

## RESPIRATORY EXCHANGE AND BODY SIZE IN THE ALDABRA GIANT TORTOISE

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### INTRODUCTION

A decrease in metabolic rate per unit body weight with increase in size has been demonstrated for a large number of organisms. Kleiber (1947), Zeuthen (1947, 1953) and Hemmingsen (1960) have given comprehensive reviews in which they point out that although in all cases the relationship

$$\text{O}_2 \text{ consumption} = aW^b$$

is applicable, there are wide variations in the value of the exponent ( $b$ ). In some cases values between 0.67 and 0.75 give the best overall fit but there are many exceptions. There is a great need, however, for study of individual species in this respect; the amount of data available for reptiles being particularly limited. Dawson & Bartholomew (1956) studied this relationship in lizards and showed that slopes of the regression line for  $\log \text{O}_2$  consumption/ $\log$  body weight ranged from 0.47 to 0.68 in *Uta* and *Sceloporus*. They obtained an overall slope for different species of lizards of 0.54 and this was subsequently modified to 0.62 (Bartholomew & Tucker, 1964). Benedict (1932) studied a variety of snakes and alligators from this point of view, and Templeton (1970) in reviewing this field provided additional data which seems to fit the overall line for lizards put forward by Bartholomew & Tucker (1964). In a study of 50 snakes, including 18 species, Galvao, Tarasantchi & Guertzenstein (1965) obtained a slope of 0.82-0.86 for the log-log regression line relating metabolism to body weight. Vinegar, Hutchinson & Dowling (1970) compare the results of Galvao *et al.* for boids with their own, which gave a slope of 0.66.

Tortoises and turtles have for some time been considered possible exceptions to this general rule. Benedict (1932) found that the metabolic rate per unit body weight was more or less constant for four species of tortoise over the weight range 5-132 kg and these results were supported by Hutton, Boyer, Williams & Campbell (1960) with *Pseudemys*, for a smaller weight range.

The purpose of the present study was to take advantage of the availability of giant tortoises having a weight range of over 300 to 1 (with) in a single species. The shell is relatively light in *Testudo gigantea* and they are all in the size/age range of juveniles, or young adults which are still actively growing (Gaymer, 1968). In addition to investigating the relationship between body size and  $\text{O}_2$  uptake, some preliminary observations were made on the relationship between metabolic rate and activity. There are relatively few observations of this kind on reptiles, although Benedict records

that a 5 kg tortoise *T. denticulata* increased its metabolism by as much as 3.5 times above its standard level at 30 °C. Bartholomew & Tucker (1964) observed the ability of *Varanus* to increase its resting metabolism by a factor of up to 10 times during activity at 20 °C. They also noted an increase in metabolic scope for activity with body temperature in these animals. Moberly (1968) measured metabolic scope in *Iguana* and found it to be greatest at body temperatures of 32 °C; the maximum O<sub>2</sub> consumption being about 4 times that of the minimum recorded under the experimental conditions. Few investigations have been made, however, of the relationship between O<sub>2</sub> uptake under resting and active conditions in relation to body weight.

#### MATERIALS AND METHODS

All nine giant tortoises used in this study were collected on south island, Aldabra, and were of the same species *Testudo gigantea* Schweigger (= *Geochelone (Aldabra = chelys) gigantea*). The three larger animals were from Anse Mais, the smaller ones were collected along the south coast, west of Dune Jean Louis (see Gaymer, 1968, for locations).

The small animals were between 1.5 and 6 years old on arrival and weighed between 100 and 600 g. Three of these have been in the laboratory for about 1 year and have grown considerably. The three large animals were aged about 15, 20 and 24 years and weighed about 20, 28 and 35 kg during the period of the experiments. The largest animal is a male, the sex of the others is as yet undetermined. European tortoises, *T. hermanni*, of mixed age and provenance were also available and used in some experiments.

The tortoises were housed in a heated room maintained at about 26 °C. Normally the temperature range was from 25 to 27 °C. Infra-red lamps were provided for basking. Lighting was on a 12 h time clock, approximating to the natural day-length on Aldabra, which lies 10° south of the equator, 260 miles north-west of Madagascar.

The tortoises were fed daily on a diet of fresh fruit and vegetables with clover hay. Vitamin syrup ('Vitavel') and a small amount of calcium phosphate were added to the food at intervals. Water was constantly available for the small tortoises and was offered to the three larger specimens at intervals of a few weeks.

All animals were acclimatized to their surroundings for several months before the experiments which, with one exception, were carried out in the animal house where the tortoises lived.

Fig. 1 shows a diagram of the apparatus used in most experiments. The animal was lifted into the respirometer box and allowed to settle down before the lid was sealed. Three different sizes of respirometer (about 3.9, 12.1 and 250 l capacity) were used according to the size of the specimen. Changes in O<sub>2</sub> and CO<sub>2</sub> content of the respirometer air were followed either (a) by withdrawing at fixed intervals samples which were analysed using a Scholander 0.5 ml gas analyser or (b) by continuous monitoring of the O<sub>2</sub> and CO<sub>2</sub> content with a Servomex industrial O<sub>2</sub> analyser and a Beckman LB1 medical CO<sub>2</sub> analyser. The analyser outputs were displayed on a Rikadenki pen recorder together with a simultaneous thermistor recording of box temperature and the output of a contact aktograph.

