTIVITY**

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### **Summary**

Oxygen consumption, lung ventilation, plasma ion concentrations and osmolality, venous blood acid–base status and gas tensions were measured in unrestrained loggerhead sea turtles in sea water at 10, 15, 20 and 30°C at rest and during routine activity. Moderate activity caused a threefold increase in oxygen consumption, accommodated by a twofold increase in ventilation (the result of increases in breathing frequency) and a 60% increase in lung oxygen extraction. There was an increase in oxygen consumption with temperature ( $Q_{10} = 2.4$ ) also due primarily to an increase in oxygen extraction (decline in air convection requirement, ACR) since neither the tidal volume nor the breathing frequency changed.

Over the temperature range 15–30°C venous blood pH decreased by 0.017 units °C<sup>-1</sup>, indicating that the maintenance of constant relative alkalinity is not confined to species of low aerobic scope. Venous blood  $P_{CO_2}$  and  $P_{O_2}$  increased with temperature. However,  $[HCO_3^-]$  decreased, suggesting that ventilatory adjustments alone are insufficient for regulating the thermally dependent shifts in blood pH. Plasma  $[K^+]$  increased with temperature, which may be related to cellular-mediated adjustments in blood pH.

Temperature-related adjustments of blood pH in the loggerhead appear to be managed both at the lung (ACR-driven changes in blood  $P_{CO_2}$ ) and tissue (ion exchange) levels. This mixed regulation is associated with the unique mode of respiration of the sea turtle.

### **Introduction**

It is well established that temperature has profound effects on the respiratory physiology and acid–base balance of reptiles. In most reptiles increasing body temperature is associated with decreasing arterial blood pH. In earlier studies it appeared that the relationship between arterial blood pH and body temperature ( $\Delta pH/\Delta T$ ) was similar to that of neutral water (from 10 to 30°C the value of

**Key words:** sea turtle, temperature, oxygen consumption, lung ventilation, pH, blood gases, blood ions, lactate, urea.

$\Delta pN/\Delta T$  ranges from  $-0.018$  to  $-0.016$ , Truchot, 1981), such that the relative alkalinity of the blood remained constant (Howell & Rahn, 1976). However, as additional data accumulated, the number of exceptions has increased sufficiently to call this generalization into doubt (Heisler, 1986). For example, although it appears that amphibians maintain constant relative alkalinity in their arterial blood (Boutilier *et al.* 1987), the average value of  $\Delta pH/\Delta T$  for various turtle species is only  $-0.012$  and the varanid lizards exhibit an almost constant arterial blood pH over a wide range of body temperatures (Wood *et al.* 1977). The pH-independence of the varanid lizards has been linked to their high aerobic capacity (Wood *et al.* 1977) and it has been suggested that the concept of constant relative alkalinity applies only to 'species of low aerobic scope under resting conditions at their preferred body temperature' (Shelton *et al.* 1986).

For most reptiles, and particularly for turtles, it appears that the temperature-related blood pH changes are achieved through ventilatory adjustments, whereby the increase in oxygen consumption ( $\dot{V}_{O_2}$ ), consequent to a rise in body temperature, is not matched by an equivalent increase in lung ventilation ( $\dot{V}_E$ ) (Glass *et al.* 1985). The ratio of  $\dot{V}_E$  to  $\dot{V}_{O_2}$  (the air convection requirement, ACR) is, therefore, reduced as temperature increases, causing an increase in arterial blood  $P_{CO_2}$ . Thus blood  $CO_2$  content is maintained at a constant level and blood pH is controlled by changing  $P_{CO_2}$  (Jackson, 1982).

However, there are a number of lizards (Wood *et al.* 1977) and snakes (Nolan & Frankel, 1982; Stinner & Wardle, 1988) in which blood  $[CO_2]$  also changes with temperature, indicating that in these species cellular-mediated adjustments also play a role in regulating blood pH.

The above considerations apply only to arterial blood. Surprisingly little, by contrast, is known of the effect of temperature on venous blood. It is very likely that the acid-base status of venous blood, which more closely represents extracellular conditions (Bickler, 1982), will be strongly influenced by tissue metabolism. The relationship between tissue pH ( $pHi$ ) and temperature is also highly variable and different tissues in the same species can have quite different values for  $\Delta pHi/\Delta T$ , suggesting that each tissue maintains a unique  $\Delta pH/\Delta T$  relationship (Boutilier *et al.* 1987).

