

## Oxygen Consumption During Swimming in Galapagos Marine Iguanas and Its Ecological Correlates

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**Summary.** 1. Oxygen consumption, undulation frequency, and tether force as an index to power output were measured in tethered, swimming marine iguanas.

2. Power output increased linearly with total oxygen consumption and mass-specific oxygen consumption increased linearly with undulation frequency (Figs. 1 and 2).

3. Velocity of free swimming iguanas is a linear function of undulation frequency and of total length (Fig. 3), which allows calculation of the equivalent velocity for tethered iguanas undulating in place on a tether.

4. Cost of transport for swimming iguanas decreases as body mass increases, and can be predicted from the equation

$$\text{ml O}_2/\text{kg} \cdot \text{m} = 0.31 M^{-0.56},$$

where  $M$  is mass in kg (Fig. 4).

5. The change in cost of transport with body mass correlates with foraging patterns of different size classes of marine iguanas. Small marine iguanas feed on algae on or near shore while adults obtain algae by swimming offshore and diving.

6. Cost of transport during swimming in marine iguanas is higher than for fish and turtles but lower than for ducks or humans (Fig. 5).

### Introduction

The foraging pattern of the Galapagos marine iguanas, *Amblyrhynchus cristatus*, is unique among li-

zards. The adults swim offshore, dive beneath the surface, and feed underwater on marine algae. A round trip to the feeding grounds may exceed 400 meters. Because swimming is central to the suite of behavioral adaptations that permits marine iguanas to exploit the littoral environment, the metabolic cost of swimming is an essential part of their energy budget.

The metabolic cost of swimming has been measured in turtles (Prange 1976), ducks (Prange and Schmidt-Nielsen 1970), human beings (DiPrampero et al. 1974), and fish (see Webb 1975 for review); but there are no published data on the cost of swimming in lizards. However, for marine iguanas data are available on related topics such as thermoregulation and cardiovascular adjustments to diving (Bartholomew and Lasiewski 1965; Bartholomew 1966; Morgareidge and White 1969; White 1973), swimming velocity (Bartholomew et al. 1976), and aerobic and anaerobic contributions to energy metabolism (Bennett et al. 1975; Gleeson 1980a, b). Gleeson (1979) measured energy cost of terrestrial locomotion of marine iguanas and compared it with the cost of swimming we discuss here.

Because of their restricted distribution and vulnerability, marine iguanas are a fully protected species which can be studied only in the Galapagos. It is improbable that a technically complete study of their locomotor adjustments will be carried out in the foreseeable future. Consequently, we undertook to study the swimming performance in the field and to supplement these studies with some physiological measurements.

We had no water tunnel. Therefore, our procedure was to determine (1) the relation of undulation frequency to swimming velocity in unrestrained iguanas of different sizes under natural conditions, and (2) the relation of  $\text{O}_2$  consumption to undulation frequency of animals of different sizes

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Abbreviations:  $\dot{V}_{\text{O}_2}$  rate of oxygen consumption;  $E_t$  cost of transport in  $\text{ml O}_2/\text{kg} \cdot \text{h}$

during tethered swimming. From these data we estimated the relation of  $O_2$  consumption to swimming velocity, the cost of transport, and the relation between body size and cost of transport. We also measured the force generated by tethered swimming iguanas in relation to oxygen consumption to evaluate the role of aerobic metabolism at the undulation frequencies characteristic of cruise swimming.

## Materials and Methods

The experiments described here took place during July, 1978 on the R/V Alpha Helix, anchored near Punta Espinosa on Isla Fernandina in the Galapagos Islands. The marine iguanas were captured on shore by noosing and held overnight on board ship before testing.

The velocity and undulation frequency of free-swimming iguanas were measured in the quiet water of a small lagoon. Swimming experiments were carried out in a tank measuring approximately  $1 \times 1 \times 1.5$  m filled to a depth of about 80 cm with seawater at a temperature of 22–24°C. We measured rates of  $O_2$  consumption and  $CO_2$  production, frequency of undulations, and obtained estimates of tether force produced by iguanas swimming in place near the middle of the tank while tethered by a nylon string looped around the neck and behind the forelimbs. The swimming iguanas were allowed to set their own pace. After each experiment we determined body temperature with a thermistor (YSI) inserted rectally to a depth of at least 6 cm, and measured body mass, body length, and tail length.