The average temperature at which experiments were performed was 25.5 °C within

range from 21.3 to 29.2 °C. The larger respirometer had a fan attached so that there was a good mixing of the air gases. Mixing in the smaller respirometer was ensured by means of a syringe before withdrawing a sample. If readings for a quiet animal were required, the respirometer box was kept in darkness, otherwise it was periodically rotated to keep the animal active. Readings were usually taken every 20 or 30 min, but if analyses were restricted to CO<sub>2</sub> they were carried out at 10 min intervals.

The volume of each tortoise was measured by water displacement. From these and from respirometer volumes the volume of air contained within the respirometer box was calculated, and from the gas samples total O<sub>2</sub> and CO<sub>2</sub> content of the respirometer were determined at different times. Controls showed that some errors arose

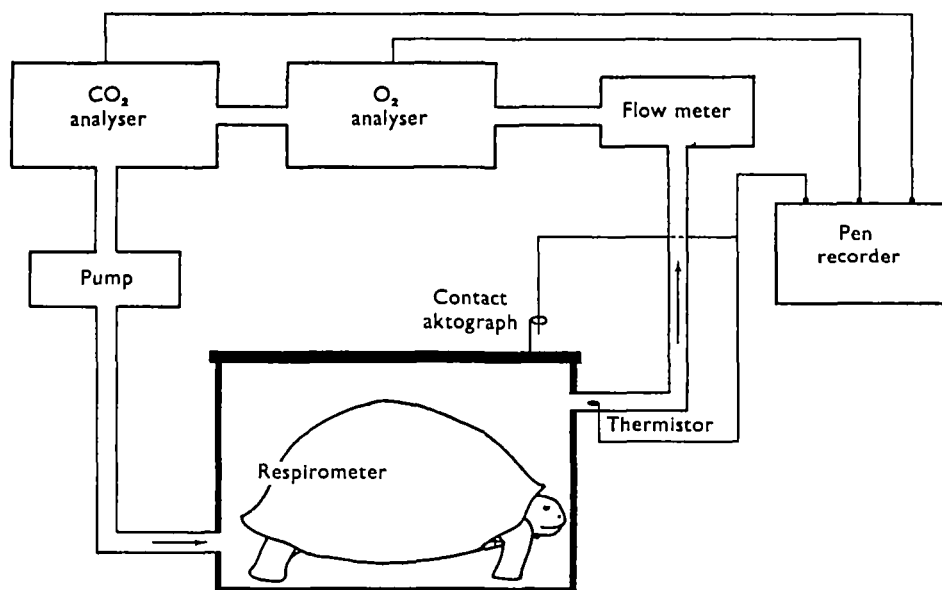


Fig. 1. Diagram of the experimental arrangement used for recording the O<sub>2</sub> uptake and CO<sub>2</sub> release of tortoises in a closed continuous-flow system.

due to slight changes in temperature, particularly when the animal was active; and also because of slight deviations from unity of the respiratory quotient. However, it would appear that these differences would not make any significant difference to the final results, especially when compared on a basis of different body weights.

From experimental results similar to those shown in Fig. 2, the rates of CO<sub>2</sub> production and O<sub>2</sub> uptake at a given time can be calculated. The results of an experiment in which the changes in gas concentrations over the first hour were not reasonably linear were rejected.

#### *Shell, flesh and body weights*

Nine *T. hermanni*, deep-frozen after terminal experiments, were dissected and the weights of the shell (plus its fused vertebrae), bones (other than those of shell), flesh (mainly muscle excluding viscera and gut contents), viscera (including heart, not gut contents) and heart were determined. Both wet and dry weights for bones and

shell were obtained. The flesh was weakened by soaking in dilute NaOH solution before separation from the bones, which were rinsed and weighed. The shell and bones were oven-dried at 90 °C to constant weight for a minimum of 3 days.

Since in most cases the tortoises had suffered some loss of weight before death, the shell weights are given as a percentage of a value for body weight calculated from plots of shell length (over the curve of the shell) against the normal live body weight. Data for *T. gigantea* was obtained from several sources. One young specimen was killed and dissected in the field. Sun-dried shells found in the wild were weighed, the weights taken as percentages of normal animals of that size.

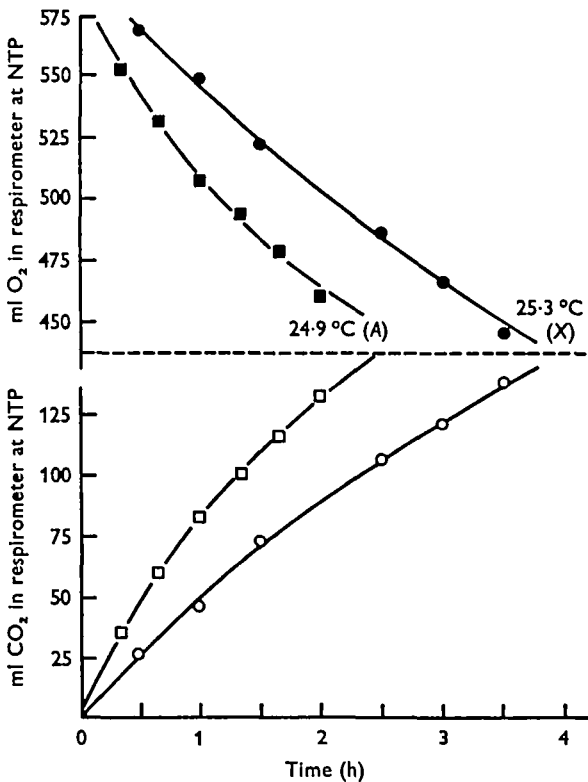


Fig. 2. Respiratory gas exchange in two specimens of *T. gigantea* at different activity levels. Plots show the changes in O<sub>2</sub> and CO<sub>2</sub> content of the closed respirometer from the beginning of the experimental observations. Body temperatures are also indicated.