Sea turtles are particularly interesting subjects for the study of the effects of temperature on respiration and acid-base balance in reptiles. They are among the largest and most active of living reptiles and have aerobic capacities that match or may even exceed those of the varanid lizards (Jackson & Prange, 1979; Lutz & Bentley, 1985). They have a greater commitment to breathhold diving than any other reptile; loggerhead sea turtles (*Caretta caretta*) routinely spend 97% of their time submerged (Lutz & Bentley, 1985) and they have pulmonary adaptations to diving that show striking similarities to those of marine mammals (Lutcavage *et al.* 1989). It is possible that sea turtles have similarly distinctive temperature-related adjustments of blood pH and gas exchange. There is, however, only one paper on the effect of temperature on acid-base balance and ventilatory changes in sea turtles (Kraus & Jackson, 1980) and the results are somewhat ambivalent. Kraus &

Jackson (1980) found no significant change in the arterial blood pH of the green sea turtle *Chelonia mydas* between 15 and 25°C, but a pH decrease between 25 and 35°C. Their respiratory measurements were performed on turtles with immobilized limbs, which may have seriously interfered with their normal ventilatory response (Lutcavage *et al.* 1989). The purpose of this study was to investigate the effect of temperature on respiration, blood gases, blood chemistry and acid-base status in free-swimming sea turtles. We wished to establish if the maintenance of constant relative alkalinity was confined to turtles of low aerobic scope and to investigate if ventilatory adjustments of blood pH sufficed for a reptile with such distinctive pulmonary adaptations.

The loggerhead sea turtle (*Caretta caretta*) used in these studies is particularly suited to investigate the effects of temperature since (with the exception of the possibly 'warm-blooded' leatherback sea turtles, Mrosovsky, 1980) loggerhead sea turtles have the widest geographical range of any of the *Chelonia*, being routinely found from the tropics to the temperate zones, and, therefore, normally experience the widest range in body temperatures.

## **Materials and methods**

### *Animals and treatment*

Eight subadult loggerheads sea turtles (mass range, 4.3–22.7 kg; mean mass, 13.02 kg) were kept outdoors in four large tanks supplied with sea water. Two days before measurements were to be made turtles were transferred to a climate-controlled laboratory which had been adjusted to the desired experimental temperature, and the turtles were held individually and without restraint in 1000 l tanks in sea water. The water was changed routinely with water at the current experimental temperature. The animals were not fed during this period. Experiments on the sea turtles were carried out at four water temperatures: 10, 15, 20 and 30°C with the turtles being held at least 2 days at each temperature.

### *Respiratory measurements*

Respiratory measurements were obtained by placing a lid with a breathing hole over the surface of the sea water in the tank. The breathing hole had to be at the edge of the lid, because the turtles showed no learning ability for finding a hole placed in any other position. A Plexiglas chamber enclosed the breathing hole to which was fitted a one-way respiratory valve (Rudolph Inc.). A flexible latex collection bag (10 l weather balloon) connected to the exhalant port of the one-way valve was used to receive the expired gas. This gas was drawn at a constant rate (200 ml min<sup>-1</sup>) through a Drierite column and then through a CO<sub>2</sub> absorbent (Ascarite) and the fractional O<sub>2</sub> concentration was measured by a differential O<sub>2</sub> analyzer (Applied Electrochemistry model S3A). Flow rates were calibrated using a bubble flowmeter. Ventilation volumes were also measured using a calibrated Fleish-type digital integrated pneumotachograph (Hewlett-Packard model 7303A) attached to the one-way valve. The pneumotachograph was calibrated

using air-tight syringes of known volume. Measurements were taken continuously for 5 h. Average oxygen consumptions and tidal volumes for 5-h periods were calculated for each animal by planimetry of the signal outputs before the group means  $\pm$  s.e. were determined.

The turtles showed some behavioural variation within runs. Typically, they rested quietly, usually on the bottom of the tank, for long periods interrupted only by slow rises to the surface to breathe. Occasionally, however, they paddled slowly and continuously round the tank for as much as 30 min. Since continuous measurements were taken, the respiratory activity was divided into 'resting' and 'routine activity' periods.

### *Blood analyses*

Venous blood was taken from hand-restrained turtles while in the experimental tanks by quickly puncturing the dorsal cervical sinus with a heparinized syringe. This sinus receives blood from the cephalic region. Arterial cannulation proved unsuitable for these experiments since after a few days the cannulated animals tended to spend a greater amount of time at the water surface. The normal diving pattern resumed after removal of the cannula. Blood gases ( $P_{O_2}$ ,  $P_{CO_2}$ ) and pH were determined immediately on whole blood using a Radiometer BMS Mk 2 blood gas analyzer. For each experimental run the blood gas analyzer was set at the current experimental temperature. Plasma [bicarbonate] was calculated from the pH and  $P_{CO_2}$  data, using the temperature- and pH-dependent  $CO_2$  solubility and dissociation constants of Severinghaus (1965). The appropriateness of these constants is considered in the Discussion.

The blood was then centrifuged and the plasma divided into two parts. One part was deproteinized with 8% chilled perchloric acid and used for plasma lactate and urea measurements using Sigma kit no. 826-uv for lactate and Sigma kit no. 640 for urea. The untreated plasma was analyzed for osmotic pressure using a Wescor 6100 osmometer, and saved frozen for measurement of chloride using an Aminco chloride titrator and plasma cations using atomic absorption spectrophotometry (Perkin Elmer PE 403).