Each iguana was fitted with a lightweight mask made of clear plastic that covered most of the head. It was open posteriorly and had a tygon tube (inside diameter 4 mm) attached near the front. In some of our initial attempts iguanas refused to swim while wearing a mask, so we routinely habituated animals by placing masks on them the night before an experiment. Behavior of conditioned animals with masks was indistinguishable from that of animals without masks.

A diaphragm pump drew air through the mask and tube and then through a column of silica gel and Drierite (anhydrous  $CaSO_4$ ) to remove water vapor. Flow rates of dry air, measured downstream from the pump with a Brooks rotameter calibrated against a Brooks mass flowmeter, were 2.5 to 4.0 l/min, depending on the size of the lizard. Part of the air stream was drawn through a Beckman  $LB_2CO_2$  analyzer and an Applied Electrochemistry S-3 $AO_2$  analyzer. Fractional concentrations of  $O_2$  and  $CO_2$  in the air stream were recorded continuously on a two-channel strip chart recorder and integrated by planimetry to determine mean rates of  $O_2$  consumption over 5 min periods. Rates of  $O_2$  consumption were calculated using equation 3b of Whithers (1977). All gas volumes are reported at standard temperature (0°C) and pressure (760 Torr = 101.3 kPa).

When a tethered iguana performs its undulatory swimming motions it generates a force that we shall call 'tether force'. This is not a measure of the thrust produced by a free-swimming iguana, but it can be used as an index to power output, or the net hydrodynamic force produced by a tethered iguana with swimming movements of different frequencies and amplitudes. We measured 'tether force' with a spring dynamometer (Chatillon) accurate to  $\pm 0.02$  Newtons. The dynamometer was attached to the tether, and held behind the iguana at an angle of 30° to the water surface. The reading oscillated about a mean value as the iguana undulated. In steady swimming, oscillations were usually less than  $\pm 0.1$  N. We estimated mean force to the nearest 0.05 N during each 30 s interval while an iguana was swimming, and calculated tether force

as the horizontal component of this measured force. The tether forces we report are the means of the values in each period for which we calculated rates of oxygen consumption.

Cruising iguanas are neutrally buoyant, so vertical force exerted by the tether did not result in any change in the metabolic expenditure necessary to stay afloat. Torque exerted by the tether did not noticeably alter the posture of the iguana in the water.

## Results

### *Behavioral Observations*

When the lizards with mask on and tether attached were first released in the tank, they usually attempted to dive and swim underwater, but after several minutes they stopped diving and began to swim steadily, cruising at the surface with head out of the water. Our observations and discussions are restricted to this cruise mode of swimming, which the iguanas can apparently maintain indefinitely (Bartholomew et al. 1976). All metabolic measurements were completed within 25 min after the iguanas began swimming in the cruise mode.

Iguanas swim by lateral undulations of the body and tail, and during cruise swimming the forelimbs are held back against the sides of the body. The amplitude of body undulations is smallest near the level of the forelimbs, so a tether at that point has a minimal effect on swimming movements. The behavior and swimming posture of masked iguanas swimming while tethered in place did not differ in any obvious way from that of free-swimming iguanas, except that they made no forward progress.

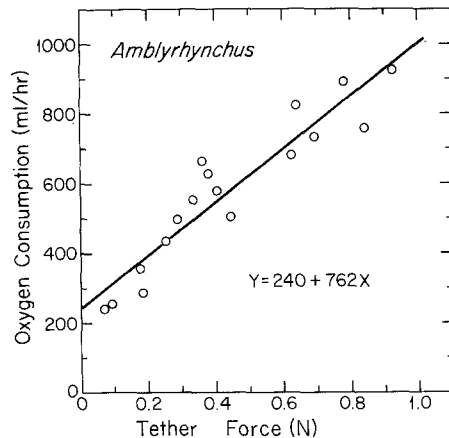
Body temperatures of iguanas at the start of experiments were usually 4 or 5°C higher than water temperature. At the end of swimming experiments body temperatures were between 24 and 28°C, which is within the range recorded by telemetry from unrestrained iguanas swimming in the sea during feeding excursions (Bartholomew and Vleck, unpublished). Bartholomew (1966) reported body temperatures of 25–26°C in iguanas returning to shore at Punta Espinosa after feeding. There was no apparent correlation between body temperature recorded at the end of an experiment and the iguana's performance during that experiment.

