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Galapagos land iguana, *Conolophus subcristatus*, feeding on *Opuntia* cactus. *Photograph: Karl H. Switak*

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Galapagos Land Iguanas: Surviving in Peril

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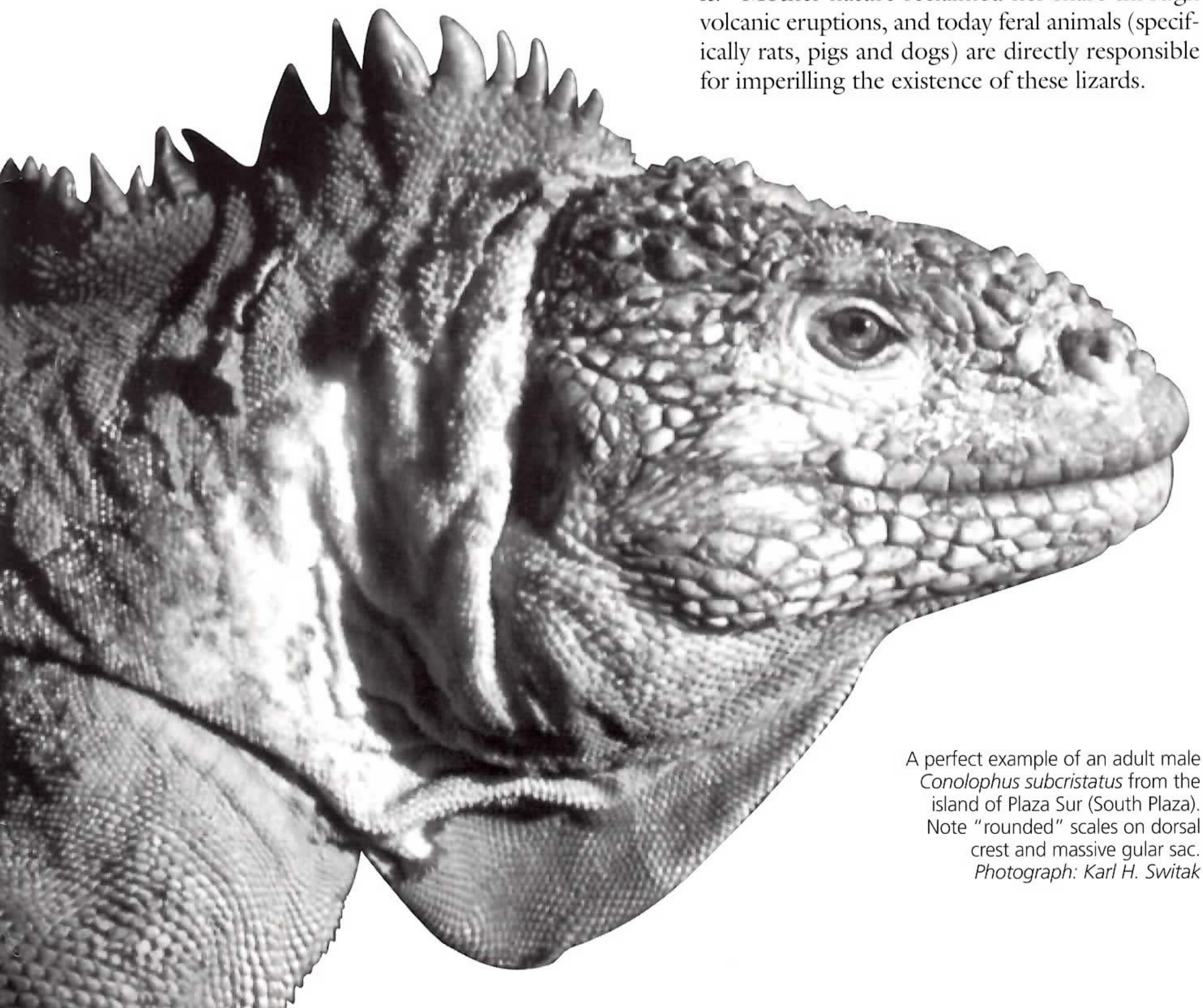