## **Results**

### *Oxygen consumption*

The oxygen consumption for resting ( $\dot{V}_{O_{2r}}$ ) and routinely active turtles ( $\dot{V}_{O_{2a}}$ ) increased with temperature (T) over the range 10–30°C (Fig. 1). The relationships were highly significant, the respective regression equations being:

$$\begin{aligned} \log \dot{V}_{O_{2r}} &= 0.038T - 1.074 \text{ (ml min}^{-1} \text{ kg}^{-1}) \quad N = 12, r = 0.817, \\ \log \dot{V}_{O_{2a}} &= 0.038T - 1.564 \text{ (ml min}^{-1} \text{ kg}^{-1}) \quad N = 11, r = 0.869. \end{aligned}$$

The  $Q_{10}$  for both resting and active oxygen consumption was 2.4.  $Q_{10}$  values of between 2 and 3 are typical for reptiles (Glass & Wood, 1983).

Over this temperature range the oxygen consumption increased about three,

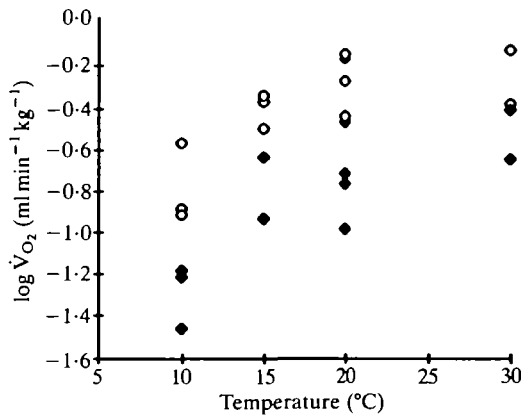


Fig. 1. The effect of temperature on the oxygen consumption of quiescent (◆) and routinely active (◇) loggerhead turtles. For each experiment measurements were taken continuously for 5 h (see text for details).

fold between rest and activity. Similar increases have been found for swimming green sea turtles (Davenport *et al.* 1982; Butler *et al.* 1984).

#### Tidal volume

There was no significant difference between the tidal volumes of the active and resting turtles, and no relationship was found between tidal volume and temperature for either group. The average tidal volume for the whole set was  $22.14 \pm 1.844$  ml kg<sup>-1</sup>,  $N = 23$ . This value is close to that found for green sea turtles ( $24.4$  ml kg<sup>-1</sup>, Butler *et al.* 1984) and for varanid lizards ( $20.5$  ml kg<sup>-1</sup> at  $25^\circ\text{C}$ , Wood *et al.* 1977). It is substantially greater than that typical of freshwater turtles ( $6.9$ – $15.7$  ml kg<sup>-1</sup>, Vitalis & Milsom, 1986).

#### Frequency

No relationship was found between respiration rate and temperature, although the respiration rate increased on activity ( $f_a/f_r = 3.05 \pm 0.501$  ( $\pm$ s.e.,  $N = 12$ )). Interestingly, for the active loggerhead turtles an increase in respiration rate was associated with a diminution in tidal volume (Fig. 2A). The average resting value for the whole set was  $0.27 \pm 0.042$  breaths min<sup>-1</sup> ( $N = 12$ ); the average for routinely active turtles was  $0.76 \pm 0.075$  breaths min<sup>-1</sup> ( $N = 13$ ). Kraus & Jackson (1980) found no change in the breathing frequency of green sea turtles over the temperature range  $15$ – $25^\circ\text{C}$  ( $0.64$ – $0.65$  breaths min<sup>-1</sup>) but they noted a slight increase at  $35^\circ\text{C}$ . A threefold increase in breathing frequency has also been found between resting and active swimming in green sea turtles (Butler *et al.* 1984).

#### Ventilation

During routine activity, lung ventilation increased two-fold ( $\dot{V}_{Ea}/\dot{V}_{Er} = 2.14 \pm 0.283$ ,  $N = 9$ ). The overall ventilation rate for routinely active turtles was

