A REAPPRAISAL OF THE AQUATIC SPECIALIZATIONS OF THE GALAPAGOS MARINE IGUANA (*AMBLYRHYNCHUS CRISTATUS*)

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It is tautological to say that an organism is adapted to its environment. It is even tautological to say that an organism is physiologically adapted to its environment. However, just as in the case of many morphological characters, it is unwarranted to conclude that all aspects of the physiology of an organism have evolved in reference to a specific milieu. It is equally gratuitous to assume that an organism will inevitably show physiological specializations in its adaptation to a particular set of conditions. All that can be concluded is that the functional capacities of an organism are sufficient to have allowed persistence within its environment. On one hand, the history of an evolutionary line may place serious constraints upon the types of further physiological changes that are readily feasible. Some changes might require excessive restructuring of the genome or might involve maladaptive changes in related functions. On the other hand, a taxon which is successful in occupying a variety of environments may be less impressive in individual physiological capacities than one with a far more limited distribution.

A case in point concerns the functional capacities of the Galapagos marine iguana (*Amblyrhynchus cristatus*), representing the large and diverse family Iguanidae that is easily the major saurian group in the Western Hemisphere. *Amblyrhynchus*, however, is unique not only among the iguanids but among all lizards in feeding exclusively on intertidal and subtidal marine products, predominantly soft-bodied macrophytic algae. It is of interest to ask how far the marine iguana has departed from general iguanid physiological patterns in following its unique mode of life. The amount of work required to harvest its algal food is of particular interest. These lizards must swim through the surf zone, dive beneath the surface (lungs remain inflated during diving so that the animals must initially overcome their own buoyancy), hold their breath during submergence, surface, and then swim back to shore through the surf (Bartholomew et al., 1976). The exertion associated with this underwater grazing must surpass the foraging of any other large iguanid, all of which are primarily herbivorous (Pough, 1973). The cool water temperatures around the Galapagos Archipelago (15–25 C) potentially hinder development of the intensity of activity required during feeding. All large iguanids so far investigated, including *Amblyrhynchus*, bask in the sun and reach body temperatures in the vicinity of 35 C. Activity in terrestrial iguanids characteristically occurs at these higher body temperatures, and the Van't Hoff effect would predict greatly depressed rates of functional processes at these lower temperatures.

Since physiological investigations have revealed that iguanids possess very little stamina, the locomotor performance required during activity is of particular interest. Other iguanids that have been investigated can sustain vigorous activity for only a minute or two and this activity is accomplished almost exclusively through anaerobic metabolism involving the production of lactic acid, rather than through greatly augmented aerobic metabolism (Moberly, 1968a; Bennett, 1972; Bennett
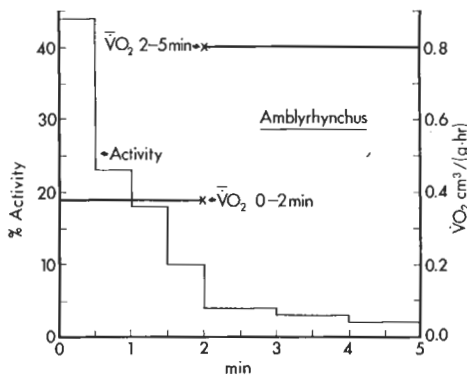
FIG. 1. Time course of activity (left hand ordinate), as indicated by movements of the left hind leg, and oxygen consumption (right hand ordinate) of marine iguanas during a 5-min period of electrical stimulation. The results are averaged for 6 animals (mean body mass, 489 g) at 30 C. The levels of oxygen consumption ($\bar{V}O_2$) indicated by the horizontal bars represent the average values for the 0-to-2- and 2-to-5-min intervals of the stimulation period, respectively.

and Dawson, 1972; Bennett and Licht, 1972). We decided that it was worthwhile determining whether the marine iguana has evolved special physiological capacities to deal with its demanding activity regime. In this investigation we have addressed several questions. Does *Amblyrhynchus* possess greater aerobic and/or anaerobic capacities than other lizards? Are marine iguanas particularly good swimmers or divers? Do these animals show physiological specializations permitting them to cope with the low body temperatures that appear to be incurred during feeding? Our observations, some of which are reported elsewhere (Bennett et al., 1975; Bartholomew et al., 1976), allow us to deal with the above questions in an evolutionary context.