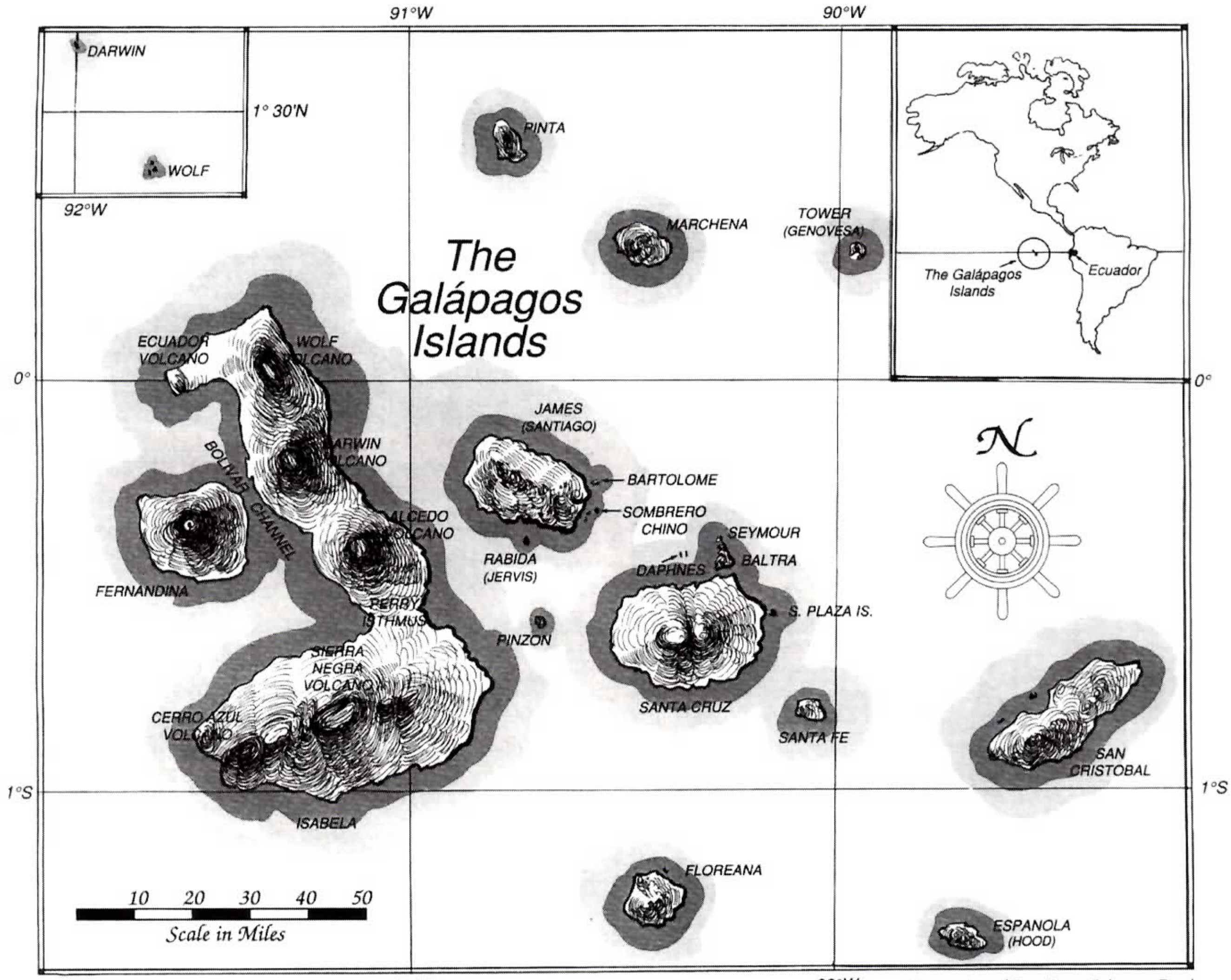
THEY ARE NOT AT ALL TIMOROUS: WHEN ATTENTIVELY WATCHING ANYONE, THEY CURL THEIR TAILS, AND RAISING THEMSELVES ON THEIR FRONT LEGS, NOD THEIR HEADS VERTICALLY, WITH A QUICK MOVEMENT, AND TRY TO LOOK VERY FIERCE: BUT IN REALITY THEY ARE NOT AT ALL SO...