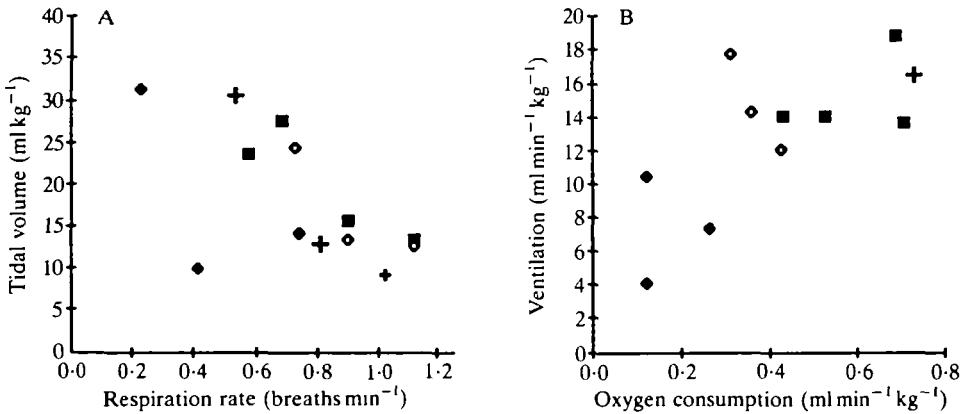


Fig. 2. The relationship between (A) respiration rate and tidal volume and (B) lung ventilation and oxygen consumption for active turtles at 10°C (◆), 15°C (◇), 20°C (■) and 30°C (+).

12.5 ± 1.6 ml min<sup>-1</sup> kg<sup>-1</sup> (N = 13). In the resting turtles no relationship was found between ventilation and temperature, and no statistically significant relationship was found between oxygen consumption and ventilation ( $P = 0.58$ ). However, in active turtles, ventilation increased with oxygen consumption (Fig. 2B,  $P < 0.5$ ).

#### *Air convection requirement*

The air convection requirement ( $ACR = \dot{V}_E / \dot{V}_{O_2}$ ) was highly variable, ranging from 16.8 to 120. Similar ranges have been reported for chelonians and saurians (Glass & Wood, 1983). However, as temperature fell, there was a tendency for the ACR to increase in both resting and active turtles, except at 10°C where there was a sharp fall in the resting turtles (Fig. 3A,B). A similar decrease in ACR with rise

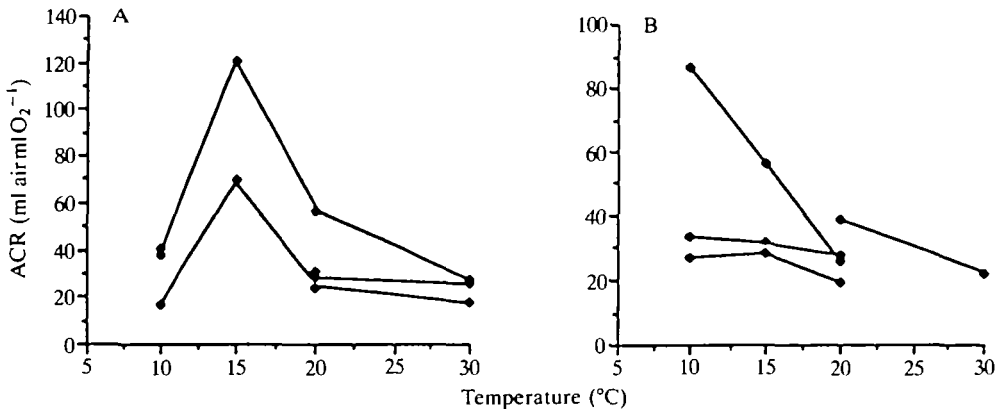


Fig. 3. The effect of temperature upon the air convection requirement (ACR) in (A) quiescent and (B) routinely active loggerhead sea turtles. Points for individuals are joined.

in temperature has been noted for various turtle species (Glass & Wood, 1983). Overall, the air convection requirement also decreased with activity ( $ACR_r/ACR_a = 1.60 \pm 0.404$ ,  $N = 10$ ), indicating an increase in oxygen extraction. At 25°C the mean resting ACR was 34.0 and the mean active ACR was 24.1. These values are very similar to those reported for the green sea turtle ( $ACR = 28.1$  at 25°C, Kraus & Jackson, 1980).

#### Blood gases and pH

A highly significant relationship was found between venous blood pH and temperature (Fig. 4A) which, over the range 15–30°C, yielded the equation:

$$pH = 7.843 - 0.017T \quad N = 23, r = 0.940.$$

The slope of the linear regression ( $\Delta pH/\Delta T = -0.017$ ) is within the range for neutral water over the temperature range 10–30°C ( $\Delta pH/\Delta T = -0.0180$  to  $-0.016$ , Truchot, 1981). Interestingly, two individuals showed a substantial fall in pH at 10°C (Fig. 4A).

Increasing temperature is associated with higher blood  $P_{CO_2}$  levels ( $P < 0.01$ ). At 10°C, however, higher blood  $P_{CO_2}$  values were found in two turtles (Fig. 4B).

