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Review Article

The Effects of Algal Abundance in an Energy Sensitive Environment on the Galapagos Island Marine Iguana

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The Galapagos Island marine iguana (*Amblyrhynchus cirstatus*) relies on energy-expensive foraging strategies in order to tolerate environments required by a strictly seaweed diet (Nagy, 1984). The quality or quantity of seaweed plays an intricate role in body size, grazing ability, and fitness of this specialist herbivore. In this review, I will discuss the relationship between algal abundance and quality and its effects on the fitness and reproductive timing of the marine iguana.

The marine iguana is thought to be evolutionarily unique. Although there are land iguanas found throughout the world, including the Galapagos Islands, the marine iguana has proven itself to be unique, as it is the only iguana that feeds exclusively underwater. Since there is food available on the islands, biologists are unsure of the origins of this adaptation. There are two suggested theories for this evolution: divergence of the two taxa from a common ancestor, or two separate ancestors colonizing the Galapagos (Rassman, 1995).

The foraging habits of the iguana can be documented as far back as Darwin (1835), the first to investigate the unique capabilities of the iguana: "I have reason to believe it (seaweed) grows at the bottom of the sea. If such be the case, the object of these animals occasionally going out to sea is explained." The iguana's body is designed for swimming and diving. The tail is long and compressed, designed as a propelling structure. Long, sharp claws permit marine iguanas to hold onto the lava reef while feeding, and serrated teeth allow them to forage on low-growing algae (Carpenter, 1966). However, May (1976) has challenged the unique evolution of the marine iguana by questioning their physiological specializations. Through his investigations he concluded that the acquisition of an aquatic foraging strategy has involved relatively little reorganization of conventional patterns of iguana physiology. Therefore, he regards the marine iguana as a member of a terrestrial line that was pre-adapted for a unique combination of circumstances. Despite the claims of May, it is well documented that the marine iguana has a specialist relationship with algae that results in adaptations in both organisms.

Herbivory on Galapagos seaweed can have severe consequences on seaweed populations because they are considered to be very small and are heavily grazed by many species (Duffy, 1990). However, seaweed has a number of defenses to prevent overgrazing. Seaweed grows rapidly, replacing the losses inflicted by grazing iguanas. However, due to their quick growth rates, the algae are dependent on the iguana to reduce intraspecific competition (Hay, 1988). Seaweed contains numerous secondary metabolites that deter herbivory (Hay, 1988, 1990). Different rates of consumption and subsequent turnover of plant material reflect the structural and morphological features of algae and their ability to reduce their vulnerability to some grazers (Choat, 1998 and Hay 1990). These adaptations can lead to digestive difficulties that hinder the iguana's ability to acquire energy and nutrients from plant material.

Similar to algal defenses, the marine iguana has evolved a number of specialized adaptations for underwater seaweed foraging. Despite having difficulty digesting seaweed because of its high content of indigestible fibers, the marine iguana is able to sufficiently digest the plant material via microbial hindgut fermentation systems similar to those of mammals (Wikelski, 1993). Marine iguanas maintain a basking temperature of 35-37°C, but forage at body temperatures 10°C lower (Bartholomew, 1965 B). This drop in temperature can cause severe physiological malfunctions because the marine iguana is an ectotherm. It would be advantageous for the marine iguana to reduce its rate of cooling while underwater and thus extend the period of potential foraging time (Bartholomew, 1965 B). In both air and water, the marine iguana cools much more slowly then it heats (Figure 1). This demonstrates that the marine iguana can cool very slowly, maintaining energy-efficient foraging, and heat very rapidly, returning to principal body temperatures after leaving the water (White, 1972). The ability of the marine iguana to maintain a relative homeostatic body temperature implicates the circulatory system as an important factor in temperature regulation (Batholomew, 1965 A). The capacity for the marine iguana to regulate circulation can be seen through ^{133}Xe deposited in marine iguanas that were heated and cooled (Figure 2). The isotope was then tracked throughout the iguana. The change in the slope of the ^{133}Xe disappearance rate in iguanas demonstrates changes in the circulatory system following localized heating or cooling. On acquiring heat from the environment, peripheral vasodilatation occurs, transporting heat from the periphery to the core, raising the slope. Cooling induces the converse response, reducing the rate of heat loss from the core to the periphery, lowering the slope (Morgareide, 1969). These adaptations help the marine iguana cope with harsh energetic foraging conditions. Marine iguanas

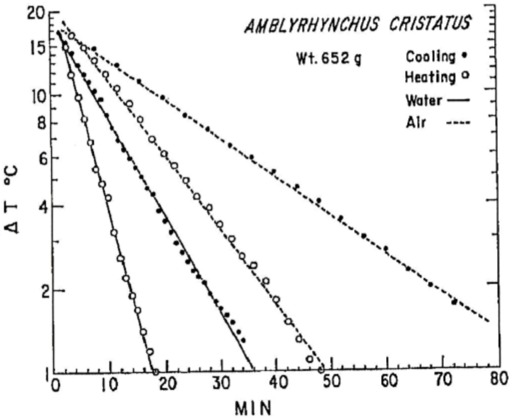

Figure 1. Heating and cooling rates in water and in air. ΔT is the difference between T_A and T_B (Bartholomew, 1965 A).