Activity metabolism.—Resting *Amblyrhynchus* were stimulated to maximal exercise for five minutes and oxygen consumption, lactate production, and gross activity output were determined (see Bennett et al., 1975, for detailed procedures). Marine iguanas fatigue rapidly; virtually all escape behavior takes place during the first two minutes of stimulation, nearly half of the total response occurring within the first half-minute (Fig. 1). Below 35 C, maximal rates of oxygen consumption do not develop until after activity has been completed. The aerobic work capacity of an animal is generally represented by its aerobic scope (Fry, 1947), the difference at any single body temperature between standard and maximal rates of oxygen consumption. The maximal aerobic scope for *Amblyrhynchus* (Fig. 2), 0.71 cc O_2/ $(g \times h)$, resembles values reported for other iguanid lizards (Bennett and Dawson, 1976).

Anaerobic metabolism overshadows aerobic metabolism during activity by marine iguanas. Average values of blood lactate after activity range between 105 and 140 mg%. This range is identical to that reported for the iguanid lizards *Iguana iguana* (Moberly, 1968a) and *Sauromalus hispidus* (Bennett, 1973) and is characteristic of physically exhausted reptiles (Bennett and Dawson, 1976). Anaerobic metabolism provides 70–90% of the total ATP generation during a burst of activity in the marine iguana and accounts for over 97% of the carbohydrate utilization (Bennett et al., 1975). This metabolic situation and the magnitude of oxygen consumption and lactate buildup in *Amblyrhynchus* are indistinguishable from those characterizing terrestrial iguanids. Neither aerobic nor anaerobic capacities have been expanded in the adaptation to the marine habitat.

Maximization of aerobic scope near preferred body temperature is a common feature of saurian metabolism (Wilson, 1974), but one that seems inappropriate for *Amblyrhynchus*. Nevertheless, aerobic scope of this lizard peaks at basking body temperature (ca. 35 C) rather than at somewhat lower temperatures (Fig. 2), at which most of the strenuous work of the animal is probably conducted as it forages in cool water. Vascular mechanisms serving to delay cooling have been found in several terrestrial lizards and are particularly well developed in marine iguanas (Bartholomew

and Lasiewski, 1965). However, the time spent in the water by *Amblyrhynchus* appears to guarantee substantial cooling during foraging. It is thus important that this animal can achieve vigorous activity at body temperatures well below 35 C (aerobic scope is maximal at 35 C), as a byproduct of primary reliance on anaerobiosis. The anaerobic component of activity metabolism is not only large but is also nearly temperature independent (Q_{10} = 1.2). Low thermal dependence of anaerobic function is characteristic of iguanids generally (Moberly, 1968a; Bennett and Licht, 1972) and appears preadaptive for operation of marine iguanas at the lower body temperatures developing in the aquatic portion of their habitat.

Swimming and diving ability.—Darwin (1883) observed that marine iguanas show "perfect ease and quickness of swimming," but our observations (Bartholomew et al., 1976) indicate that they swim rather slowly and have little stamina. When released in the water, they attempted to escape from us by bursts of swimming lasting less than 2 min. The fastest adult marine iguana we observed (snout-vent length, 55 cm; total length, 106.5 cm) swam at 0.85 m/sec (47.9 body lengths/min), and the mean velocity for burst swimming by five adults (mean snout-vent length, 43.2 cm; mean total length, 97.0 cm) was 0.74 m/sec (46 body lengths/min). Following the brief period of burst swimming, adult marine iguanas cruised at velocities averaging only 0.45 m/sec (28 body lengths/min). Thus peak burst velocities are only about twice cruise velocities, a situation equivalent to a terrestrial herbivore being able to run only twice as fast as it can walk. The average burst velocities for adult marine iguanas are less than 10% of the peak burst velocities of fish of similar body length, including predatory species (Walters and Fierstine, 1964; Webb, 1975; Wardle, 1975). *Amblyrhynchus* are not uncommonly found in the stomachs of sharks around the Galapagos (Heller, 1903). These lizards with their
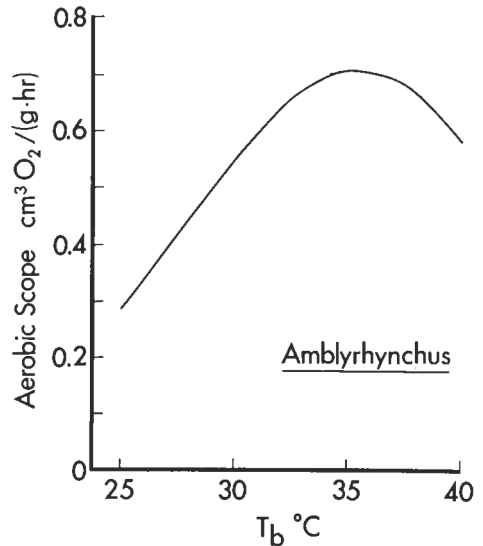

FIG. 2. The relation of aerobic scope of marine iguanas (mean body mass, 489 g) to body temperature (T_b). Values for aerobic scope are calculated from Bennett et al. (1975) and this reference should be consulted for details of procedure.

weak swimming abilities would appear to be easy prey for such predators.

