

## Swimming, Diving and Lactate Production of the Marine Iguana, *Amblyrhynchus cristatus*

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The swimming and diving performance of hatchling, juvenile and adult marine iguanas, and the effects of these activities on blood lactate in juveniles were studied under field conditions at Academy Bay, on Isla Santa Cruz, in the Galapagos Islands.

By appropriate selection of microclimate, all size classes of marine iguanas maintain body temperatures between 35 and 37 C during the hours of daylight. Despite strong sexual dimorphism no pronounced allometry in body proportions occurs during growth. Newly hatched young are effective swimmers but do not voluntarily enter the water. They feed on algae exposed in the intertidal. Juvenile animals confine their aquatic activity to shallow water and feed mostly in the intertidal zone. Adults also feed in the intertidal but do much of their feeding underwater in subtidal areas.

During both burst and cruise swimming, velocity and distance traveled per undulation increase directly with size, whereas body lengths/sec, body length/undulation and rate of undulation are inversely related to body size. The absolute velocity and the length-specific velocity of both the burst and cruise swimming of marine iguanas are very slow when compared with bony fish of similar size.

The burst swimming of unrestrained marine iguanas results in a sharp increase in blood lactate, but cruise swimming is apparently supported aerobically. After 10 min of forced submergence under water mean blood lactate of juveniles increased about 38 mg%; after one hour of forced submergence it increased by 137 mg%. Marine iguanas appeared exhausted after one hour underwater, could not right themselves, and could not be induced to run.

The role of anaerobiosis in both the aquatic and terrestrial activity of *Amblyrhynchus* is discussed and the zoogeographic implications of its swimming performance are examined.

THE marine iguana, *Amblyrhynchus cristatus*, of the Galapagos Islands is the only lizard that feeds underwater in the sea. The degree to which its habits are adjusted to the marine environment makes it unique among lizards, but few quantitative data are available on the adaptations that accommodate it to its remarkable mode of life. Aside from measurements of body temperature, only a small amount of quantitative information on this species exists in the natural history literature and no systematic field studies of its aquatic performance have been published. We undertook to investigate aspects of the physiology and behavior of this reptile in a series of studies carried out at the Darwin Biological Research Station on Isla Santa Cruz in the Galapagos Islands during the summer of 1974. Our laboratory investigation of its energetics (Bennett, et al., 1975) and our comparison of its physiology and behavior with that of

other iguanids (Dawson, et al., 1977) are published elsewhere. Here we report the results of our field observations on the ecology of the marine iguana with special emphasis on its swimming and diving.

### BODY SIZE AND BEHAVIOR

The highly social nature of marine iguanas, their tameness, their remarkable population density and the localized nature of their foraging make the relationship between population structure and resource utilization unusually amenable to observation. During July, 1974, in the vicinity of the Darwin Station at Academy Bay on Isla Santa Cruz, four readily distinguishable size classes were present in the population: hatchlings with snout-vent (S-V) lengths of 10.5 to 13.0 cm, juveniles with S-V lengths of 19 to 28 cm, adult females and small