### *Oxygen Consumption*

We measured oxygen consumption during tethered swimming in 13 marine iguanas ranging in mass from 0.958 to 4.08 kg (Table 1). The rate of oxygen consumption ( $\dot{V}_{O_2}$ ) increased linearly with tether force (Fig. 1). The relationship between these parameters is described by the equation,

**Table 1.** Morphometric and physiological parameters related to swimming energetics of marine iguanas

Mass (kg)	Total length (m)	Tether force (Newtons)	Undulations/s	Calculated velocity (m/s)	Oxygen consumption (ml/kg·h)
4.08	0.92	0.29	0.63	0.28	122
3.23	0.86	0.36	0.81	0.34	206
3.13	0.98	0.45	0.63	0.30	161
3.03	0.86	—	0.57	0.24	182
3.02	0.87	0.64	0.88	0.37	273
		0.38	0.81	0.34	208
2.92	0.84	0.26	0.64	0.26	149
2.87	0.96	0.63	0.80	0.37	238
		0.78	0.86	0.40	311
2.85	0.88	0.34	0.63	0.27	194
		0.41	0.74	0.32	203
2.80	1.00	0.70	0.78	0.38	262
		0.84	0.85	0.40	271
		0.93	0.92	0.45	331
1.83	0.78	—	0.78	0.29	202
1.33	0.65	0.07	0.73	0.22	181
1.23	0.74	0.19	0.79	0.28	234
		0.10	0.73	0.26	208
0.96	0.63	0.18	0.82	0.25	373

**Fig. 1.** Rate of total oxygen consumption as a function of tether force generated by swimming marine iguanas. See text for definition of tether force

$$\dot{V}_{O_2} = 240 + 762F \quad (1)$$

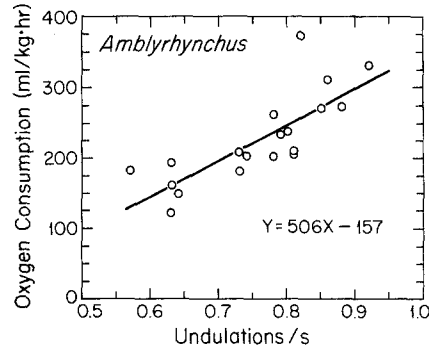
( $n = 17$ ;  $r^2 = 0.88$ )

where  $\dot{V}_{O_2}$  is ml/h and tether force ( $F$ ) is Newtons. Mass-specific  $\dot{V}_{O_2}$  increases with the number of undulations/sec ( $f$ ),

$$\dot{V}_{O_2}/M = 506f - 157 \quad (2)$$

( $n = 19$ ;  $r^2 = 0.61$ )

where  $M$  is body mass in kg (Fig. 2).

**Fig. 2.** Mass-Specific rate of oxygen consumption as a function of undulation frequency in tethered marine iguanas

At any given undulation frequency mass-specific  $\dot{V}_{O_2}$  is independent of body size; for the intervals 0.61–0.70, 0.71–0.80, and 0.81–0.90 undulations per second (Table 1), mass-specific  $\dot{V}_{O_2}$  and mass are not correlated (Spearman Rank Correlation  $P > 0.05$ ). This is consistent with the hypothesis that muscle mass used in swimming is directly proportional to total mass, and suggests that in the size range we studied (1–4 kg), marine iguanas are geometrically similar. This is reasonable in view of the fact that over a much wider range of body size (20 g–4 kg), total length, tail length, and snout-vent length all increase with  $(\text{mass})^{1/3}$ , as expected for geometrically similar animals (Bartholomew et al. 1976).