#### RESULTS

Data obtained from experiments on *T. gigantea* and *T. hermanni* in which the gas-exchange rates remain constant during the first hour are given in Table 1. The results of these experiments indicate the animal's metabolic rate under fairly constant conditions, as in this period there would be relatively little change in the O<sub>2</sub> and CO<sub>2</sub> content of the inspired air. In some cases the animal was acclimatized to the respirometer before it was closed, but no significant differences were noted between the results of these experiments and ones in which measurements were started immediately

After the tortoise had been placed in the respirometer. In most cases the animals settled down immediately and the changes in O<sub>2</sub> and CO<sub>2</sub> content of the respirometer were similar to those shown in Fig. 2.

Table 1. *Respiratory rates of Testudo gigantea and T. hermanni over the first 60 min of the experiment*

Wt (g)	O <sub>2</sub> at NTP (ml/kg/h)	RQ	Body temp. (°C)	Activity*
<i>T. gigantea</i>				
118	102.7	1.1	27.3	I
119	130.3	1.1	25.7	A
134	181.8	1.2	25.5	A
323	46.9	—	25.4	I
327	92.0	1.0	26.6	A
336	116.6	1.2	26.6	A
534	26.8	0.8	22.9	I
562	73.5	1.2	25.7	I
615	69.2	1.0	25.3	I
631	149.7	1.0	26.0	A
667	122.2	1.0	24.9	A
710	155.6	1.1	26.9	A
743	79.7	—	27.5	I
772	46.8	—	28.2	I
807	80.8	—	26.9	I
1253	137.9	—	28.7	A
1361	70.2	—	26.9	I
1368	60.4	—	28.4	I
1378	48.8	—	26.2	I
1468	104.8	—	—	I
1806	46.2	1.0	27.5	I
1885	145.0	0.9	26.8	A
1302	90.1	1.0	—	I
1616	109.1	—	29.0	A
1656	56.7	0.9	26.2	I
1732	80.2	1.1	26.2	I
19550	16.6	1.2	24.0	I
	120.0	0.9	28.0	A
	126.5	0.9	29.0	A
28400	123.5	1.0	29.0	A
	147.1	1.0	31.0	A
	68.2	1.0	26.0	I
	48.9	—	25.3	I
	30.1	—	26.0	I
35450	30.7	—	—	I
	48.7	1.0	—	I
	119.8	1.2	—	A
<i>T. hermanni</i>				
665	150.75	0.85	—	I
637	63.04	1.2	—	I
663	131.58	0.88	—	I
672	29.76	0.6	24.6	I
2164	12.78	1.0	23.4	I

\* A = active; I = inactive.

*Gas-exchange ratios*

Data from all experiments in which the concentrations of both  $O_2$  and  $CO_2$  were monitored (including some not represented in Table 1 because the gas-exchange rates changed significantly during the first hour) were included in the calculation of the gas-exchange ratios (RQ).

The mean value of the RQ for all nine specimens of *T. gigantea* was 1.01 (range 0.8–1.2 S.E. 0.017) (Table 1). In *T. hermanni* the results of six experiments using four animals were perhaps more variable and gave a mean value of 0.91 and a range of 0.6–1.1 (S.E. 0.024). It is possible that any greater variability of the results obtained for *T. hermanni* is related to the greater range of relative ages and conditions among these animals. For either species there appeared to be no significant difference in RQ between active and inactive periods or between animals of different body size.

*Change in gas content of the closed respirometer*

Fig. 2 shows the change in gas composition within the respirometer for two experiments in which tortoises of similar weights and volumes showed different levels of activity over prolonged periods. Both graphs show a reduction in  $O_2$  content and an increase in  $CO_2$  content of the respirometer air, the rates of change being greater for the more active animal. In both cases there is also a gradual decrease in the  $O_2$  and  $CO_2$  exchange rates which characterizes these experiments. These changes are probably caused by the build-up of  $CO_2$  in the respirometer since they occurred in both active and inactive animals and were unrelated to the time spent in the respirometer prior to its closure at the beginning of the experiment. The progressive hypoxia under such conditions is likely to have much less effect than the  $CO_2$  increase and is certainly insignificant during the first hour.

*The effects of activity*

The rates of  $O_2$  uptake and  $CO_2$  release were significantly increased in animals which moved about in the respirometer as against those which remained stationary. In all experiments direct observation was made of their activity states and a division made into 'active' and 'inactive' on this basis. In Table 1, no distinction is made between the different degrees of activity but data for the 'inactive' condition are comparable to one another.