Darwin 1839

Land iguanas, like all other animals that abound within the confines of the Galapagos Archipelago, have struggled through centuries of turbulent times. In the past many were killed by visiting sailors and used as a food supplement, while others were shot "just for the sport of it." Mother nature reclaimed her share through volcanic eruptions, and today feral animals (specifically rats, pigs and dogs) are directly responsible for imperilling the existence of these lizards.



A perfect example of an adult male *Conolophus subcristatus* from the island of Plaza Sur (South Plaza). Note "rounded" scales on dorsal crest and massive gular sac. *Photograph: Karl H. Switak*



Map courtesy of Barry Boyce, Galapagos Travel.

Some interesting field notes recorded during the California Academy of Sciences expedition of 1905–06 read as follows:

> Sixteen or eighteen specimens were secured on South Seymour, two at Tagus Cove, Albemarle, and twenty-one on Narborough. [Author's note: by "secured" I assume they meant killed.]

> Land iguanas are common [South Seymour, Nov. 21, 1905], and are scattered all about, not living in colonies like those on Barrington Island. There are a few burrows, but most of the iguanas live in the broken lava. I saw one large male eating on a cactus, and our mate, Mr. Nelson, said that one came and drank the blood of a goat he had shot.

> April 6, 1906 [Narborough Island]. Land iguanas are common. They live in cracks in the lava. No colonies of burrows were observed. April 17, 1906—We made a landing on a slope of cinders and lava, over which we climbed to the top... Here we found iguanas scattered over the lava. They were wild and had to be shot.

> Oct. 20, 1905. Anchored on N.W. coast of Barrington, and went ashore and a mile inland to the iguana colony on a plateau at an elevation of about three hundred feet. The burrows resemble those of a ground-squirrel only larger. We found the iguanas common here. They were awkward in their movements but covered the ground at good speed. They are very vicious, seizing one another by the jaws and drawing blood. One

WE CAUGHT TORE THE WHOLE LOWER JAW OFF ANOTHER. JULY 10, 1906.

WE DID NOT SEE ANY YOUNG SPECIMENS. TEN EGGS WERE TAKEN FROM ONE FEMALE AND SEVEN FROM ANOTHER.

VAN DENBURGH & SLEVIN 1913. THE ACADEMY COLLECTION INCLUDES TWENTY-FIVE ADULT SPECIMENS IN ALCOHOL, AND SOME SKINS AND BONES. [AUTHOR'S NOTE: THE VARIETY REFERRED TO HERE IS *CONOLOPHUS PALLIDUS*, ENDEMIC TO THE ISLAND OF BARRINGTON.]

TAGUS COVE, ALBEMARLE ISLAND, MARCH 23, 1906. BECK REPORTS SEEING ABOUT SIX LAND IGUANAS, OF WHICH HE SECURED ONE. THEY ARE EXTREMELY WILD. HE NOTICED ONE VERY LARGE BRIGHTLY COLORED MALE. THE ONE TAKEN WAS A FEMALE IN THE ACT OF SHEDDING ITS SKIN. MARCH 24, 1906. I SAW ONLY ONE IGUANA TODAY. THEY ARE VERY RARE; PROBABLY ONLY SIX OR EIGHT ARE LEFT IN THE COLONY. JUDGING FROM THE NUMBER OF BURROWS ONE MAY SAFELY SAY THERE WERE AT ONE TIME AS MANY AS A THOUSAND IN THIS COLONY.

The islands of the Galapagos are known by two names, one being English, the other Spanish (several by three names). Older literature (journals, etc.) uses only the English names. I have used the current Spanish names under the specific distribution section and include the English versions in parentheses. Most present day writers use only the Spanish names, making it difficult to cross-reference material from days gone by (Darwin, *et al.*).