#### Undulation Frequency and Swimming Velocity

Large iguanas produce more tether force per undulation than do small ones (see Table 1). In general, large iguanas undulate more slowly but swim more rapidly than do small ones (Bartholomew et al. 1976). The iguanas we used were mostly adults and there was no strong relationship between undulation frequency and body mass. Undulation frequencies during metabolic measurements ranged from 0.57 to 0.92 cycles/s. For comparison, in 26 iguanas with masses from 0.96–3.6 kg swimming across a quiet lagoon they ranged from 0.4–1.5 cycles/s and the mean was not statistically distinguishable from that of the tethered iguanas. Bartholomew et al. (1976) reported a mean undulation frequency in voluntarily swimming adult male iguanas of 0.97 cycles/s.

We were constrained to measuring  $\dot{V}_{O_2}$  of iguanas swimming while tethered in place, and therefore do not have a direct measure of swimming velocity associated with a given  $\dot{V}_{O_2}$ . However, our observations on free-swimming iguanas provide the data necessary to calculate the velocity a tethered iguana would achieve if unrestrained. For free-swimming iguanas, distance traveled per undulation, or stride

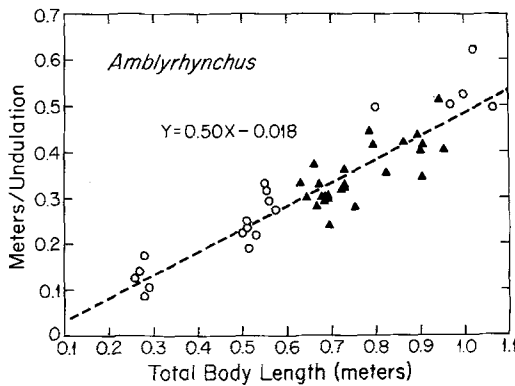


Fig. 3. Stride length, or distance traveled per undulation, as a function of total length in free-swimming marine iguanas. Open circles are data collected during a previous Galapagos expedition; mean values based on these data were published by Bartholomew et al. (1976). Solid triangles are data from this study

length, plotted against total length ( $L$ ) yields a straight line (Fig. 3) described by the equation,

$$\text{stride length} = 0.50L - 0.018. \quad (3)$$

( $n = 45$  iguanas;  $r^2 = 0.85$ )

The swimming velocity of an iguana of length  $L$  can be predicted by multiplying Eq. (3) by undulation frequency. For example, a 1 m iguana undulating at 0.85 cycles/s moves through the water at about 0.4 m/s. Because undulation frequencies of free-swimming and tethered iguanas were not different, we used this procedure to calculate from  $f$  and  $L$  the velocities our experimental iguanas would have achieved had they not been tethered. Calculated velocities ranged from 0.24 to 0.45 m/s (Table 1).

## Discussion

In the population we studied, adult *Amblyrhynchus* routinely swim as far as 400 meters during feeding excursions. This distance is much greater than they ordinarily travel on land. Their energy expenditure during swimming is, therefore, not only of interest for interspecific comparisons, but also of direct ecological importance.

### Oxygen Consumption and Energy Expenditure

In most lizards, including *Amblyrhynchus*, intense activity such as sprint swimming is anaerobically supported. Therefore, measurements of oxygen consumption underestimate energy expenditure during such burst activities (Bennett et al. 1975). However, several lines of evidence strongly indicate that in marine iguanas cruise swimming at the surface is entirely supported aerobically. (1) Free-swimming iguanas

can cruise indefinitely without becoming exhausted (Bartholomew et al. 1976). Tethered iguanas can undulate continuously as in cruise swimming for at least an hour. (2) Lactate levels in the blood of marine iguanas returning to shore after feeding in the sea do not differ from those in resting iguanas, and blood lactate concentrations are actually reduced during 60 min of tethered cruise swimming (Gleeson 1980a). High blood lactate concentrations reported in marine iguanas cruise swimming in experimental circumstances (Bartholomew et al. 1976; Gleeson 1980a) result from anaerobic metabolism during preceding attempts to escape by diving (Gleeson 1980a, b). (3)  $\dot{V}_{O_2}$  increases linearly with tether force in iguanas undulating at frequencies characteristic of cruise swimming (Fig. 1), and changes in  $\dot{V}_{O_2}$  account for 88% of the variability in tether force. Increases in tether force, or power output, are accompanied by proportional increases in  $\dot{V}_{O_2}$ , or aerobic power input.