Some measure of the degree of activity was obtained using a contact aktograph, and a part of a continuous record is shown in Fig. 3. In this recording there are two periods during which the animal was clearly active and when the rates of  $O_2$  uptake and  $CO_2$  release increased noticeably, as did the temperature inside the respirometer. These changes are related to the duration of the activity, which is adequately recorded by the aktograph, although it does not accurately record the intensity of activity. It is noticeable that the highest rate found over short periods in this recording (for a 28 kg animal) is somewhat greater than the results from the long-term experiments discussed below.

Possibly such high rates would be maintained for longer periods if the tortoises were stimulated electrically, as has been done in experiments with other reptiles (Bartholomew & Tucker, 1964).

In Fig. 4 the  $O_2$  uptake of all the animals is plotted and shows the ranges of metabolic activity obtained for animals of different weight when inactive or when showing varying degrees of activity. Maximum rates given here are lower than those obtained for brief periods such as are shown in the recording of Fig. 3.

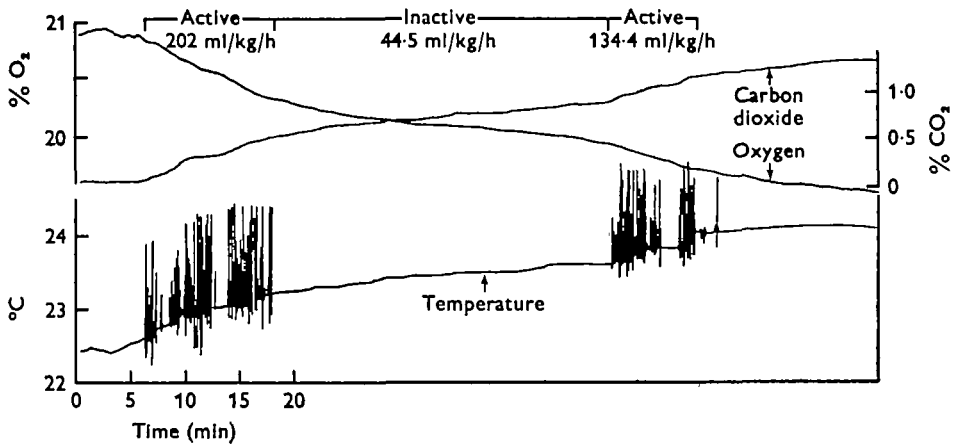


Fig. 3. Tracing of part of a recording from an experiment on *T. gigantea* in a continuous-flow respirometer (Fig. 1). The two upper traces show the changes in  $O_2$  and  $CO_2$  content and the lower one indicates the temperature within the respirometer; the output of a contact aktograph is superimposed upon this trace.

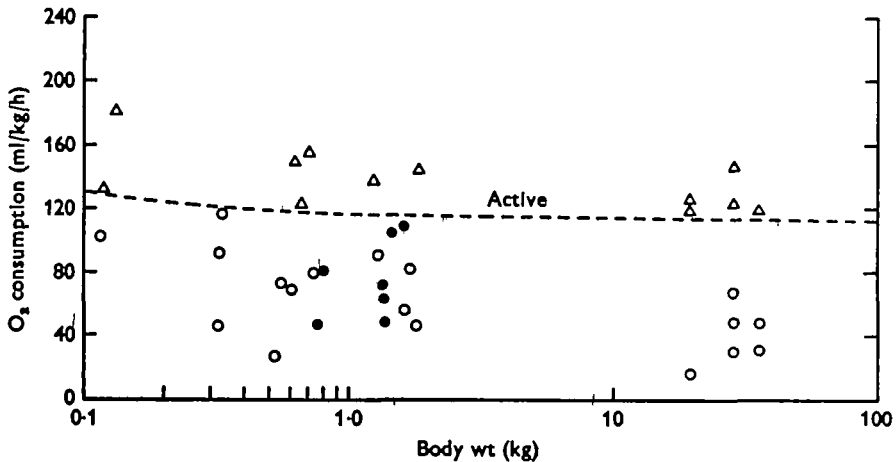


Fig. 4. *T. gigantea* and *T. hermanni*. Semi-logarithmic plot of  $O_2$  consumption against body weight. Experiments in which the animal was active are indicated by triangles and the circles represent inactive or partially active animals. Solid circles indicate points which were obtained indirectly from the  $CO_2$  measurements using an RQ of 1.0.

*O<sub>2</sub> uptake and body size*

It is already clear from Fig. 4 that the weight-specific  $O_2$  consumption tends to fall with increasing body weight. The same data has been plotted out on log/log coordinates in Figs. 5 and 6, and the best-fitting straight line obtained by the method of least squares. The confidence and tolerance limits are given in Table 3.