Today, at the near closure of the twentieth century, land iguanas frequent the more arid regions on seven of the islands in the archipelago. There are two recognized species: *Conolophus subcristatus* and *Conolophus pallidus.* The former occurs on the islands of Santa Cruz (Indefatigable), Plaza Sur (South Plaza), Isabela (Albemarle), and Fernandina (Narborough). In years past *C. subcristatus* was introduced onto Seymour (North Seymour) and was recently repatriated on Baltra (South Seymour). *Pallidus* is endemic to the island of Santa Fe (Barrington). They are extinct on Santiago (James).

For ease of identification, or for placing a specific land iguana within a given locale, I decided to establish two separate common names. The

Habitat for *Conolophus subcristatus* on Plaza Sur (South Plaza) Island. Ground cover is *Sesuvium,* tall cactus is *Opuntia.* *Photograph: Karl H. Switak*

Barrington Land Iguana, *Conolophus pallidus* (found only on Santa Fe) and the Galapagos Land Iguana, *Conolophus subcristatus,* found elsewhere in the archipelago.

Land iguanas are large and robust reptiles. They range in size from 0.91 m to 1.07 m (3 to 3 ½ feet), with males attaining greater proportions. Jackson (1993) estimates them to grow to more than a meter, weighing as much as 13 kg (28.7 pounds). The latter was a huge specimen brought to the Darwin Research Station from North Seymour Island, which has since bred successfully in captivity. Sprackland (1992) estimates the size up to 1.1 meters (3.6 feet) and a weight of 4.5–6.8 kg (10–15 pounds).

I have personally observed land iguanas on the islands of Isabela, Plaza Sur, and Santa Fe, starting in 1986. The largest iguana was encountered in January of 1991 at Urvina Bay on the west side of Isabela very near the ocean. Two of the specimens observed on Santa Fe, both males, were also of considerable size. During my April 1995 visit I also found a large male on Plaza Sur that must have exceeded 1.1 meters in total length. Males are distinguished from females by having a much more pronounced dorsal crest of "rounded" scales, a larger head with bulky jowls, and a larger gular fold that is extended during territorial and/or courtship displays. In April of 1995, on Plaza Sur, we found land iguanas of mixed sizes, but no juveniles. One young individual, perhaps 35 cm (14 inches) in length, was seen running from one bush to another in late afternoon. But nothing is more impressive than the sight of an adult male. With gular sac fully extended, the forward part of his body raised high off the ground, and a pair of powerful eyes reflecting the golden hue of a setting sun, he certainly exemplifies the definition of prehistoric origin.

Conolophus feed on a great variety of plant species, such as *Sesuvium, Portulaca, Scalesia,* plus the fruit, stem and spinose pads of *Opuntia* cactus—just to mention a few. Harris (1996) writes that caterpillars and grasshoppers are commonly eaten, and that young land iguanas will jump into the air to catch grasshoppers on the wing. Beebe (1924) made some noteworthy observations regarding the feeding habits of this species.

Large adult female *C. subcristatus* on Plaza Sur, resting in the shade of a tree-like *Opuntia* cactus. *Photograph: Karl H. Switak*

Galapagos land iguana, *C. subcristatus,* at the edge of a hundred foot cliff on Plaza Sur (South Plaza). *Photograph: Karl H. Switak*

Adult *Conolophus pallidus* from the island of Santa Fe (Barrington). This individual, an adult, was quite skittish. This island boasts some of the tallest *Opuntia* cactus in the world. Iguanas are found very near the water's edge and far inland. *Photograph: Karl H. Switak*