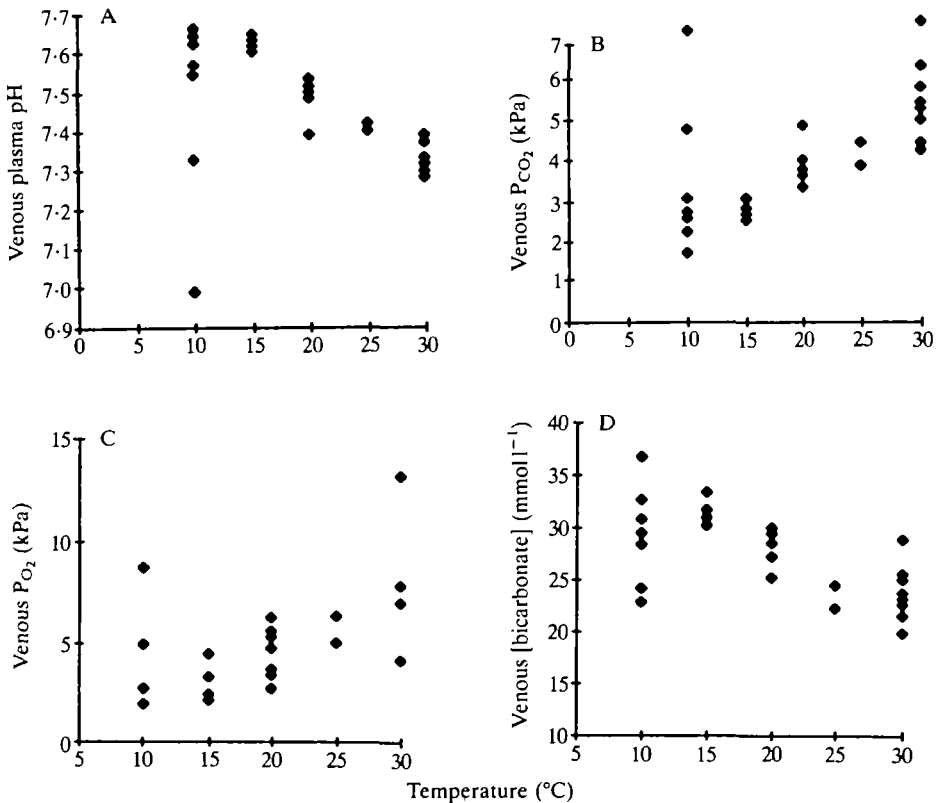


Fig. 4. The effect of temperature on (A) venous blood pH, (B) venous  $P_{CO_2}$ , (C) venous  $P_{O_2}$ , (D) venous bicarbonate concentration, in the loggerhead sea turtle.

The analyses of covariance on the relationship between  $\log P_{\text{CO}_2}$  and pH gave a highly significant correlation ( $P < 0.001$ ) with the slope  $\Delta \log P_{\text{CO}_2} / \Delta \text{pH} = -0.296 \text{ kPa pH unit}^{-1}$ .

The change in venous blood oxygen levels paralleled that of  $P_{\text{CO}_2}$ :  $P_{\text{O}_2}$  fell with temperature from 30 to 15°C ( $P < 0.01$ ) but, as with  $P_{\text{CO}_2}$ , for two individuals this trend was reversed at 10°C (Fig. 4C).

The bicarbonate concentration of loggerhead sea turtle blood ( $25.9 \text{ mmol l}^{-1}$  at 25°C) was similar to that found for the green sea turtle by Kraus & Jackson (1980) ( $27.8 \text{ mmol l}^{-1}$  at 25°C). Over the range 15–30°C venous blood bicarbonate decreased with temperature (Fig. 4D). The linear regression for this relationship is:

$$\text{HCO}_3^- (\text{mmol l}^{-1}) = 38.67 - 0.51T \quad N = 23, r = 0.823.$$

At 10°C there was some evidence of a decrease in blood bicarbonate (Fig. 4D).

#### *Blood ion concentrations*

Temperature had no significant effect on blood calcium, magnesium or chloride concentrations, all of which were maintained within rather narrow limits (Table 1). Between 15 and 30°C, however, potassium level increased significantly with temperature (Table 1, Fig. 5A), yielding the following linear regression:

$$\text{K}^+ (\text{mmol l}^{-1}) = 1.228 - 0.157T \quad N = 18, r = 0.71.$$

The mean values for osmolality declined over the range 30–15°C but the changes were not significant (Table 1).

Although urea values varied widely from 0.9 to 15.1  $\text{mmol l}^{-1}$  (Table 1), higher temperatures appeared to be associated with higher urea levels (Fig. 5B).

Over the range 15–30°C blood lactate levels were very low, less than 1  $\text{mmol l}^{-1}$ , and appeared to be temperature-independent. At 10°C a large and highly significant increase (Student's *t*-test,  $P < 0.001$ ) was seen, although the animals were particularly quiescent at this temperature (Fig. 5C, Table 1).

### **Discussion**

#### *Oxygen consumption*

Over the temperature range of these experiments, moderate routine activity caused a threefold increase in oxygen consumption from resting rates. Since there was no corresponding change in tidal volume, this increase in oxygen consumption was accommodated by a matching threefold increase in respiratory frequency. However, the change in respiratory frequency is not the whole answer, as active turtles showed a decrease in tidal volume at higher respiratory frequencies, the result being that, on average, lung ventilation only increased twofold on activity. This proportionately smaller increase in lung ventilation is compensated for by an activity-related 60% increase in oxygen extraction.