Table 2. Statistical data relating to regression lines plotted in Figs. 5 and 6

	Wt. (kg)	O <sub>2</sub> cons.	95 % confidence limits	Tolerance limits
Fig. 5. Log/log plot of O <sub>2</sub> consumption in ml/h against body wt in kg				
(1) Maximum rates				
Slope (b)	0.969	15.14	11.91-19.24	9.65-23.73
S.D.	± 0.028	140.8	122.7-161.4	93.99-211.0
Intercept (a)	140.8	1310	1114-1539	866.8-1980
S.D.	± 1.059	12190	9196-16150	7593-19560
(2) Minimum rates				
Slope (b)	0.820	6.88	3.91-12.10	2.34-20.23
S.D.	± 0.066	45.47	32.78-63.06	17.13-120.7
Intercept (a)	45.47	300.7	202.9-445.3	110.6-817.5
S.D.	± 1.148	1987	1008-3918	633.6-6234
Fig. 6. Log/log plot of O <sub>2</sub> consumption in ml/kg body wt/h against body wt in kg				
(1) Maximum rates				
Slope (b)	-0.031	151.4	119.1-192.4	96.49-237.4
S.D.	± 0.028	140.8	122.7-161.4	93.96-211.1
Intercept (a)	140.8	131.0	111.4-153.9	86.64-198.1
S.D.	± 1.059	121.9	91.91-161.5	75.88-195.7
(2) Minimum rates				
Slope (b)	-0.179	68.6	38.84-121.4	23.26-202.6
S.D.	± 0.066	45.43	32.70-63.14	17.10-120.8
Intercept (a)	45.43	30.08	20.35-44.46	11.07-81.77
S.D.	1.149	19.92	10.13-39.17	6.354-62.41



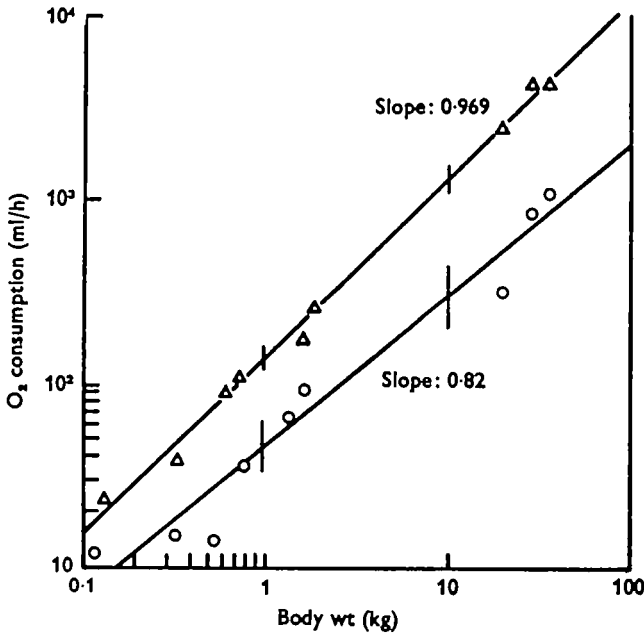


Fig. 5. *T. gigantea*. Log/log plot showing the relationship between  $O_2$  consumption and body weight. Regression lines are plotted for the data giving the minimal and maximal levels for each individual. Vertical bars indicate 95% confidence limits at 1 and 10 kg.

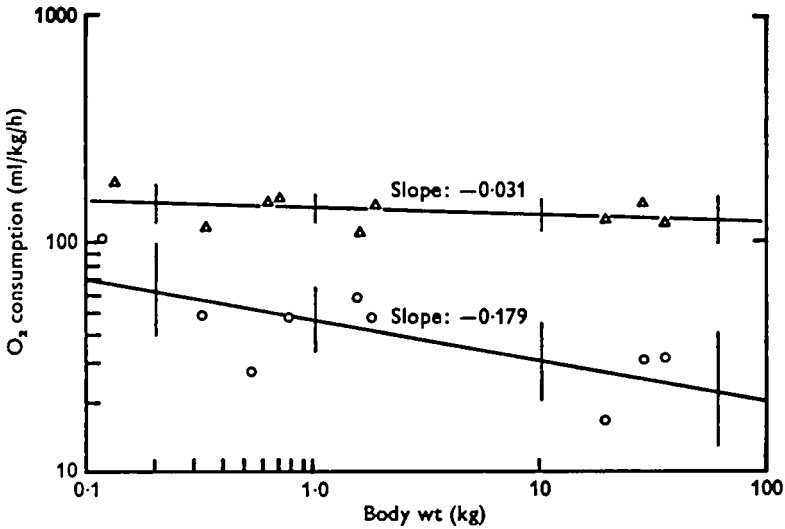


Fig. 6. *T. gigantea*. Logarithmic plots of weight-specific  $O_2$  consumption versus body weight for nine specimens. The regression lines are drawn through the maximum and minimum points for each animal. Ninety-five% confidence limits are indicated by vertical lines at 0.2, 1.0, 10 and 60 kg.

This work indicates that the relationship

$$\dot{V}_{O_2} = aW^b$$

is applicable, or

$$\log \dot{V}_{O_2} = \log a + b \log W,$$

where  $\dot{V}_{O_2}$  is the rate of oxygen consumption.