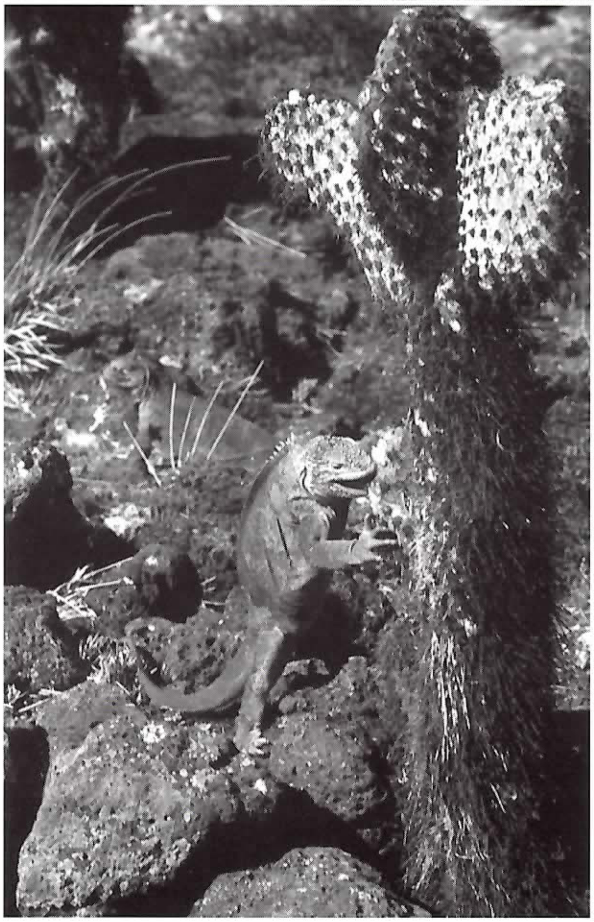
In the stomachs of two which I examined were enormous quantities of the leaves of several plants, especially *Cordia* and *Maytenus*, and many flowers of the former. One had swallowed whole five cactus fruits and another three. Twice I saw *Conolophus* getting the cactus fruit which they seemed to love. To my surprise it was a deliberate attempt—the nearest to an intelligent action which I have ever observed in any reptile. Two were close together at the base of an *Opuntia*, and one stretched up and struck the spiny base slowly, but repeatedly with one foot. Nothing happened at first, but finally two fruits fell at once. The second lizard rushed up and gulped down both, spines and all without a second's delay or mastication.

I saw circumstantial evidence of these lizards actually eating the pads of *Opuntia*, spines and all, but I could hardly believe this, until, in a number of cases, following the capture of those which I took on board the Noma, I found their droppings to be a mass of full-length spines. How it is possible for any creature to swallow such needle-length and steel-hard spines and not perish, I cannot conceive.

[Beebe (1924) goes on to write...] *Conolophus* is essentially herbivorous, but that it occasionally partakes of animal food I can attest to, from finding one and three grasshoppers respectively in the stomachs of two individuals. This is very unusual, and I question the accuracy of the statement made by the mate of a vessel, that they were seen drinking the blood of a slain goat.

Personally I have no problem whatsoever with the fact that *Conolophus* is not a strict herbivore, nor that it might lick up the blood from a slain goat. Rather, I believe these lizards to be opportunistic feeders, consuming mostly plant and occa-

"Active" burrow for *C. subcristatus* on Plaza Sur (South Plaza); plant is *Sesuvium*. *Photograph: Karl H. Switak*



When feeding on *Opuntia* cactus, Galapagos land iguanas also ingest the needle-sharp and steel-hard spines. However, given a choice, they prefer the softer fruit of this cactus species on the island of Plaza Sur (South Plaza). Note marine iguana in the background (out of focus). *Photograph: Karl H. Switak*

sional animal matter as dictated by providence. After all, hunger has forced both man and beast to prey upon that which isn't considered normal. In April of 1995 our group, consisting primarily of Chapman University students and their guru Dr. Fred Caporaso, was fortunate to observe the non-botanical feeding habits of a land iguana on the island of Plaza Sur.

...The time was 1430 when I spotted a land iguana leisurely walking over the smooth and rather flat rocks near the ocean's shore. The smoothness of said rocks was primarily sea lion activity, of which many abounded within close proximity. First the lizard investigated a number of brown spots (dried sea lion urine) and pieces of fecal matter. Each spot was carefully "tasted" with tongue and nostrils, two pieces of fecal matter were picked up, but neither ingested.