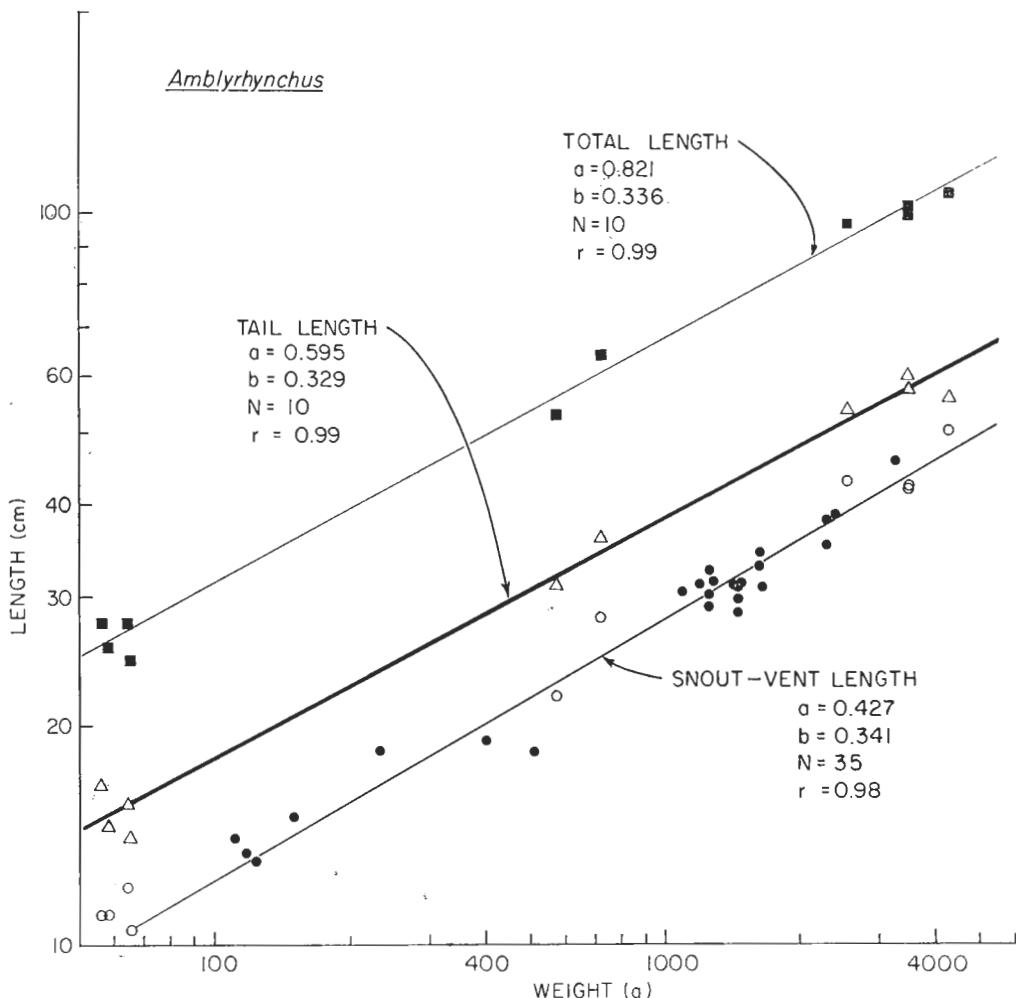


Fig. 1. Linear regressions of the log-transformed values of snout-vent length, tail length, and total length on body weight in *Amblyrhynchus*. Symbols: N, number of individuals; a, y-intercept; b, slope; r, correlation coefficient. The shaded circles represent animals from Punta Espinosa, Isla Fernandina. The unshaded circles represent animals from Academy Bay, Isla Santa Cruz. The regressions of snout-vent length on body weight in these two populations are statistically indistinguishable.

adult males with S-V lengths of 29 to ~35 cm and large adult males with S-V lengths of 35 to 51 cm.

Despite the conspicuous sexual dimorphism and the massive appearance of the large males, no pronounced allometry is apparent in the body proportions of marine iguanas during growth. The log-transformed values of S-V length, tail length and total length all increase linearly with the log-transformed values of body weight (Fig. 1). The slopes of all three regressions are statistically indistinguishable and

fall between 0.33 and 0.34. Thus, no major changes occur during ontogeny in the relations of S-V length, tail length and total length to body weight. However, the length of the tail relative to S-V length increases somewhat with increasing size. The least squares regressions of tail length on S-V length has a slope of 1.21 ( $r = 0.98$ ).

Despite that fact that their geographic range straddles the equator, marine iguanas have a clearly defined breeding season. The annual cycle varies only a few weeks from island to

island. The eggs are laid in February and early March and hatching occurs from early May through early June (Dowling, 1962; Carpenter, 1966). In the last week of June, 1974, many hatchlings with fresh umbilical scars were present along the shore east of the Darwin Station. Their weights approximated those of freshly laid eggs, 80–120 g (Bartholomew, 1966). The hatchlings aggregated in the deep central fissures present in most of the lava flows along the shore. Although the hatchlings could swim, we never saw any of them voluntarily enter the water—even in sheltered tide pools. They were feeding on algae, primarily *Ulva*, as were adults, but they foraged terrestrially in rocky areas exposed at low tide. Their small size allowed them to reach algae growing in cracks and crevices that the much larger juveniles and adults could not enter.

The juvenile animals (age 1 to 2 years, S-V length 19–28 cm) do not hesitate to enter the sea, but they confine their aquatic activity mainly to tide pools and shallow water. In our experience they do not dive to feed, but forage in the rocky areas awash at low tide. Waves sometimes break over them but their feeding activities appear to be confined exclusively to the intertidal zone.

Adult animals, both female and male, feed intertidally when algae are available. However, they do most of their feeding beneath the surface, sometimes at depths in excess of 12 m (Hobson, 1965, 1969) and as far as 200 m from shore. We did not notice any consistent differences in the feeding behavior of the very large males as compared with the adult females and the smaller adult males.

#### THERMAL RELATIONS

The only detailed studies of behavioral thermoregulation in marine iguanas (Bartholomew, 1966; White, 1973) have been carried out on Isla Fernandina at Punta Espinosa, which is on a lee shore in the rain shadow of Volcan Fernandina. This locality is characterized by persistent conditions of severe aridity, high air and substrate temperatures, and intense solar radiation. During the daylight hours at Punta Espinosa, the typical body temperature of adult marine iguanas is between 35 and 37 C. Body temperature is regulated within this range by behavioral and postural adjustments that control rates of heat exchange.

The marine iguanas at Academy Bay live in a climatic regime that contrasts sharply with that at Punta Espinosa, especially during the

garua season (June through September). During this period the rocky shores where these lizards spend their time are swept by the cool, boisterous southeast trade winds and pounded by a heavy surf; the sky is persistently overcast, and light-to-heavy mist falls frequently nearly every day. The substrate is often cool and damp; daytime air temperatures characteristically remain between 21 and 24 C.