### Cost of Transport

On the basis of the evidence summarized above we conclude the  $\dot{V}_{O_2}$  is a realistic measure of energy expenditure in marine iguanas swimming in the cruise mode, and therefore it can be used to calculate the cost of transport in this species. The energy cost of transport ( $E_t$ ) is the energy expended in moving a unit of mass a unit distance. The accuracy of determining  $E_t$  for *Amblyrhynchus* from our data depends on the metabolic cost of undulating at a given frequency being the same in tethered and free-swimming iguanas. Despite the obvious hydrodynamic differences between the two, the assumption of equivalence seems justifiable, particularly for intraspecific comparisons, because the tether did not perceptibly alter the swimming program. Tethered and free-swimming iguanas of the same size undulated at the same frequencies. If the tether were released, the undulating animal did not change the frequency or amplitude of its undulations, it merely moved forward across the tank.

We calculated  $E_t$  by dividing the measured metabolic rate of an undulating iguana by its body mass and calculated velocity. In swimming *Amblyrhynchus*,  $E_t$  declines as body size increases, as is true in other animals (Taylor et al. 1970; Tucker 1970; Schmidt-Nielsen 1972; Fedak et al. 1974). On logarithmic coordinates the  $E_t$  of marine iguanas plotted against body mass is approximated by a straight line (Fig. 4) defined by the equation,

$$E_t = 0.31 M^{-0.56} \quad (4)$$

( $n = 13$ ;  $r^2 = 0.73$ )

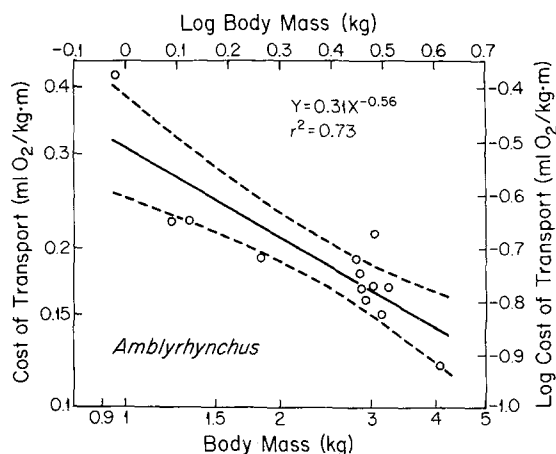


Fig. 4. Cost of transport for swimming *Amblyrhynchus* as a function of body mass. Only the lowest value for cost of transport measured for each individual is plotted. Dashed lines indicate the 95% confidence interval for prediction of the mean value of cost of transport for iguanas of a given body mass

where  $E_t$  is in  $\text{ml O}_2/(\text{kg} \cdot \text{m})$  and  $M$  is mass in kg. The 95% confidence interval for the exponent in Eq. (4) extends from  $-0.34$  to  $-0.80$ , in part because the iguanas we measure span less than an order of magnitude in body mass.

Equation (4) indicates that mass-specific cost of transport decreases by about one-third as body size doubles. Of course, the total energy cost for an iguana to swim a given distance always increases with body size. Total cost of transport ( $E_t'$ ) for an iguana of mass  $M$  can be calculated by multiplying both sides of Eq. (4) by  $M$ :

$$E_t' = 0.31 M^{0.44}.$$

Body mass of *Amblyrhynchus* spans almost two orders of magnitude, ranging from 60 g in hatchlings to more than 4 kg in adult males. An average adult of 2.5 kg is about 40 times the mass of a 60 g hatchling and its resting  $\dot{V}_{\text{O}_2}$  at 25°C is 18 times that of the hatchling (Bartholomew and Vleck 1979), yet such an adult would expend only about 5.2 times as much energy as the hatchling in swimming a given distance. The change in cost of transport with body size may be one of the factors controlling foraging patterns of different size classes of marine iguanas.