A somewhat similar response to activity was found for green turtles by Jackson



Table 1. The effect of temperature on the osmotic and ionic composition of loggerhead sea turtle blood

Temperature (°C)	[K <sup>+</sup> ] (mmol l <sup>-1</sup> )	[Ca <sup>2+</sup> ] (mmol l <sup>-1</sup> )	[Mg <sup>2+</sup> ] (mmol l <sup>-1</sup> )	[Cl <sup>-</sup> ] (mmol l <sup>-1</sup> )	[Lactate] (mmol l <sup>-1</sup> )	[Bicarbonate] (mmol l <sup>-1</sup> )	[Urea] (mmol l <sup>-1</sup> )	Osmolality (mosmol kg <sup>-1</sup> )
30	4.35 ± 0.24 (6)	1.42 ± 0.155 (7)	1.60 ± 0.113 (8)	110.9 ± 1.56 (8)	0.260 ± 0.045 (8)	23.8 ± 0.97 (8)	10.28 ± 1.559 (7)	325.2 ± 11.31 (8)
25	3.81 (2)	2.17 (2)	1.34 ± 0.152 (3)	120.7 ± 4.43 (3)	0.207 ± 0.003 (3)	23.24 (2)	7.37 ± 0.906 (3)	304.5 ± 7.44 (3)
20	3.53 ± 1.78 (7)	1.48 ± 0.204 (8)	2.13 ± 0.254 (7)	109.2 ± 1.273 (8)	0.434 ± 0.14 (7)	28.64 ± 0.61 (7)	4.03 ± 0.614 (6)	295.3 ± 14.8 (7)
15	2.86 ± 0.47 (5)	1.19 ± 0.060 (5)	1.86 ± 0.165 (5)	107.6 ± 2.02 (5)	0.502 ± 0.114 (4)	30.15 ± 0.57 (6)	3.60 ± 0.923 (4)	306.9 ± 13.4 (5)
10	4.03 ± 0.28 (4)	1.28 ± 0.132 (6)	2.03 ± 0.215 (7)	108.3 ± 2.41 (7)	1.605 ± 0.49 (7)	29.27 ± 1.82 (7)	4.17 ± 0.526 (7)	298.9 ± 11.9 (7)

Values are means ± s.e. (N).

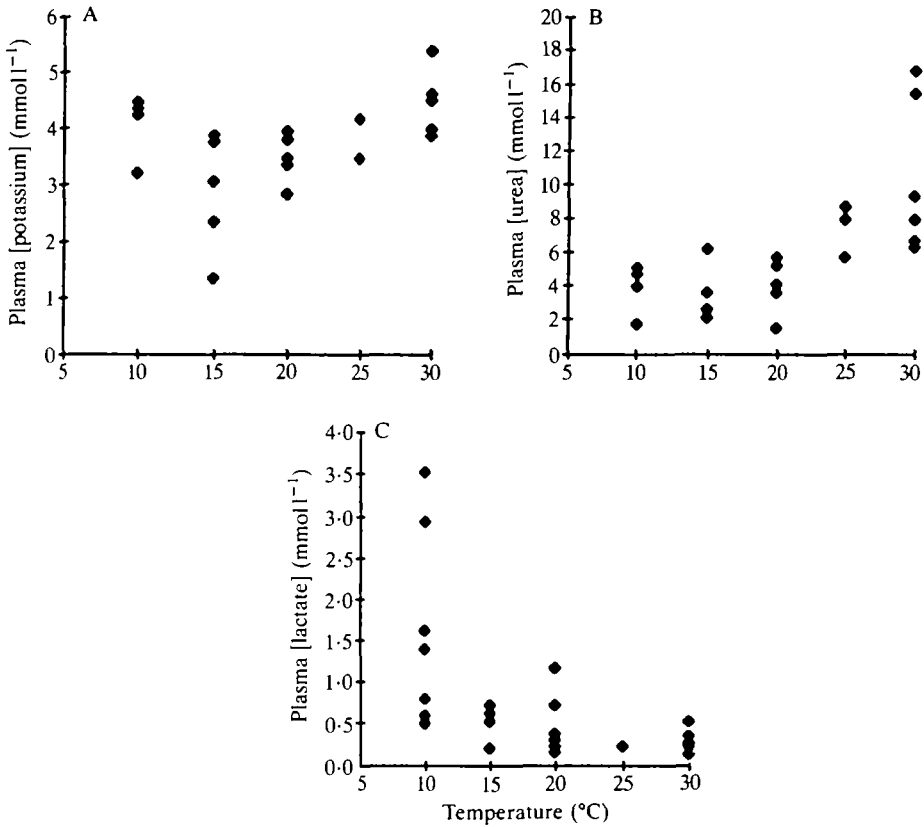


Fig. 5. The effect of temperature on plasma concentrations of (A) potassium, (B) urea and (C) lactate in the loggerhead sea turtle.