In view of the marked differences in local climate between the windward shore of outer Academy Bay and Punta Espinosa, it is of interest to compare the body temperatures maintained by the lizards in the two areas. The limited data (Dowling, 1962) on temperatures of the iguanas of Jensen Island, which lies at the entrance to Academy Bay within a kilometer of our study area, suggested that the terrestrial thermal regime of the *Amblyrhynchus* there is similar to that reported for the Punta Espinosa population.

Our observations are consistent with this suggestion and further indicate that the body temperatures maintained on land by marine iguanas are essentially the same in all size classes. However, the animals at Punta Espinosa spend the mid-day hours making the necessary behavioral adjustments to avoid overheating, whereas those at Academy Bay devote most of their thermoregulatory behavior to attaining the highest possible body temperatures, seeking out warm areas sheltered from the wind and assuming a prostrate basking posture. The hatchlings, of course, warmed somewhat faster than the yearlings and adults, but all size classes had the same range of body temperatures. For example, the body temperatures of 10 hatchlings at mid-morning on a clear day (air temp. 24–25 C) averaged 36.8 ( $\pm$  0.4 SE). This figure does not differ significantly from that for adults measured at the same time. It is also in the range (35 to 37) observed in adult iguanas at Punta Espinosa on Isla Fernandina.

The hatchlings remained as warm as possible on overcast days by staying in the lee of rocks and boulders where shelter from the wind allowed them to receive the maximum benefit from solar heating. The temperature of the lava surface was 8 to 10 C warmer in such situations than the 22 to 24° characteristic of rock surfaces directly exposed to the SE trade-winds, even though the lee and windward surfaces might be only 30 to 40 cm apart.

Outside the feeding periods some of the juveniles and most of the adults, particularly the large males, moved inland and congregated



Fig. 2. Aggregation of marine iguanas in a sheltered area 15 m inland from beach.

in a depression about 15 m from the high tide line and partly covered by thickets of *Cryptocarpus pyriformis* (Fig. 2). The lava ridges together with the bushes completely blocked the wind at ground level so the iguanas were able to spend their time in a sheltered, warm habitat and maintain themselves at temperatures near 35 C despite the cool, windy conditions on the shore only a few meters away.

#### SWIMMING

##### General Observations

The swimming of the marine iguana is anguilliform: the legs are held back against the sides, and thrust is developed by strong lateral undulations of the entire body and tail. The posterior third of the tail is somewhat flattened, but not conspicuously more than in other iguanids. Many naturalists have commented on the webbing between the heavy toes of *Amblyrhynchus*. Nevertheless, the webbed area is hardly more extensive than that of *Iguana iguana*.

When swimming at top speed along the bottom, marine iguanas often extend their front legs laterally and push themselves forward in

synchrony with their body undulations as if running. At low to moderate swimming speeds they never use their limbs for thrust, although they do sometimes use the front legs for balance. While swimming on the surface the animals float with head and back well above water (Fig. 3). When moving slowly after being forced to swim until fatigued they have a tendency to roll, which they counteract by moving the front limbs vertically in synchrony with their undulations. The digits are spread on the down stroke and held together on the up stroke, maximizing any effect of the webbing between the toes.

Swimming by members of all size classes of *Amblyrhynchus* falls into two principal modes, burst and cruise. When attempting to escape the lizards swim as rapidly as possible. They have limited stamina and this burst of activity can rarely be sustained for more than a minute. Even when being chased, they soon slow down to cruise velocity, which they can apparently maintain indefinitely.

#### Field Experiments

We assessed in the field the swimming performance of members of the three principal size

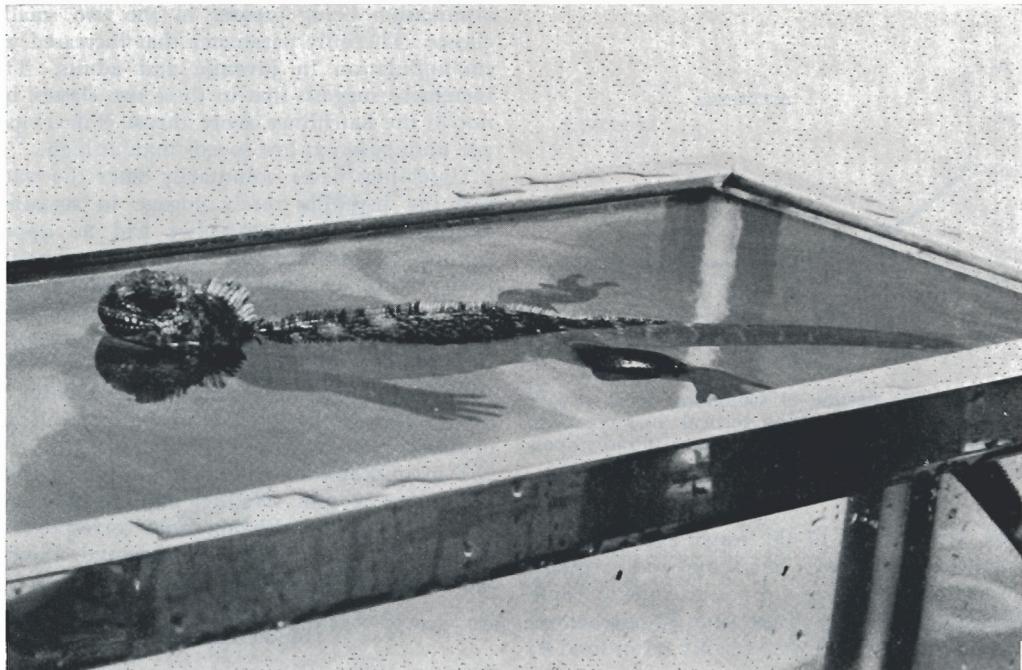


Fig. 3. When swimming at the surface, marine iguanas float buoyantly with head and back above the water.