Only the larger marine iguanas are sufficiently powerful to swim through breaking waves. Even the largest animals may have difficulty returning to shore through heavy surf. The hatchlings forage exclusively on the rocks exposed at low tide, not entering the water voluntarily. Hatchlings that we placed in the water beyond the surf invariably swam immediately toward shore and often became exhausted in the surf. They reached shore only by floating in on a favorable wave, their own locomotion being insufficient without such assistance. We also observed adult animals feeding on macrophytic algae exposed at low tide; indeed, during the lowest tides, they did so almost to the exclusion of entering the water. Marine iguanas swim with inflated lungs and their buoyancy eliminates any risk of drowning (Bartholomew et al., 1976). Individuals may occasionally be carried from one island to

another in the Galapagos Archipelago by the swift currents prevailing there. However, their relatively weak swimming capacities would make any directed long distance movements between islands improbable. The variation in color apparent among the populations inhabiting the different islands suggests a low level of genetic interchange among insular groups of *Amblyrhynchus*.

By mammalian or avian standards, the capacities of marine iguanas for tolerating submergence are quite impressive. Natural dives generally last 5–10 min and are relatively shallow (1.5–5 m) (Bartholomew et al., 1976; G. Wellington, pers. comm.), but these lizards sometimes descend to depths as great as 12 m and remain submerged for as long as 30 min (Hobson, 1965, 1969). Darwin (1883) reported that an animal tied underwater for an hour was still alert when released. These observations naturally led to the conclusion that marine iguanas have unusual capacities for remaining submerged. However, recent investigations have established that lizards as a group are very tolerant of anoxia: terrestrial iguanid lizards survive in an atmosphere of pure nitrogen for over an hour (Belkin, 1963). This tolerance results from a combination of low metabolic rates and high tolerance of lactic acid. Moreover the common iguana, *Iguana iguana*, which occasionally dives into streams as an escape response, will voluntarily tolerate submergence for up to 4 hr (Moberly, 1968*b*). Evidently the diving abilities of *Amblyrhynchus* do not surpass those of other iguanids. In fact, our observations on marine iguanas indicate that enforced dives of one hour are sufficiently stressful to produce a pronounced loss of locomotor coordination. We observed increases in concentrations of blood lactate averaging 137 mg% following such dives. Diving by marine iguanas requires vigorous effort. Individuals approaching exhaustion in our tests after 1–2 min of burst swimming could not develop the thrust necessary to submerge and remained in a diving posture at the surface, making futile undulatory movements.

Diving mammals and birds show a suite of physiological specializations that prolong the time they can remain submerged and facilitate recovery after diving. These adaptations include a high aerobic scope, large hematocrit and blood oxygen capacity, and high myoglobin concentrations in skeletal muscle. None of these factors in *Amblyrhynchus* departs significantly from levels found in other iguanid lizards. Aerobic scope is low (Fig. 2); hematocrit values average 31.5% (± 4.5 *s.d.*), a figure characteristic of that reported for iguanid lizards as a group (Dessauer, 1970; Bennett, 1973); and skeletal muscle tissue appears as white as fish hypaxial muscle, indicating very low myoglobin content. Even the bradycardia reported for *Amblyrhynchus* during a dive (Bartholomew and Lasiewski, 1965) appears to be a response generally evident in terrestrial vertebrates during submergence rather than a specialized adaptation.

Evolution of Amblyrhynchus.—Our study indicates that the mode of life of the marine iguana has entailed surprisingly little departure from capacities for activity and locomotion characterizing terrestrial iguanids. Aerobic scope and its thermal dependence, reliance on anaerobiosis, and restricted stamina evident in *Amblyrhynchus* are consistent with data obtained for other iguanid lizards. Other functional characteristics of marine iguanas previously thought to be unique are now known to resemble qualitatively those of terrestrial iguanids, e.g., circulatory responses to diving (Bartholomew and Lasiewski, 1965), tolerance of submergence, nasal salt secreting glands (Schmidt-Nielsen and Fänge, 1958; Dunson, 1969). We do not wish to minimize the impressive osmoregulatory capacity manifested in the nasal gland of *Amblyrhynchus*: it has the highest mass-specific secretory rate established for reptilian salt glands (Dunson, 1969). However, this is a quantitative improvement rather than a unique development among

iguanid lizards. It is the sole physiological specialization thus far observed in this species. The partially webbed feet and laterally compressed tail specified as adaptations of marine iguanas for swimming and diving (Darwin, 1883) do not differ greatly from those of *Iguana iguana*. These morphological features were not distinctive enough to merit special comment in the original description of *Amblyrhynchus cristatus* (Bell, 1825), which was made without information on the behavior and ecology of this species.