& Prange (1979), an increase in breathing frequency but no change in tidal volume. However, they reported that exercise caused a much greater (200%) increase in the air convection requirement, but this occurred on land under conditions of maximum effort. Butler *et al.* (1984) also found that green turtles increased lung ventilation during swimming solely by increasing breathing frequency.

It appears that in both loggerheads and green turtles the increase in oxygen uptake due to activity is not matched by an equivalent rise in lung ventilation. Higher oxygen demands are accommodated by increases in ventilation (due solely to changes in breathing frequency, not tidal volume) and by increases in the amount of oxygen taken at each breath. It is very likely that sea turtles have only a limited scope to increase their tidal volume since, like many marine mammals, it typically accounts for more than 50% of the total lung volume (Lutcavage *et al.* 1987).

However, the increase of oxygen uptake with temperature could not be attributed to changes in either tidal volume or breathing frequency, suggesting

that it is principally accommodated by an increase in the amount of oxygen taken per breath. A decrease in the ACR as body temperature increases appears to be common for turtles (Glass & Wood, 1983), including the green sea turtle (Kraus & Jackson, 1980). The freshwater turtle *Pseudemys scripta* also shows no change in ventilation with temperature (Jackson *et al.* 1974; Hitzig, 1982). However, an increase in ventilation with temperature has been found for some other freshwater turtles due to changes in breathing frequency or tidal volume or, in some cases, both (see Shelton *et al.* 1986), and Kraus & Jackson (1980) also found a substantial increase in ventilation with temperature in green sea turtles.

It appears that in the sea turtle the increase in O<sub>2</sub> consumption that accompanies routine activity or a rise in body temperature is accommodated by a rise in both breathing frequency and the amount of oxygen taken at each breath, the former being of greater importance for activity, the latter predominating as temperature increases. The tidal volume occupies such a large proportion of the resting lung volume that, as in marine mammals, the scope for increased tidal volume is limited.

#### *Blood gases*

An increase in arterial blood P<sub>CO<sub>2</sub></sub> with temperature has been widely recorded for reptiles (Glass *et al.* 1985; Boutilier *et al.* 1987) and appears to be mainly the result of ventilatory adjustments whereby the ACR is reduced as temperature rises (Shelton *et al.* 1986).

A temperature-related increase in the P<sub>O<sub>2</sub></sub> of arterial blood has also been recorded for many reptiles (Wood, 1984; Boutilier *et al.* 1987). Wood (1984) has suggested that, in reptiles that use cardiovascular shunts, the arterial oxygen content will depend on the degree of shunting and that a decrease in blood oxygen-affinity caused by increasing body temperature would produce higher P<sub>O<sub>2</sub></sub> levels. Although the oxygen content of venous blood will be determined by the rates of tissue oxygen delivery and oxygen demand, as for arterial blood, any effect that produces a decrease in oxygen affinity (such as an increase in temperature, P<sub>CO<sub>2</sub></sub> or [H<sup>+</sup>]) would result in higher venous P<sub>O<sub>2</sub></sub> levels. This would particularly apply if the venous oxygen content remained reasonably constant as temperature changed. An increased venous P<sub>O<sub>2</sub></sub> at higher temperatures could reflect a higher capillary-to-tissue P<sub>O<sub>2</sub></sub> gradient and, therefore, an enhanced driving gradient to accommodate the increased metabolic rates.

#### *Ionic and osmotic composition*

Temperature had no effect on loggerhead turtle plasma chloride, calcium or magnesium levels or osmotic pressure. By contrast, plasma K<sup>+</sup> level increased with temperature in an identical manner to that found in a field study of a large number of 'wild' loggerheads (Lutz & Dunbar-Cooper, 1987). We are not aware of this relationship being reported before, but clearly it is not a laboratory artefact. The elevated plasma urea could be related to increased protein catabolism at higher temperatures.

*Acid-base balance*

Over the temperature range 15–30°C the venous blood of the loggerhead sea turtle conforms to the general rule for poikilotherms: (arterial) blood pH declines as body temperature falls (Truchot, 1981). For this animal, the slope of the regression between venous pH and body temperature ( $\Delta\text{pH}/\Delta\text{T}$ ) parallels the neutral line for water, suggesting that constant relative alkalinity is maintained. However, as for arterial blood (Heisler, 1986), there are probably a wide range of values for this parameter among different animals. Bickler (1982), for example, obtained a value of  $-0.012$  for venous blood of the lizard *Dipsosaurus dorsalis*. The more data are gathered, the less common constant relative alkalinity appears to be (Heisler, 1986).