classes of marine iguanas by measuring velocity, frequency of undulation, distance traveled, and blood lactate levels prior to and after standard periods of burst and cruise swimming.

**Methods.**—Two to 3 hr before experimentation, the animals were captured on land by noosing, measured to the nearest 0.5 cm, and placed in cloth sacks in which they remained quiet. Their swimming performance was measured in water 0.75 to 1.75 m deep in a sheltered cove with a sandy bottom. During the periods of measurement currents were absent or negligible; the water was clear and the surface was quiet except for small ripples. The lizards were slowly lowered into the water and released when all but the head was submerged. The iguanas swam slowly enough, even when exerting maximal effort, that we could readily maintain position just behind them by wading or swimming. We recaptured them by hand after a timed interval, and measured the distance swum with a line marked at 1 m intervals. With three observers, it was possible to measure distance swum, velocity, and frequency of undulation. We followed the change of these functions during periods of 6 to 8 min of continuous swimming or until velocity became constant.

**Results.**—When released the lizards immediately dove and swam away at burst velocity. The angle of dive was usually about 30°. Since they dove with lungs inflated, to remain submerged at the shallow depths at which they were tested they had to swim at a slight downward angle. They gradually surfaced as they tired and their velocity decreased.

The swimming performance of members of all three size classes during their attempted escapes were qualitatively similar, but the velocities and distances achieved increased directly with increasing size. Maximum velocity occurred during the initial burst. Thereafter, the rate decreased rapidly and stabilized at the cruise velocity within 3 or 4 min (Fig. 4). While swimming at cruise speed, they floated at the surface with the head and the dorsal part of the thorax above water (Fig. 3).

Once the iguanas were swimming at cruise speed, they always headed steadily toward shore and made no effort to dive, or otherwise escape, even when closely approached and touched. When picked up and rotated so they were headed away from shore they invariably turned and resumed their landward heading. When permitted, they swam slowly and steadily toward

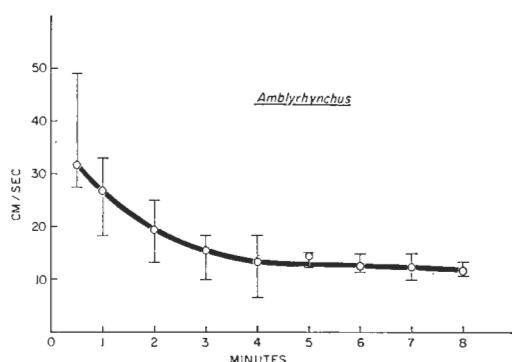


Fig. 4. The decline of swimming velocity with time spent swimming. The vertical lines represent the range and the circles the mean of 10 individuals (S-V length, 22.0 to 23.5 cm).

shore, crawled out of the water and remained stationary with heavy breathing and frequent gular pumping. They did not attempt to evade capture at this time. Even after 30 min ashore they did not run and were readily recaptured by hand.

During burst swimming, absolute velocity (cm/sec) and cm/undulation increased directly with size, whereas specific velocity (body lengths/sec), body lengths per undulation, and undulations/sec decreased with size (Table 1, Fig. 5). During cruise swimming, the same situation obtained (Table 1, Fig. 6).

In comparing burst and cruise swimming within each age class, most of the parameters examined showed a decrease when the animals were in the cruise mode (Table 2) with the

attenuation being greater in the two smaller classes. The only parameter that increased was cm/undulation in juvenile and adults. This increment suggests that in these two classes, but not in the hatchlings, more thrust is developed per undulation at low speeds than at high.

Hatchlings never voluntarily enter the water and the juveniles rarely engage in sustained swimming. Consequently, we had no opportunities to measure the voluntary swimming performance in these age classes. Adults, however, often enter the water and swim for considerable distances. We were able to measure the velocity and undulation frequency of 6 adult males that were voluntarily swimming in quiet water during low tide in the cove in front of the Darwin Station. Their mean velocity was 25.4 m/min and their mean frequency of undulation was 58/min. Neither of these figures is statistically distinguishable from corresponding measurements on adult experimental animals swimming in the cruise mode (Table 1).