The slopes ( $b$ ) of the regression lines are 0.82 for the minimum values of  $O_2$  uptake obtained for each tortoise, and 0.97 for maximum values:

$$\text{minimum } \dot{V}_{O_2} = 45.5W^{0.82},$$

$$\text{maximum } \dot{V}_{O_2} = 140.8W^{0.97}.$$

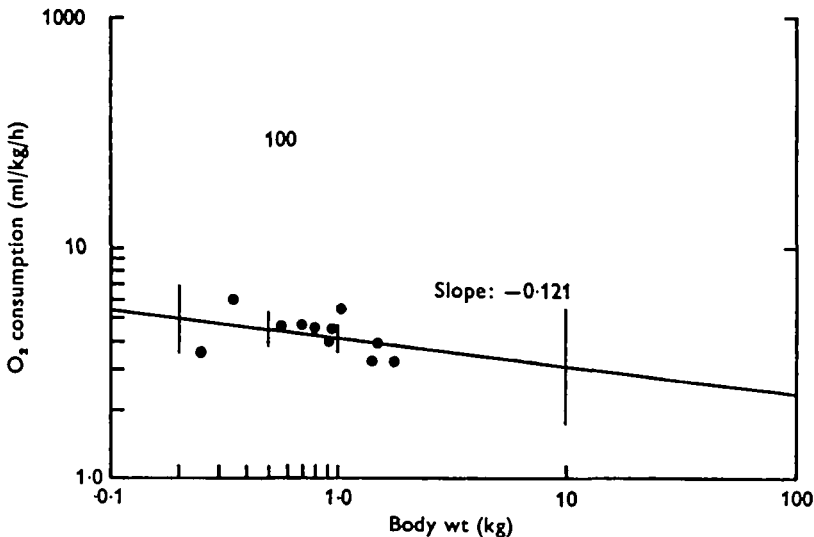


Fig. 7. *Pseudemys*. Log/log plots showing the relationship between weight-specific  $O_2$  consumption at 30 °C and body weight, based upon data contained in Fig. 3 of Hutton *et al.* (1960). Ninety-five % confidence limits shown by vertical bars at 0.2, 0.5, 1.0 and 10 kg.

In plots of  $O_2$  consumption per unit body weight (Fig. 6) the corresponding slopes of the regression lines are -0.179 and -0.03.

From the statistical data relating to these regression lines (Table 3) it may be concluded (a) that the  $O_2$  consumption per unit body weight reduces with increasing size for giant tortoises, and (b) that the rate of decrease is greater for the animals at rest than when they are active. Even for the active condition, the slope is different from zero.

The slope for the overall data lies between 0.8 and 1.0 and clearly depends upon the proportion of the measurements and degree of activity of the animal and is therefore not of particular value except as a general guide.

The difference between standard  $O_2$  consumption of a fish and its maximum active metabolism has been referred to as the 'scope for activity' (Fry, 1947). In *T. gigantea* it appears that scope for activity increases with body weight and the slope for the corresponding regression line would be  $0.97 - 0.82 = 0.15$ . Thus it seems that these tortoises can increase their metabolism when becoming active by an amount

Table 3. The percentage of body weight represented by the shell, bones (% *lo wt.*) flesh and viscera (% *dead wt.*) in *Testudo hermanni* and *T. gigantea*

<i>lo</i> (cm)*	Dead wt. kg	<i>lo wt.</i> (kg)†	Shell		Bones exc. shell		Flesh and bones exc. shell (%)	Flesh only (%)	Viscera exc. gut contents (%)	Heart only (%)
			Wet wt. (%)	Dry wt. (%)	Wet (%)	Dry (%)				
<i>T. hermanni</i>										
14.4	0.209	0.28	27.9	17.8	—	2.6	1.4	—	17.5	0.29
15.3	0.318	0.38	24.2	13.9	1.9	3.7	1.5	—	26.8	0.28
16.1	0.284	0.39	29.9	19.0	—	3.3	1.3	—	23.2	0.35
16.2	0.278	0.42	30.9	24.0	—	4.6	2.0	—	13.8	0.60
17.2	0.367	0.51	33.8	24.9	2.4	3.0	1.6	—	10.9	0.33
17.3	0.380	0.52	37.1	28.2	—	3.5	2.2	—	9.5	0.24
18.9	0.425	0.65	38.9	27.6	1.9	2.9	1.5	—	10.7	0.26
20.6	0.695	0.83	27.1	20.6	1.9	4.3	2.0	—	14.5	0.43
21.3	0.830	0.89	30.4	22.7	1.7	3.8	2.0	—	9.1	0.46
<i>T. gigantea</i>										
22.6	0.622	0.8	18.2	8.2	—	2.6	1.45	29.8	17.3	0.32
77.5	—	32.0	—	11.0	—	—	—	—	—	—
86.5	—	44.0	—	13.6	—	—	—	—	—	—
89.5	38.0	47.0	19.0	—	—	—	—	39.89	—	0.18
95.5	—	53.0	—	10.8	—	—	—	—	—	—
99.7	56.1	63.0	19.0	—	—	—	—	27.72	—	0.17
105.5	—	65.0	—	11.6	2.4	—	—	—	—	—
113.5	—	76.0	—	10.6	—	—	—	—	—	—

\* *lo* (cm) = length in cm over curve of carapace.  
 † *lo wt.* = weight in kg calculated from the length (*lo*) using a graph of *lo* × normal body weight (Gaymer, 1968).

which increases with body size and consequently larger animals can become relatively more active than smaller ones.

Another way of expressing this relationship is to compare the maximum and minimum rates as a ratio. This has been called the 'index of the expansibility of metabolism' by Drabkin (1950), and data for each individual tortoise is plotted out in Fig. 8. The predicted line obtained from the two regression lines of fig. 6 is also shown. Thus a tortoise of about 100 g body weight can increase its metabolism twofold whereas for animals of 100 kg the possible increase is at least six times.