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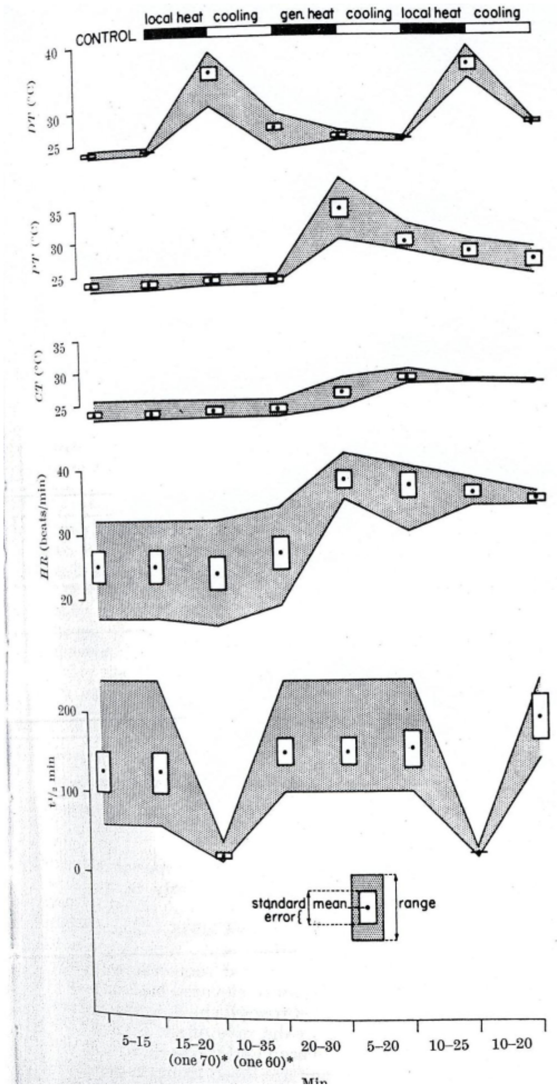

Figure 2. The results of heating and cooling in the marine iguana. DT, temperature at the site of ^{133}Xe deposit; PT, temperature proximal to the DT; CT, hindgut temperature; HR, heart rate; t1/2, ^{133}Xe disappearance (Morgareide, 1969).

are able to forage for seaweed via numerous physiological adaptations in digestion and temperature regulation. Without these adaptations the iguana could not hold such a strong grip on their specialist niche and therefore maintain their relationship with the algae.

The marine iguana is thought to be a food-limited species (Rubenstien, 2003). This creates a fixed ecological relationship between the iguana and its algae, as any slight difference in algae abundance can cause large changes in marine iguana body condition, survival, and reproduction (Rubenstien, 2003). Each of these circumstances can be related back to the need of the iguanas to be energy efficient, as they are foraging on specialized plant material in a cold, aqueous environment. Therefore, if algae are not plentiful, valuable foraging energy will be wasted, leading to adverse effects on fitness.

The abundance of algae in the Galapagos Archipelago is considered to be seasonal. Algal biomass and cover declines from the cool season to the hot season: there is a sharp increase in algae in late November and a rapid decrease as the warmer months begin (Figure 3). This annual change has a remarkable effect on the marine iguana, as algal abundance is positively correlated with iguana fitness. As a result, marine iguanas can utilize this proximate environmental cue to influence the timing of reproduction. This can be achieved through synchronizing breeding times and favoring such times when food is most available for the hatchlings (Rubenstein, 2003). Iguanas would then benefit from breeding during the cool season, when algae is most available for hatchlings. The peak in copulation among marine iguanas is seen in late December (Figure 4), coinciding with the spike in algal populations (Figure 3). Demonstrating the marine iguana's ability to utilize algal quantity to cue reproduction shows the remarkable connection between the iguana and its food source.