#### Blood Lactate

*Methods.*—Blood lactate concentrations of juvenile lizards (S-V length 20–25 cm) were measured before and after 2-min bursts of underwater swimming, and before and after a 7-min period that included 2 min of burst swimming underwater followed by 5 min of cruise swimming on the surface. Small samples of blood (0.3 cc) were obtained by cardiac puncture. Aliquots were precipitated in 0.6 N perchloric acid and centrifuged at 3,000 rpm for 10 min. Lactate concentrations were measured after return to the U.S.A., with biochemical kits manufactured by

TABLE 1. SWIMMING PERFORMANCE OF MARINE IGUANAS.

	Weight <sup>a</sup> (g)	Total length (cm)	cm/sec	Burst				Cruise			
				undulations/sec	cm/undulation	lengths/sec	Lengths/un- dulations	cm/sec	undulations/sec	cm/undulation	lengths/sec
Hatchlings	72.2	27.8	42.5	2.5	16.7	1.53	0.60	15.1	1.2	12.5	0.55
(N = 6)	S.E.	—	0.53	4.2	0.2	—	—	2.1	0.1	—	—
Juveniles	540	54.9	46.3	2.2	21.3	0.84	0.39	21.3	0.8	25.7	0.39
(N = 10)	S.E.	—	1.71	2.6	0.1	—	—	2.0	0.1	—	—
Adults	2903	97.0	74.3	1.8	42.3	0.77	0.44	45.3	0.9	50.4	0.47
(N = 5)	S.E.	—	4.64	3.4	0.2	—	—	2.6	0.1	—	—

<sup>a</sup> Calculated from regression lines in Fig. 1.

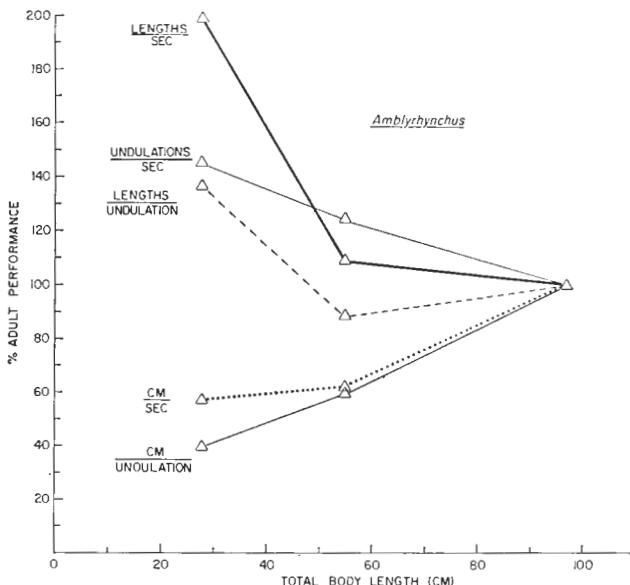


Fig. 5. The relation of performance to size during burst swimming in *Amblyrhynchus*. See Table 1 for original data.

Boehringer Mannheim Corporation. The animals were captured and handled as previously described. Blood samples from control animals showed that the handling involved in cardiac punctures did not lead to increases in levels of blood lactate. Post-exercise samples were taken 5 to 10 min after the cessation of swimming. This interval was chosen because blood lactate concentration does not reach a maximum level in other iguanids until 5 to 10 min after exertion (Moberly, 1968; Bennett, 1973). Blood lactate was measured immediately before the swimming tests because the elimination of lactate burdens requires many hours in lizards, and the behavior of the experimental animals prior to the 1 to 3 hr of rest that preceded testing was unknown.

**Results.**—Blood lactate concentration in 14 juvenile iguanas averaged  $36.5 \pm 6.3$  SE mg% prior

to swimming. This figure is significantly higher than the mean value of 8 mg% obtained from animals that had been kept undisturbed in the dark in the laboratory at 25°C for 8 hr (Bennett et al., 1975).

Following 2 min of sustained underwater burst swimming, the mean blood lactate of 6 animals was increased by an average of  $31.5 \pm 10.4$  SE mg% (Table 3). Eight individuals that had been forced to swim underwater at burst speed for 1 to 2 min and then to swim steadily at the surface in cruise mode for 5 min showed an average increase in blood lactate of  $60.2 \pm 10.4$  SE mg%. These increments in concentration of lactate following activity supply the first information on the extent of the lactate

TABLE 3. BLOOD LACTATE OF JUVENILE MARINE IGUANAS BEFORE AND AFTER SWIMMING.

TABLE 2. PERFORMANCE RATIOS (CRUISE/BURST) DURING SWIMMING IN MARINE IGUANAS. Data from Table 1.