#### DISCUSSION

The experiments described in this paper provide information which has the advantage over previous studies with chelonians and other reptiles of being based on a greater range in body size for a single species. Consequently, apart from the absolute levels of  $O_2$  consumption, the data obtained in relation to body size is of particular interest. It seems justifiable, even from a relatively limited number of animals at present available, to conclude that the weight-specific  $O_2$  consumption decreases with body weight and that this relationship varies according to the level of activity of the animals. There is a scarcely significant difference between individuals of different sizes for the most active animals, but when at rest the relationship is very clear. These results are to be contrasted with those obtained by previous authors who have concluded that chelonians of all sizes have the same  $O_2$  consumption/unit body weight. Of these studies, only those of Hutton, Boyer, Williams & Campbell (1960) have been based upon a survey of a single species and in that case the range of body weights was much smaller than in the present study. Studies using different species, even within the Chelonia, have a number of disadvantages as discussed below. In fact, we have re-plotted the data at 30 °C obtained for *Pseudemys* by Hutton *et al.* (1960) on log/log co-ordinates (Fig. 7). Employing the same methods which have been used for *T. gigantea*, a significant departure from a slope of 1 has been obtained. As shown in Fig. 7, the  $O_2$  consumption/unit body weight when plotted against body weight on log/log co-ordinates has a slope of  $-0.121$  (S.D.  $\pm 0.0985$ ). It is therefore significantly different from zero but not significantly different (5% level) from our figure of  $-0.179$  for *T. gigantea*. Again there is the problem of relatively small numbers, and if the point for the smallest specimen of *Pseudemys* were omitted from the data, the slope of the line would be very much greater.

The difference in slope of the regression lines for resting and active tortoises indicates that the scope for activity (Fry, 1947) increases for larger animals. This may have survival value and perhaps can be interpreted in relation to the increased body weight which the animal must support during its active movements. This is most likely to be related to the cube of the linear dimension (i.e. directly to body weight), whereas the resting  $O_2$  consumption, as in other animals, seems to be related to some surface-dependent factor. On this basis a difference in the slope of the regression lines between 1.0 and 0.67 would be expected between active and quiet animals.

Variations in the scope for activity have also been observed by other workers on reptiles. Bartholomew & Tucker (1964) noted that it generally increases with body temperature, but this is not always so, and there seems to be some correlation between

The relationship of scope and temperature and the habits of animals in the field. The results on *T. gigantea* consequently suggest comparisons between relative activity of small and large animals in their normal environment. As has been pointed out, the same data may be interpreted in terms of the 'index of the expansibility of metabolism' (Drabkin, 1950), which is the ratio between the maximal and minimal rates of respiration; in the case of *T. gigantea* this increases from twofold for small animals to at least sixfold. Increases of about tenfold have been observed in some varanid lizards, and this should be taken into account when field observations are made.

Some advantages of the large size in giant tortoises may be suggested in relation to their survival on isolated islands. The lightness of the carapace and the large size of the lungs provide considerable buoyancy, so that they be readily dispersed by ocean winds and currents. The relatively lowered metabolic rate would increase the time for which they could survive.

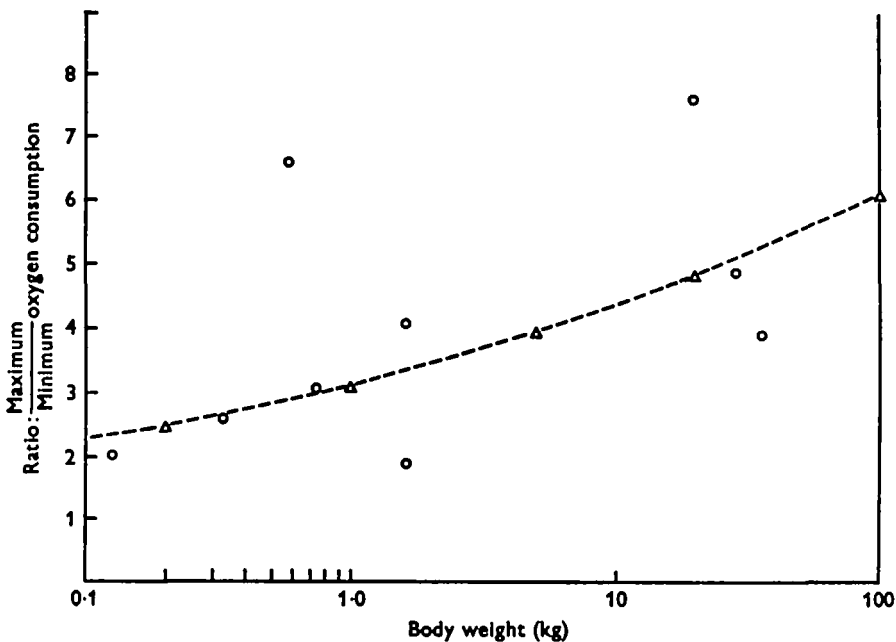


Fig. 8. *T. gigantea*. Ratio of maximum to minimum oxygen consumption for each of nine specimens, plotted against logarithm of the body weight. Individual data are indicated by circles. The triangles and dashed line are based on the two regression lines shown in Fig. 6.