The effectiveness of the marine iguana's ability to retrieve energy and nutrients from algae is based not only on the quantity of available algae but also on the quality of the algae. The quality of algae is based on the carbon content, nitrogen content and carbon to nitrogen ratio (Hemmi, 2002). Leading up to mating, the marine iguana should ingest the algae of the highest quality. The mean foraging of iguanas increases linearly as the first day of copulation approaches, while after copulation (shown by the dotted line) foraging decreases and becomes nonlinear (Figure 5). Not only are iguanas ingesting more algae, they are ingesting algae of the highest quality. Wikelski (1997) observed that marine iguanas preferred the algae *Gelidium* over other species. *Gelidium* was also the species of algae that had the highest nutritional value on the basis of carbon and nitrogen content and carbon to nitrogen ratio (Figure 6). Overall, iguanas are foraging more frequently on algae with the most nutrients and energy, and they are doing so when the algae are most available. This energy efficient foraging is linked to the timing of their copulation.

Another possible factor in marine iguana reproductive timing is sea surface temperature. Sea surface temperature could give the primary cue to commence reproduction. However, sea surface temperature data suggests this to be an unreliable source as El Niño events have no effects on iguana reproduction (Wikelski, 2000). This concludes that food quality and quantity are the most reliable queues for reproduction. and that the availability of plentiful and nutritious algae affects both reproduction and iguana fitness.

Galapagos marine iguana populations show considerable differences in body size. Adult body mass varies by more than 10-fold, even though predation and site-specific food competition are largely absent (Wellington, 1975). Since predation and food competition do not influence body size, mass can be more accurately predicted by foraging capabilities and, consequently, fitness. Foraging efficiency and its relationship to food intake is therefore the main constraint on body size (Frost, 1983). Wikelski (1994) compared the foraging capabilities of both large and small iguanas. He showed that small iguanas were limited in duration of feeding due to wave force, whereas large iguanas were constrained by a decrease in bite rate. He also showed that small iguanas had a natural advantage in foraging, as they grazed the algae closer to shore more frequently than the large iguanas. More frequent foraging was possible for small iguanas because they are able to warm themselves more rapidly than large iguanas (Bartholomew, 1964). Their

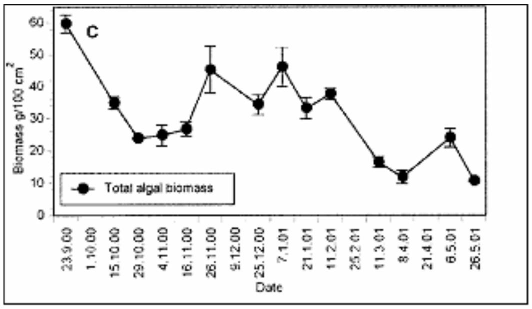

Figure 3. Algal cover and fresh weight biomass (Shepherd, 2005).

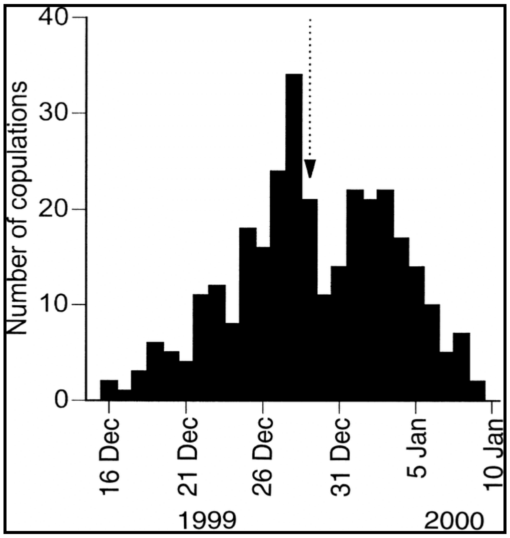

Figure 4. Copulations observed from December 16 to January 10. The arrow depicts the median copulation date (29 December 1999) (Rubenstien, 2003).

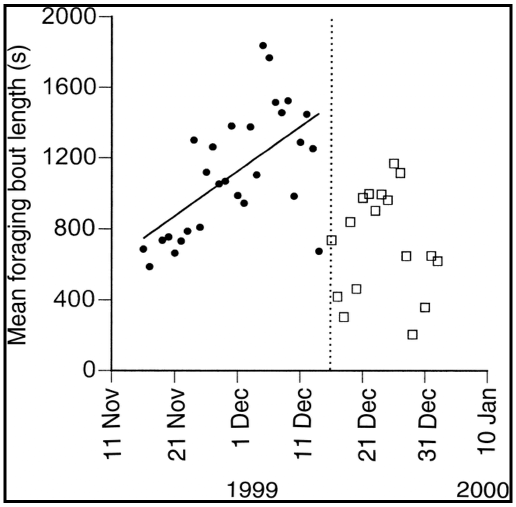

Figure 5. The mean foraging bout length The mean foraging bout length varied over the course of the breeding season. The day the first of copulation is depicted by the dotted line (Rubenstien, 2003).