Age class	cm/sec	Undulations/sec	cm/undulation
Hatchlings	0.36	0.48	0.75
Juveniles	0.46	0.38	1.21
Adults	0.61	0.51	1.19

Swimming regime	Blood lactate (mg%)						
	N	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
2 min at burst speed	6	23.6	3.6	55.1	8.2	31.5	10.4
2 min at burst speed plus 5 min at cruise speed	8	46.2	8.3	106.4	10.7	60.2	10.4

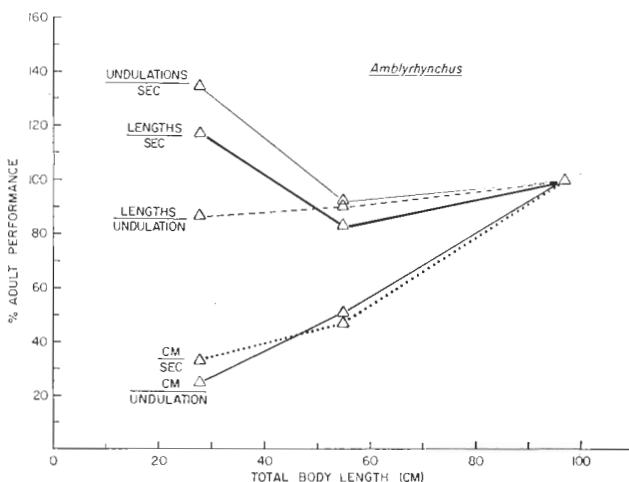


Fig. 6. The relation of performance to size during cruise swimming in *Amblyrhynchus*. See Table I for original data.

burdens developed by unrestrained active lizards under field conditions (see Discussion).

#### DIVING

##### General Observations

The diving of *Amblyrhynchus* is unique among lizards in that it is an integral part of feeding behavior rather than a mechanism for escape from potential terrestrial predators. Moreover, lizards that dive to escape typically remain quiet while submerged, whereas *Amblyrhynchus* feeds actively and moves about while underwater.

In our experience marine iguanas dive with lungs inflated. Thus, in the initial stages of diving the animals must work to overcome their buoyancy and in shallow water they must swim to stay submerged. In deeper water, however, their buoyancy becomes neutral as a result of compression of the air in their lungs and they can hang motionless in mid-water (Hobson, 1965, 1969). They also occasionally exhale small amounts of air while submerged. Buoyancy associated with feeding in shallow water does not present serious problems, however, because the algae that the iguanas eat grow on rocks to which the grazing lizards cling with their large recurved claws.

Marine iguanas dive by submerging the head and swimming obliquely downward with powerful undulations of the body. After they are a couple of meters below the surface their descent

becomes vertical. The thrust required at the start of a dive is considerable and propulsive power generated by the tail is essential. We captured an adult male that had lost most of its tail but otherwise was in good condition. The completely healed stump was 15.5 cm in length. The burst velocity of this animal was 28.3 cm/sec (38% of average burst velocity for normal individuals), and it was unable to submerge when it attempted to escape by diving.

The natural dives of feeding marine iguanas are, of course, variable and depend in part on depth of water and food availability. Voluntary dives lasting 30 min have been observed in the field (Hobson, 1965). Hobson (1969) reported that animals feeding in water 0.5 to 1 m deep had an average submergence time of 3.06 min (range 0.75 to 6.25 min). Carpenter (1966) estimated that marine iguanas feeding at depths of 7 m remained submerged for as long as 15 to 20 min. We observed dives by adult males feeding just outside the surf in water 2 to 3 m deep at Academy Bay. Durations of the dives for which we could be confident were 4.5, 2.6 and 2.7 min.

Iguanas tolerate prolonged periods of enforced submergence. Darwin's anecdote in the "Voyage of the Beagle" concerning an iguana that was "quite active" after a forced submergence of an hour is often quoted. In one instance a captive animal stayed submerged voluntarily for 50 min (Bartholomew and Lasienski, 1965).

TABLE 4. BLOOD LACTATE OF JUVENILE MARINE IGUANAS BEFORE AND AFTER PERIODS OF ENFORCED SUBMERGENCE.

Duration of submergence (min)	N	Blood lactate (mg%)					
		Pre		Post		Increase	
		$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
10 min	6	15.5	2.2	54.3	10.6	38.8	11.3
60 min	8	33.0	7.1	170.1	14.7	137.1	10.4

### Field Experiments

*Methods.*—We measured the levels of blood lactate before and after periods of forced submergence. The animals were tethered to rocks by lines secured in such a manner that they could cling to the rocks in their natural posture. They were submerged in clear sheltered water 0.5 to 1.0 m deep and kept under observation during the enforced dives. Some of the animals struggled occasionally, but most remained quiet throughout the period of submergence.

During the 10-min enforced dives, mean blood lactate concentration increased by an average of 39 mg% (Table 4). During the 1-hr enforced dives, the average increase was 137 mg%. The levels of lactate following dives did not overlap between the 10-min and 1-hr groups. Blood samples were taken from two animals at intervals for 30 min following forced submergence of 1 hr; during this period, lactate levels showed an irregular increase (Table 5). The highest blood lactate level measured during either swimming or enforced submergence was 295.5 mg% obtained 30 min after a 1-hr dive.

After the 10-min periods of submergence, the lizards appeared normally active. However, they were poorly coordinated following the 1-hr period of submergence, walking slowly and awkwardly and not attempting to escape except by wedging themselves into rock crevices. The animals submerged for an hour were unable to right themselves when turned on their backs. All eventually recovered, but even an hour after removal from the water, they moved only slowly and could not be induced to run.