After some twenty feet of strolling and continuously tasting the ground, this iguana came upon a dead sea lion. From its appearance, partially mummified, I suspected this pinniped to have died at least two weeks prior. Not much flesh adhered to the already bleached out bones and the remaining skin could best be described as being the consistency of parched leather.

As soon as the iguana made contact with the dead sea lion, it started tearing away at those dried-out remains. Using its sharp and serrated teeth, plus a set of extremely powerful jaws, it bit off pieces of skin and tore away at the mammal's exposed rib cage. Even with all that adequate equipment, the lizard's job was an arduous task. But it prevailed. Sea lion was on the menu, and sea lion it would have!

This feeding spectacle consumed at least ten minutes, and none of our group's movements deterred the iguana from its primary objective. A short while later, after everyone except myself had wandered off to investigate other animal activities, I observed this same iguana feeding on the plant *Sesuvium* within the splash zone of the ocean. With no fresh water on this island, except for accumulations during excessive downpours, *Conolophus* obtains bodily moisture from the plants it consumes. I suppose that after several mouths full of that dried-up sea lion carcass, that juicy *Sesuvium* went down like proper dessert.

Present population densities of both *Conolophus pallidus* and *subcristatus* may be directly associated with favorable or adverse weather conditions of any given season. During drought years, such as witnessed in 1990–91, when plant species are at low productivity, the iguanas tend to diminish in numbers. While investigating the population status of *C. subcristatus* on the small island of Plaza Sur in January of 1991, we found the iguana colonies to be quite low in numbers and the vegetation of sparse distribution. An adult iguana was found mummified near the downward slope of the island. Others, few in number, were of meager appearance. Then, in April of 1995, the story had changed dramatically. Vegetation was plentiful and so were the lizards. During our walk across part of Plaza Sur we encountered no less than 50–60 iguanas, most of which were sub-adult or adult size, including several "brutes." The animals were in excellent condition and from all indications this promised to be a very good year for *Conolophus* on Plaza Sur. It has been estimated by some that during such an obliging year this island (a mere .13 square kilometers in size) may support as many as 300 land iguanas.

Whalers and buccaneers ceased using land iguanas for food long ago, and scientists no longer need to collect specimens to fill those infamous formaldehyde bottles. These, plus the control of feral animals (particularly rats, pigs and dogs), and the repatriation program by the Charles Darwin Research Station and Ecuador's National Park Service, all add up to a bright future for a truly magnificent beast. We must never stop our vigil to protect and nurture a heritage that can never be

Conolophus subcristatus feeding on the leathery remains of a dead sea lion on the island of Plaza Sur (South Plaza). The immediate presence of live sea lions didn't bother this lizard at all. *Photograph: Karl H. Switak*

This adult female *Conolophus subcristatus* was photographed on Plaza Sur (South Plaza) in 1986. *Photograph: Karl H. Switak*

replaced. Extinction is forever. The process cannot be reversed!

Conclusion

It goes without saying that visiting the Galapagos Islands is much like traveling to paradise. Although reptiles have always been the primary purpose for seeking out these enchanted isles, and I suppose always will be, I cannot help but wonder how so many animal species live in such harmony. And to this end I must once again quote from the works of the person who really sorted out the lot.

> ...WHEN WE REMEMBER THE WELL-BEATEN PATHS MADE BY THE MANY HUNDRED GREAT TORTOISES, THE WARRENS OF THE TERRESTRIAL *AMBLYRHYNCHUS* [=*CONOLOPHUS*], AND THE GROUPS OF THE AQUATIC SPECIES (REPTILES) BASKING ON THE COAST-ROCKS, WE MUST ADMIT THAT THERE IS NO OTHER QUARTER OF THE WORLD WHERE THIS ORDER REPLACES THE HERBIVOROUS MAMMALIA IN SUCH EXTRAORDINARY A MANNER.
>
> *Charles Darwin 1839*

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Editor's Note: The West Indies also had giant tortoises and a tremendous biological diversity, many species of which were extinct by Darwin's time.