If the physiological grade represented by the family Iguanidae is in a sense preadaptive for the mode of existence followed by *Amblyrhynchus cristatus*, why are there no other marine iguanids? Any examination of this question requires definition of the major features of the particular environment occupied by marine iguanas. As in the areas in which most large iguanids live, the terrestrial environment of *Amblyrhynchus* is relatively warm and equable. The equatorial location of the Galapagos Archipelago also ensures that strong insolation occurs throughout the year on the leeward sides of the islands and at least seasonally on the windward sides, important considerations for heliothermic lizards. The cool waters surrounding the Galapagos Islands, the upwelling occurring at many points off them, and the extensive rocky or lava substrates allow an abundant and diverse flora of soft-bodied macrophytic algae of the types utilized by *Amblyrhynchus* (Carpenter, 1966; Silva, 1966). We should note here that the upwelling is quite localized even within the Galapagos Archipelago, with a corresponding concentration of marine iguanas on adjacent shores. It is of interest that the social organization of this lizard parallels that of sea lions and other otariids, which assemble in dense concentrations on shore. Until the introduction of dogs, cats, pigs, and rats by man, the Galapagos Islands have been free of terrestrial mammalian predators, which might abort any evolutionary experiment involving the grouping of potential prey in large sedentary concentrations in relatively exposed positions.

Within the geographic range occupied by members of the family Iguanidae, the combination of physical and biological circumstances evident in the Galapagos appears unique. Continental islands or mainland coasts are likely to have mammalian predators. Other tropical islands are likely to offer fewer food resources because coralline algae rather than softer-bodied forms utilized by *Amblyrhynchus* predominate in the warmer waters surrounding them (Carpenter, 1966; W. R. Taylor, pers. comm.). Islands located at higher latitudes may offer the food resources, but have cool temperatures and few sunny days. In addition to these considerations, the Galapagos Archipelago lies astride the equatorial current. This location facilitates rafting from tropical America, where the family Iguanidae has its greatest radiation. Moreover, most of the islands in this archipelago are large enough to support a reasonably diverse biota that would have made them hospitable to large iguanid immigrants.

Immunological evidence (Higgins and Rand, 1974, 1975; Higgins et al., 1974), suggests that the Galapagos marine iguana and the Galapagos land iguana (*Conolophus* spp.) are more closely related to one another than either is to any mainland iguana. These two insular forms probably differentiated within the Archipelago from a common ancestor, presumably a terrestrial herbivore. This differentiation must have occurred in substantially less than the several million to 10 million years regarded as the maximum age of the Archipelago (Cox, 1971), for the ancestral form could not have survived before the establishment of a flora offering suitable food resources. In the case of *Amblyrhynchus*, the evolutionary events leading from the ancestral form have resulted in a number of habits that have been interpreted as indicating a high degree of specialization for marine situations. However, aside from osmoregulation and, possibly, processing of food, the major portion of these adaptations is

behavioral. These reflect the fact that the behavioral repertoire of marine iguanas has evolved in a manner permitting recognition and procurement of macrophytic algae as food and the establishment of a social order permitting the concentration of large numbers of these lizards on shore at points adjacent to locally abundant food resources. That foraging by marine iguanas is accomplished under conditions in which temperature regulation is not feasible indicates a further behavioral distinction between these animals and other heliothermic lizards. The acquisition of a semi-aquatic habit has involved relatively little reorganization of conventional patterns of iguanid physiology. With regard to metabolism and capacities for swimming and diving, we feel justified in regarding the marine iguana as a member of a terrestrial line that was preadapted for exploiting a unique combination of circumstances.

Summary

Contrary to earlier descriptions, the Galapagos marine iguana is not a particularly fast swimmer, the mean velocity for burst swimming by large adults being only 0.85 m/s. Moreover, this lizard depends on physiological patterns characteristic of terrestrial iguanids in its amphibious existence. Aerobic metabolic scope is relatively restricted and highly dependent upon body temperature. This function reaches a maximum at 35 C, a value characteristic of basking marine iguanas, but substantially higher than the water temperatures at which the most strenuous activities of this species occur. Its abilities to forage in cool waters appear to depend upon substantial anaerobic capacities, which resemble those of terrestrial iguanids. As in these other lizards, anaerobic metabolic scope appears relatively independent of temperature in the marine iguana. Physiological results and a review of the probable events leading to the evolution of the Galagapos marine iguana support a view of this animal as a representative of a terrestrial line that was preadapted for exploiting a unique combination of circumstances.

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