In the enforced dives, the animals were immersed slowly and in a horizontal position. The lizards invariably inflated their lungs prior to submergence and kept them at least partly inflated while submerged. They emitted bursts of 10 to 20 bubbles at irregular intervals. At the end of the period of submergence, they were slowly lifted to the surface. Most of the lizards

TABLE 5. BLOOD LACTATE IN TWO JUVENILE IGUANAS BEFORE, AND AT INTERVALS AFTER, ENFORCED SUBMERGENCE OF 60 MIN.

S-V length (cm)		Blood lactate (mg%)					
		Pre-submergence	Minutes Post-submergence				
			5	10	15	20	30
25.0		78.8	243.9	247.2	272.9	273.3	295.5
23.5		30.2	159.2	185.2	198.0	179.2	192.6

did not immediately begin breathing. They began strong gular pumping movements as soon as their heads were in the air, and these movements returned the lungs to what appeared to be maximum inflation. The lizards did not initiate their usual thoracic respiratory movements for 30 sec to 5 min after removal from water. For the first 3 or 4 min after emergence, thoracic breathing was extremely irregular.

### DISCUSSION

Our measurements of the swimming and diving performance of *Amblyrhynchus*, together with our laboratory data on aerobic and anaerobic metabolism in relation to ambient temperature (Bennett, et al., 1975), supply some new insights concerning the biology of this lizard.

*Physiology.*—Because the level of blood lactate is affected by rates of removal as well as rates of production and rates of release, it can be used only as a rough index to the extent of glycolysis during activity. Even so, it is clear that *Amblyrhynchus* depends significantly on anaerobiosis during diving and burst swimming, and develops a substantial lactate burden. To our knowledge these measurements of blood lactate in *Amblyrhynchus* are the first direct demonstration of lactate accumulation in reptiles active under field conditions. On the basis of our data, we conclude that *Amblyrhynchus* routinely develops substantial lactate burdens incidental to swimming, feeding, and diving. Similar lactate burdens may also develop during certain activities associated with reproduction, such as agonistic encounters between males and nest hole digging by females.

After 2 min of burst swimming followed by 5 min of cruise swimming, the mean increase in blood lactate was 60 mg% (Table 3), a much lower figure than the 100 mg% increase in animals forced to run to exhaustion under laboratory conditions (Bennett et al., 1975). Moreover, lizards that had sustained underwater

burst swimming for 2 min and then surfaced to begin cruise swimming showed an increase in blood lactate of only 31 mg% at the time they changed from burst to cruise. We interpret these data to indicate that marine iguanas terminate burst swimming prior to the build-up of blood lactate to levels associated with exhaustion. Such behavior is compatible with the inference that even during the intense activity associated with attempted escape, some anaerobic capacity is held in reserve. Presumably a similar reserve of anaerobic capacity is maintained while the animals are diving and feeding underwater—activities which presumably are less demanding than the burst swimming associated with attempts to escape. The physiological parameters which the animals monitor to retain this reserve capacity are unknown but might involve pH,  $[H^+]/[OH^-]$ , or  $P_{O_2}$  of the blood.

Because marine iguanas appear able to swim at cruising velocity indefinitely, this mode of swimming is probably sustained aerobically. Nevertheless, the mean level of blood lactate after 2 min of burst swimming followed by 5 min of cruise swimming was 60 mg% above pre-activity levels, whereas after 2 min of burst swimming, the increase was only 31 mg%. We are uncertain whether this difference represents an actual increase in the amount of lactate produced or simply reflects a normal delay for washout of lactate from the muscles.

The relationship between high levels of blood lactate and exhaustion may be correlative rather than causal. However, all *Amblyrhynchus* having concentrations of 100 mg% or higher appeared exhausted, moved slowly, and were poorly coordinated. The period required for the iguanas to eliminate a lactate burden was not determined, but several hours are probably necessary for blood lactate to return to a resting level as is the case in *Iguana* (Moberly, 1968). During the first half-hour after enforced dives, blood lactate in *Amblyrhynchus* remained constant or increased slightly. Because marine iguanas appear to incur lactate burdens frequently in the normal course of their activities, it would seem advantageous for them to eliminate these as rapidly as possible. In relation to this, it is noteworthy that the maximal aerobic scope in these lizards develops near 35°C (Bennett et al., 1975), which is the same temperature they characteristically maintain by behavioral thermoregulation. If oxygen debt and removal of lactate are closely associated in lizards, the typical daytime body temperature of *Ambly-*

*rhynchus* coincides with the body temperature which would favor the most rapid elimination of a lactate burden (Bennett and Dawson, 1976; Dawson, 1975).

*Swimming performance.*—It is difficult to find an appropriate frame of reference for evaluating the swimming performance of marine iguanas. Their mode of swimming is anguilliform, and few comparative data are available on fish that employ this type of propulsion. Moreover, most determinations of the burst velocities of fish have been made in water tunnels over intervals lasting only a few seconds, whereas cruise velocities of fish have been measured over periods lasting from minutes to hours. However, the swimming performance of *Amblyrhynchus* can be placed in partial perspective by comparing it with appropriate data selected from the large literature on the locomotion of salmon, the swimming of which is intermediate between the anguilliform and carangiform (propulsion by caudal fin only) patterns, the latter of which is employed by most fast-swimming fish (Webb, 1975).