RESEARCH ARTICLE

Morphologic Characters of Herbivorous Lizards

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Introduction

Many lizards are omnivorous (Sokol 1967), however, only iguanines, two species among the gerrhosaurids and cordylids, and relatively few agamids and scincids have significant morphological specializations for a true herbivorous diet (Pough 1973; Iverson 1982). These herbivorous groups comprise approximately 2% of all lizard species (Zimmerman and Tracy 1989), which inhabit three distinct regions: 1) the neotropics and subtropics into the Mohave Desert of the Southwest United States (all *Iguaninae* except two species), 2) the Near and Middle East from North Africa to Southwest Asia (*Uromastyx*), and 3) the Philippines and Indonesia (*Hydrosaurus*), and the Solomon Islands (*Corucia*). They are found on continents, but more abundantly on islands (Iverson 1982). While they are most commonly found in xeric conditions, they also inhabit mesic and hydric habitats.

Two factors make digestion of plant material more difficult than digestion of animal material: 1) digesting the fibrous portions of the plant material such as cellulose, lignin and pectins, and 2) the need to separate the non-fibrous material from the plant fiber, so digestive enzymes are more effective (Throckmorton 1973). These factors may explain why digestive efficiencies of carnivorous lizards are known to vary from 70–90%, while herbivorous lizards normally range from 30–70% (Table 1). Throckmorton (1973) and Hansen and Sylber (in Iverson, 1982) have reported higher efficiencies for the herbivorous lizards *Ctenosaura pectinata* and *Sauromalus varius*. However, in the studies, *Ctenosaura* were fed sweet potato tubers, while *Sauromalus* were fed dandelion flowers, shredded carrots and "chick starter." Iverson (1982) felt that these two species are not able to obtain such easily digestible foods in nature throughout most of the year. For example, during the non-fruit and flower portions of the year, the herbivorous iguanines *Dipsosaurus dorsalis* (Minnich 1970), *Cyclura carinata* (Iverson 1979), and *Iguana iguana* (Rand 1978) each primarily rely on leaves which are fibrous and difficult to digest. Whole ingested leaves have been observed to pass through the entire gastrointestinal tract of *C. carinata* (Iverson 1979), *C. cornuta stejnegeri* (Wiewandt 1977) and *C. cychlura figginsi* (Knapp, per. obs.). The energy derived from ingested food items is also lower for fibrous plant material. Fibrous plant material contains an energy content of 3,600–4,200 cal/g of dry weight. In contrast, vertebrate animal tissue contains 5,200 cal/g and insects 5,400 cal/g (Golley 1961).

In order to deal with the difficulties of a plant material diet, herbivorous lizards share multiple, analogous characters. The majority of species possess a large body size, modified dentition, nasal glands, and a large population of colic nematodes. Each of these character complexes is considered adaptive in permitting the increased use of plant material for food by lizards. However, all true herbivorous lizards, regardless of family, share one significant morphological adaptation not found in other extant lizards; they all have a distinctly enlarged, partitioned colon (Iverson 1980). Although numerous ecological adaptations, such as search patterns and repetitive browsing, are also associated with lizard herbivory (Auffenberg 1982), this paper will explore the morphological characters that allow these lizards to exploit an abundant, yet difficult to utilize resource.

Table 1. Apparent Digestibility Coefficients (ADC) of lizards, where ADC = (calories consumed – calories of fecal waste) x (100) / calories consumed.