This work clearly indicates the need for more extended studies to be made on a larger number of giant tortoises in order to obtain more data on this important relationship for a single species. Relatively little work has been devoted to this field in reptiles and there are many dangers in generalizing from relationships based upon interspecific plots. For such plots it is essential that comparable stages in the life cycle are chosen; for the slopes of the log/log plot will vary during the life-cycle, particularly in the earlier and later stages. Nevertheless, the relationship (Fig. 9) between  $O_2$  consumption and body weight given by plotting recently collected

chelonian data (Altman & Dittmer, 1971, p. 479) is surprisingly close to that obtained for resting *T. gigantea* in the present study.

Although variations in activity were recorded in the present experiments, more detailed information of this kind is required. It would also be of interest to investigate the effect of variations in temperature.

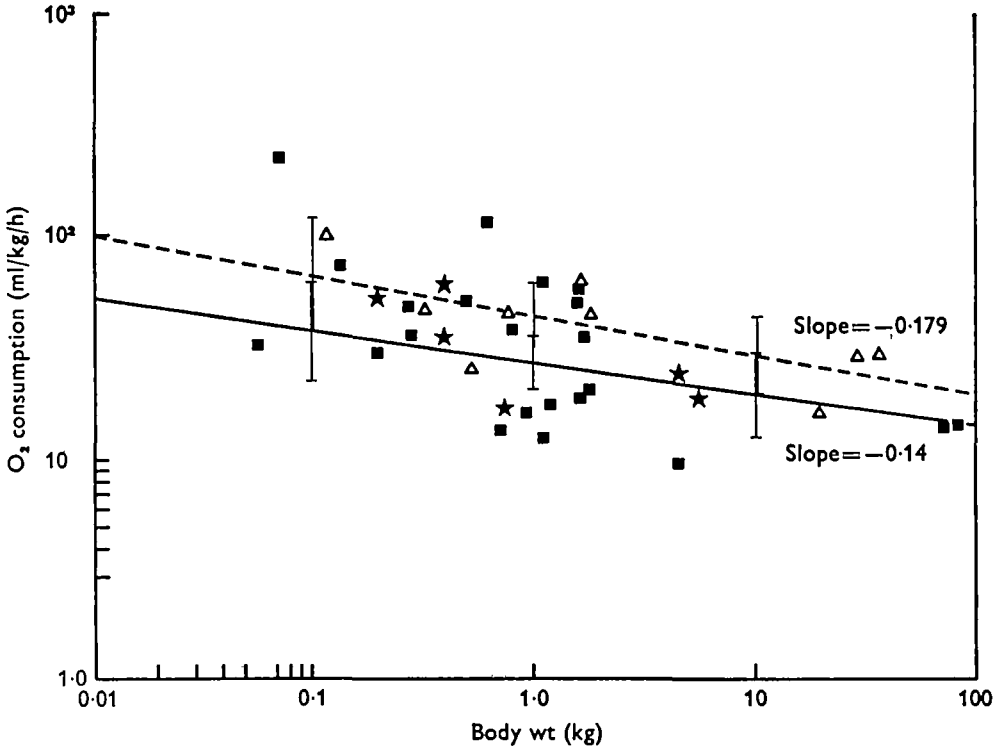


Fig. 9. Log/log plot of body weight against  $O_2$  consumption per unit weight for a number of chelonian species. ■, Values obtained at temperatures between 18 and 22 °C; ★, temperatures 25–29 °C (Altman & Dittmer, 1971). The dotted regression line and the triangles are the data obtained from *T. gigantea* (inactive), plotted in Fig. 6. Ninety-five % confidence limits are shown for both lines.

#### SUMMARY

1. The  $O_2$  consumption and  $CO_2$  release of nine giant tortoises *Testudo gigantea* (weight range 118 g–35.5 kg) were measured at a temperature of about 25.5 °C. Four European tortoises *Testudo hermanni* (weight range 640 g–2.16 kg) were also used. The mean RQ values obtained were 1.01 for *T. gigantea* and 0.97 for *T. hermanni*. These values were not influenced by activity or size.

2. The data was analysed by plotting log/log regression lines relating body weight to  $O_2$  consumption. Both maximum and minimum metabolic rates recorded for each individual *T. gigantea* showed a negative correlation with body weight. For active rates the relation was  $O_2$  consumption =  $140.8W^{0.97}$ , whereas for inactive animals  $O_2$  consumption =  $45.47W^{0.82}$ .

3. The maximum rates were obtained from animals that were observed to be active in the respirometer and the minimum rates from animals that remained quiet throughout. The scope for activity increased with body size, being 82 ml/kg/h for animals of

100 g and 103 ml/kg/h for 100 kg animals. The corresponding ratio between maximum and minimum rates increases from about 2 to 6 for the same weight range.

4. Values for metabolic rate in *T. hermanni* seem to be rather lower than in *T. gigantea*. Analysis of the relative proportion of the shell and other organs indicates that the shell forms about 31 % of the body weight in adult *T. hermanni* but only about 18 % in *T. gigantea* of similar size. The shell is not appreciably heavier in adult *T. gigantea* (about 20 %).

5. Data obtained for inactive animals is in good agreement with results of other workers using lizards and snakes. Previous evidence suggesting that chelonians show no reduction in metabolic rate with increasing size is not considered to conflict with data obtained in the present work.

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