#### Swimming Costs and Foraging Economics

Gleeson (1979) has estimated that foraging costs account for somewhat less than 10% of the total energy budget of an adult marine iguana. The energy spent in swimming must be a major part of the energy cost of foraging, and is equal to  $(d) \cdot (0.31 M^{0.44})$ , where  $d$  is the distance traveled.

Energy gained during a foraging trip should be proportional to the volume of algae harvested. No data are available on the relation of stomach size to body mass in *Amblyrhynchus*, nor are such data apt to become available in the foreseeable future because of the totally protected status of the species. However, if one assumes that stomach volume is proportional to body mass, as is generally true for capacity variables (Calder 1974), we can infer that the maximum quantity of algae, and thus energy, that can be harvested on a foraging trip is also proportional to body mass. The ratio of energy gained during foraging to energy expended on swimming is then:

$$\frac{\text{energy gain}}{\text{energy cost}} \propto \frac{M}{d \cdot M^{0.44}} = \frac{M^{0.56}}{d}.$$

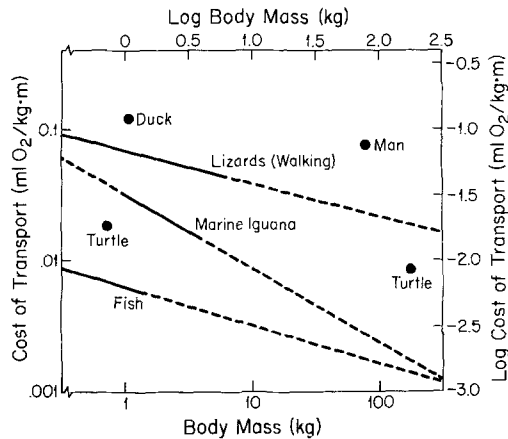
This means that all other things being equal, foraging efficiency for marine iguanas feeding on subtidal algae is directly proportional to the 0.56 power of body mass, and inversely proportional to the distance to the feeding area. If both swim the same distance, a 2.5 kg adult iguana need eat only 5.2 times as much as a 60 g hatchling to meet the cost of swimming. If both eat the same ration per unit body mass, an adult could afford to swim 8 times as far as a hatchling for that ration.

The relationship between foraging efficiency and body mass indicates that foraging by swimming is more economical for large iguanas than for small ones, and that as distance to a feeding area increases, the minimum size of iguana that can economically exploit that area increases. This is consistent with the observation that both large and small marine iguanas feed on or near shore, but only large ones swim out and dive to subtidal feeding areas (Bartholomew et al. 1976). Large iguanas do feed inshore as well, but in areas where iguanas are abundant, intertidal and near-shore algae are heavily grazed and may be restricted to crevices too small for large iguanas to enter, whereas subtidal foraging areas support a more luxuriant standing crop of algae.

It should of course be recognized that the feeding patterns of marine iguanas must be affected by factors other than locomotor energetics – danger from aquatic predators comes immediately to mind.

#### Comparative Values for Cost of Transport

It is of interest to compare  $E_t$  for different kinds of swimmers. In ducks, sea turtles, and fish,  $E_t$  is minimal at some intermediate velocity and increases at both higher and lower velocities (Brett 1965; Prange and Schmidt-Nielsen 1970; Prange 1976). We do not



**Fig. 5.** Cost of transport as a function of body mass in swimming vertebrates and walking lizards. Dashed lines indicate extrapolation beyond the range of measurements. The value for humans is from DiPrampo et al. (1974); that for the duck is from Prange and Schmidt-Nielsen (1970). Sea turtle data is from Prange (1976); the value for a 735 g turtle is a measured minimum cost of transport and the value for a 175 kg adult turtle is an estimate. The line for fish is the regression line calculated by Tucker (1973) from data in Schmidt-Nielsen (1972). The line for walking lizards is from Gleeson (1979), and the line for swimming iguanas from Fig. 4

have measurements over a broad enough range of velocities to define a similar relationship between  $E_t$  and velocity in *Amblyrhynchus*. However, ducks and migrating salmon that are free to choose, select velocities near their minimum  $E_t$  velocity (Brett 1965; Prange and Schmidt-Nielsen 1970). We allowed swimming iguanas to set their own pace, and the undulation frequencies they selected were not significantly different from those chosen by free-swimming iguanas in the field. Therefore, we can reasonably compare the  $E_t$  we calculated for swimming iguanas with the minimum  $E_t$  reported for other swimmers (Fig. 5).