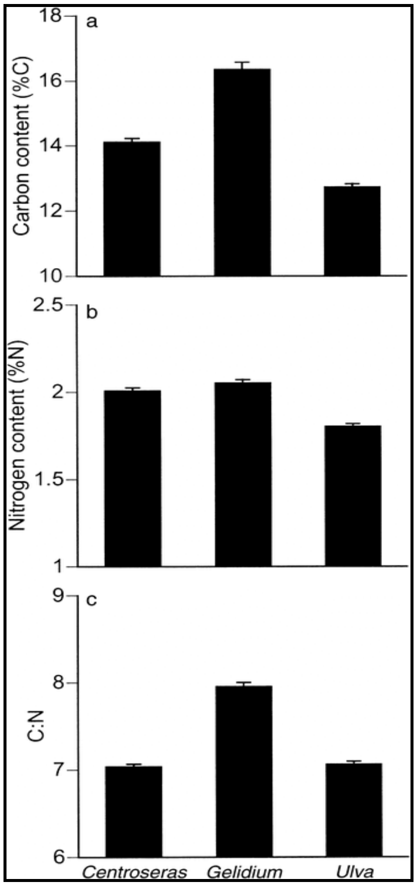

Figure 6. Carbon content, nitrogen content, and C:N ratios differed among the three species of macroalgae (Rubenstien, 2003).

ability to heat themselves quickly allows for rapid return to the sea to forage in the cool temperatures. As small iguanas foraged more frequently, they kept the algae closer to shore grazed down. This left no algae for the large iguanas and forced them to feed farther out.

Inefficient foraging in large iguanas causes a higher vulnerability to decreases in food abundance and therefore a higher mortality rate (Wikelski, 1994). An increase in the mortality rate of large-bodied iguanas would tend to imply that natural selection favors small body size over the larger body size. However, reproductive performance in males increases with body size and is reinforced by a higher survival rate of larger hatchlings from larger females (Frost, 1983). If reproductive performance favors increased body size, an evolutionary increase in body size can be predicted regardless of the overall limit imposed by foraging performance.

This information brings up many intriguing questions for iguana fitness and evolution. If marine iguanas are imposing both positive and negative forces on the evolution of body size, why is there such great disparity in iguana mass? Natural selection acting in either direction would cause the pronounced differences in adult body mass, ranging from 1kg to 12kg (Wikelski, 1997), to gradually shrink. However, unidirectional change in body size is not seen on the islands. Secondly, a large increase in algal abundance would cause an increase in iguana body size, but would be beneficial for only a short amount of time, as any environmental change can causes large shifts in algae population. Rapid temperature increases, such as the El Nino events, would cause a decrease in the quantity and quality of algae populations (Wikelski, 2000). Large iguanas would not forage small algae populations efficiently and would have an increase in their energy expenditure. Consequently, these large iguanas would have a higher mortality rate implying that surplus algae may circumstantially hurt iguanas.

Temperature change at a world wide scale can also significantly affect the marine iguana. Global warming may have large effects on the marine iguana, with the possibility of increasing or decreasing body size. As sea temperatures increase, algae quantity and quality will decrease. Smaller populations of algae are foraged more effective by small-bodied iguanas, leading to a decrease in body size. However, iguana activity is dependent upon environmental temperatures. A slow relaxation of constraints on foraging performance due to increased sea temperatures could result in an overall increase in body size (Wikelski, 2003). Therefore, the expectation is thatbody size of Galapagos marine iguanas may increase along with global warming trends and warmer sea surface temperatures. Along with global warming and El Niño, pollution may be another unnatural forces affecting iguana body size,

As the Galapagos Islands become a hub for tourism, the amount of cruise ships entering and leaving the islands can effect algae populations and consequently iguanas. Large ocean-going ships are known for increasing levels of nitrogen emission (Corbett, 1990). Nitrogen levels can significantly increase the algal biomass of nitrogen deficient algae populations. As previously stated, an increase in algae quantity can have negative effects on large-bodied iguanas. Overall, there are many possible factors inducing possible changes in iguana body size.

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Conclusion

The marine iguana has a dependant relationship with the underwater algal beds of the Galapagos Islands. Its reproductive timing, body size, and fitness are all related to both the quantity and quality of the algal beds. Contrasting opinions on the forces of natural selection on marine iguana body size has sparked a controversy over their fitness. Both small and large iguanas have evidence to support the unidirectional evolution of body size. The evolution of body size may be affected by the El Nino events, global warming, and pollution. Future research could approach this dilemma both phylogenetically and observationally. The evolutionary phylogeny of the marine iguana could be used to compare body sizes and their increase or decrease. Similarly, iguanas could be physically measured to calculate any general trends in growth or shrinkage. Evolutionary change in marine iguanas is ultimately related to algal quality and quantity, emphasizing the delicate relationship between the fitness of the marine iguana and Galapagos Island algae.

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