The burst velocities of marine iguanas are much slower than those of salmon of similar size (Table 6). However, the general relation of burst velocity to length is similar in fish and iguanas. Absolute velocity (cm/sec) increases with size while specific velocity (lengths/sec) decreases. The absolute velocity of cruising marine iguanas is less than  $\frac{1}{6}$  that of sockeye salmon, and on the basis of specific velocity of cruising, the comparison is even less favorable. Even the burst velocity of iguanas is less than half the critical velocity (the velocity that can be maintained for one hour) of sockeye salmon of the same length. Marine iguanas are more elongate than salmon. Consequently, if comparisons of swimming performance are made on the basis of body weight rather than length, the iguana appears in a slightly more favorable light (Table 6).

Compared with fish that employ carangiform swimming, the burst velocity of marine iguanas is modest indeed. For example, a conservative estimate (Walters and Fierstine, 1964) of the burst velocity of a hooked wahoo (*Acanthocybium solanderi*) 100 cm long is 12 body lengths/sec, a speed almost 16 times the maximum reached by marine iguanas of the same length. Even when compared with fish which swim in the anguilliform mode, the burst speed of the marine iguana is still extremely modest. Blaxter (1969) reported that a 60-cm eel (*Anguilla*) achieved a burst velocity of 1.9

TABLE 6. COMPARISON OF SWIMMING SPEEDS OF MARINE IGUANAS AND SOCKEYE SALMON (*Oncorhynchus nerka*). The left column pairs salmon with iguanas of equal length. The right column pairs salmon with iguanas of equal weight. Water temperature 20–22 C.

Salmon <sup>a</sup>			Iguana						Salmon <sup>a</sup>		
Critical speed <sup>b</sup>		Total length (cm)	Cruise speed		Burst speed		Body <sup>c</sup> weight (g)	Critical speed <sup>b</sup>			
(cm/sec)	(L/sec)	(cm)	(cm/sec)	(L/sec)	(cm/sec)	(L/sec)	(g)	(cm/sec)	(L/sec)		
103	3.68	28	15.1	0.54	42.5	2.81	74	80	2.86		
158	2.87	55	21.3	0.39	46.3	0.84	543	125	2.27		
230	2.37	97	45.3	0.47	74.0	0.76	2903	175	1.80		

<sup>a</sup> Recalculated from Brett and Glass (1973).

<sup>b</sup> Maximum speed that can be maintained for 60 min.

<sup>c</sup> Calculated from regression of total length on body weight, Fig. 1.

lengths/sec. This value is 2.3 times the burst velocities we recorded in marine iguanas with a mean length of 55 cm (Table 6).

The absolute and the length-specific burst velocities of marine iguanas are very slow when compared with those of fish of similar size. The burst velocity of these lizards is also slow when compared with their cruise velocity. Burst velocity is only 1.3 to 3.0 times cruise velocity in the various size classes (Table 2). Clearly, the capacity of marine iguanas to escape from aquatic predators by speed alone is extremely limited.

**Zoogeographic considerations.**—Marine iguanas occur only in the Galapagos Islands and they have dispersed throughout the archipelago. Populations have become established even on small and remote islands such as Wenman (Isla Wolf). Several of the populations are readily recognizable on the basis of size and color and seven insular subspecies have been described (Eibl-Eibesfeldt, 1962).

The present distribution of marine iguanas has almost certainly resulted from waif-dispersal. The cruising velocity of even the largest male iguanas is about 1.6 km/hr while that of the hatchlings is only about 0.5 km/hr. Currents of 3 or more km/hr are commonplace in the Galapagos. Marine iguanas can swim only a few meters at burst velocity, and at cruise velocity they are at the mercy of both wave surge and currents. The weakness of their swimming plus the frequency with which they enter the sea predisposes them for waif-dispersal.

Persistent strong currents serve not only to disperse iguanas but can also act as barriers to inter-island movements. The existence on adjacent islands of sharply differentiated populations argues strongly for a lack of frequent movements of individuals between islands. A

strong current flows northward in the Bolivar Channel between Isla Fernandina and Isla Isabella, which are separated by only 5 km, yet the marine iguanas on the two islands (*A. c. cristatus* on Fernandina and *A. c. albemarlensis* on Isabella) differ markedly in size and color.

Marine iguanas are occasionally exhausted by the strenuous swimming required to get through the heavy surge on the windward sides of islands such as Española and can be seen drifting almost helpless in the wave currents. They are in no danger of drowning, however, if completely exhausted. They float high and buoyantly because of their inflated lungs. In the absence of osmotic problems, they should be able to survive for many weeks while floating at sea. Fasts of a month or more are tolerated without difficulty by large iguanids including *Amblyrhynchus* (Bartholomew, personal observation). This period should provide more than enough time to drift from island to island. Moreover, it should even allow adequate time to drift from the mainland of South America to the Galapagos on the equatorial current which during the southern hemisphere winter has a velocity of as much as 2 km/hr. At this speed, less than 3 weeks would be required to drift from the mainland to the Galapagos.

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