The cost of transport for swimming reflects the importance of swimming to the group in question and indicates the extent of their adaptive compromise with alternate forms of locomotion. For their body mass humans, even trained swimmers, have very high  $E_t$  for swimming. Ducks, which also fly and walk, have a relatively high  $E_t$  for swimming; fish which are totally aquatic have the lowest  $E_t$ , and amphibious marine iguanas and sea turtles are intermediate.

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## References

- Bartholomew GA (1966) A field study of temperature relations in the Galapagos marine iguana. *Copeia* 1966: 241-250
- Bartholomew GA, Bennett AF, Dawson WR (1976) Swimming, diving, and lactate production of the marine iguana, *Amblyrhynchus cristatus*. *Copeia* 1976: 709-720
- Bartholomew GA, Lasiewski RC (1965) Heating and cooling rates, heart rate, and simulated diving in the Galapagos marine iguana. *Comp Biochem Physiol* 16: 573-582
- Bartholomew GA, Vleck D (1979) The relation of oxygen consumption to body size and to heating and cooling in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *J Comp Physiol* 132: 285-288
- Bennett AF, Dawson WR, Bartholomew GA (1975) Effects of activity and temperature on aerobic and anaerobic metabolism in the Galapagos marine iguana. *J Comp Physiol* 100: 317-329
- Brett JR (1965) The swimming energetics of salmon. *Sci Am* 213: 80-85
- Calder WA (1974) Consequences of body size for avian energetics. In: Paynter RA Jr (ed) *Avian energetics*. Nuttall Ornithological Club, Cambridge, Mass, pp 86-144
- DiPrampo PE, Pendergast DR, Wilson DW, Rennie DW (1974) Energetics of swimming in man. *J Appl Physiol* 37: 1-5
- Fedak MA, Pinshow B, Schmidt-Nielsen K (1974) Energy cost of bipedal running. *Am J Physiol* 227: 1038-1044
- Gleeson TT (1979) Foraging and transport costs in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *Physiol Zool* 52: 549-557
- Gleeson TT (1980a) Lactic acid production during field activity in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *Physiol Zool* 53: 157-162
- Gleeson TT (1980b) Metabolic recovery from exhaustive activity by a large lizard. *J Appl Physiol* 48: 689-694
- Morgareidge KR, White FN (1969) Cutaneous vascular changes during heating and cooling in the Galapagos marine iguana. *Nature (London)* 223: 587-591
- Prange HD (1976) Energetics of swimming of a sea turtle. *J Exp Biol* 64: 1-12
- Prange HD, Schmidt-Nielsen K (1970) The metabolic cost of swimming in ducks. *J. Exp Biol* 53: 763-777
- Schmidt-Nielsen K (1972) Locomotion: energy cost of swimming, flying, and running. *Science* 177: 222-228
- Taylor CR, Schmidt-Nielsen K, Raab JL (1970) Scaling of energetic cost of running to body size in animals. *Am J Physiol* 219: 1104-1107
- Tucker VA (1970) Energetic cost of locomotion in animals. *Comp Biochem Physiol* 34: 841-846
- Tucker VA (1973) Aerial and terrestrial locomotion: a comparison of energetics. In: Bolis L, Schmidt-Nielsen K, Maddrell SHP (eds) *Comparative physiology: locomotion, respiration, transport and blood*. North-Holland, Amsterdam, pp 63-76
- Webb PW (1975) Hydrodynamics and energetics of fish propulsion. *Bull Fish Res Board Can* 190: 1-158
- White FN (1973) Temperature and the Galapagos marine iguana - insights into reptilian thermoregulation. *Comp Biochem Physiol* 45A: 503-513
- Withers PC (1977) Measurements of  $\dot{V}_{O_2}$ ,  $\dot{V}_{CO_2}$ , and evaporative water loss with a flow-through mask. *J Appl Physiol* 42: 120-123