The suggestion that only species of low aerobic scope maintain constant relative alkalinity (Shelton *et al.* 1986) is insufficient, since sea turtles have the highest aerobic capacities of any reptiles (Lutcavage *et al.* 1987). It is possible that values for  $\Delta\text{pH}/\Delta\text{T}$  are widely scattered throughout the reptiles and that it is merely a coincidence that a few species have relationships similar to that for neutral water. Or it may be a common feature for both freshwater and sea turtles, and characteristic of Chelonia.

*Regulation of pH*

In many reptiles it appears that ventilatory adjustments are solely responsible for temperature-related shifts in arterial pH, the decrease in ACR with temperature causing a rise in arterial  $\text{P}_{\text{CO}_2}$  which produces a fall in arterial pH (Shelton *et al.* 1986). In this scheme total blood  $[\text{CO}_2]$  and, therefore, blood  $[\text{HCO}_3^-]$  remain relatively constant. However, there appear to be a number of exceptions (lizards, Wood *et al.* 1977; snakes, Nolan & Frankel, 1982; Stinner & Wardle, 1988) and the issue is somewhat confused by the fact that different authors have used different functions in calculating the value of the apparent pK for the Henderson-Hasselbalch equation. One of the most widely used set of values (Reeves, 1976) only accounts for the effect of temperature on apparent pK and makes no correction for the effect of pH. The functions given by Severinghaus (1965) and Siggaard-Andersen (1974) take into account both pH and temperature. As far as the freshwater turtle *Chrysemys picta belli* is concerned, calculations of bicarbonate levels using either set of functions agree with direct measurements in showing that bicarbonate level is independent of temperature (Nicol *et al.* 1983). However, applying the Severinghaus *et al.* (1956) functions to the data for the green turtle of Kraus & Jackson (1980) indicates a decline in bicarbonate level with temperature (35°C, 24.8 mmol l<sup>-1</sup>; 25°C, 27.7 mmol l<sup>-1</sup>; 15°C, 32.0 mmol l<sup>-1</sup> HCO<sub>3</sub><sup>-</sup>) although, using the Reeves (1976) functions, the original paper (Kraus & Jackson, 1980) reported no change in bicarbonate level.

In the loggerhead sea turtle, increasing body temperature is associated with increasing venous  $\text{P}_{\text{CO}_2}$  and a fall in ACR, indicating that ventilatory adjustments play a role in managing the thermally dependent shifts in blood pH. But in thi

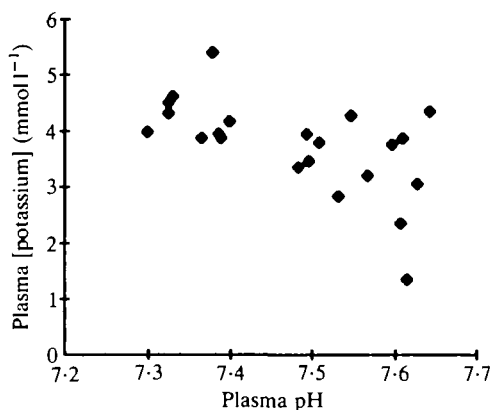


Fig. 6. Relationship between plasma pH and potassium concentration in the loggerhead sea turtle.

animal blood  $[\text{HCO}_3^-]$  also declines with temperature from 15 to 30°C. The lack of change in blood lactate level over this temperature range indicates that bicarbonate is not being consumed by acid titration, but rather that transcellular ion exchange processes using  $\text{HCO}_3^-$  are involved.

More direct evidence of ion exchange mechanisms being involved in pH regulation are seen in the temperature-related changes in potassium level (Fig. 5). For the whole set of loggerhead sea turtles increasing venous blood [potassium] is associated with increasing  $[\text{H}^+]$  (Fig. 6):

$$[\text{K}^+] = 34.93 - 4.173\text{pH} \quad N = 22, r = 0.568.$$

A similar phenomenon is found in mammals and is thought to be the result of intracellular buffering of blood pH whereby extracellular protons are taken up by the cell in exchange for  $\text{K}^+$  (Rose, 1977). The magnitudes of the shifts are also similar; in the loggerhead sea turtle a fall of 0.1 pH units is accompanied by a rise of  $0.4 \text{ mmol l}^{-1} \text{ K}^+$  and in man the change is  $0.6 \text{ mmol l}^{-1}$  (Rose, 1977).

Temperature-related adjustments of blood pH in sea turtle appear to be managed both at the lung and tissue (ion exchange) levels. One advantage of ventilatory control of blood pH, allowing a rapid response to changes in temperature (Wood, 1984), would be of little value to sea turtles entrained to the slow changes of the ocean and it is possible that the mode of respiration of sea turtles – infrequent breathing, explosive ventilation, breathhold diving from minutes to hours – is unsuited for a complete reliance on ventilatory adjustments of blood pH.

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