Species	ADC *(in %)*	Food	Source
Anolis carolinensis	54.4 88.9 69.5	*Tenebrio* adults *Tenebrio* larvae crickets	Licht & Jones 1967
Dipsosaurus dorsalis	3070*	natural diets	Minnich 1970 Porter *et al.* 1973
Sceloporus grasiosus and *S. occidentalis*	83	*Tenebrio* larvae	Mueller 1970
Ctenosaura pectinata	86.3 (77.894.0)	Sweet potato tubers (*Ipomea*)	Throckmorton 1971, 1973
Lacerta vivipara	89 (8491)	*Tenebrio* larvae	Avery 1971
Anolis carolinensis	*69.972.2*	*Tenebrio* larvae	Kitchell & Windell 1972
Crotaphytus wislizeni *Cnemidophorus tigris* *Uta stansburiana*	77.878 79.8 83.585.8	natural diets	Essghaier & Johnson 1975
Dipsosaurus dorsalis	57	natural vegetation (flowers)	Nagy and Shoemaker 1975
Sauromalus obesus	56	natural vegetation	Nagy and Shoemaker 1975
Sceloporus olivaceus	83.5	crickets	Dutton *et al.* 1975
Dipsosaurus dorsalis	54.3 @ 33'C 62.8 @ 37'C 69.5 @ 41'C	commercial rabbit food	Harlow *et al.* 1976

*Method of calculation of digestive efficiency was not indicated. (Source: Iverson 1979)

Body Size

Of approximately 3,000 extant lizard species, no more than 60 attain an adult body size exceeding one kilogram (Alberts 1994). With the exception of the specialized varanid carnivores, the majority of these large lizards are herbivorous. Several hypotheses have been offered to explain the adaptive significance of this correlation between large body size and herbivory.

One adaptive advantage of a large body size is the increased mechanical strength for reducing vegetation for consumption (Iverson 1982). Also, because mass specific energy requirements decrease with increasing body mass, larger body size may be an adaptation to a diet that is typically energy deficient. For example, the metabolic rate per gram of a 100 gram lizard is 1/6 that of a 1 gram lizard while a lizard weighing 1 kilogram would have an estimated weight-specific metabolic rate about 1/2 that of a 100 gram lizard (Pough 1973). Similarly, large body size may serve as an energy buffer against a seasonal and fluctuating food supply. Therefore, the mass-specific rate of energy reserve depletion would be lower for larger than for smaller animals (Case 1982).

Larger body size in herbivorous lizards may also be a thermoregulatory adaptation to aid in digestion. Body size of ectotherms influences the rate at which heat is exchanged with the environment. Thus, larger ectotherms are temporally less responsive to their thermal environment than smaller ectotherms. This causes them to heat and cool more slowly in relation to a fluctuating thermal environment. The high thermal and stable environment in the gut presumably allows gut symbionts to ferment the cell walls of plants more efficiently (Zimmerman and Tracy 1989). For example, greater digestive efficiency at elevated, opposed to reduced, body temperatures have been demonstrated in *I. iguana* (Troyer 1987) and *Sauromalus obesus* (Zimmerman and Tracy 1989). Furthermore, in the lizard *D. dorsalis,* Harlow *et al.* (1976) demonstrated a significant correlation between body temperatures and the proportion of ingested food utilized. At temperatures of 33, 37 and 41°C, apparent digestibility coefficients were 54.3%, 62.8% and 69.5% respectively. Even though *D. dorsalis* is smaller (25-75g) than most herbivorous lizards, it is the most thermophilic of all North American reptiles. Its tolerance of body temperatures exceeds 40°C (Norris 1953). Pough (1973) postulates that few insects are active at these extreme temperatures; therefore, the unique ecological specialization of *D. dorsalis* has forced it into a herbivorous diet, despite its small body size.

Greater digestion efficiencies at elevated temperatures are not, however, restricted to herbivorous lizards. With increasing temperature, Hardwood (1979) reported the increased digestive coefficient in three carnivorous species, and Waldschmidt *et al.* (1986) in one species. Although greater digestive efficiencies at elevated temperatures may not be a unique characteristic among herbivorous lizards, increased body size provides the advantage of greater thermal inertia. This allows the maintenance of elevated body temperatures and facilitates the consistent assimilation of fibrous vegetative material despite fluctuating temperatures. Therefore, excluding the unique ecological situation associated with *D. dorsalis,* large body size may, in part, be a thermoregulatory adaptation co-evolved with an herbivorous feeding strategy (Zimmerman and Tracy 1989).

Szarski (1962) suggested that poor assimilation of plant material reduced the energy herbivorous lizards had available for reproduction, leading to reproductive rates lower than those of carnivorous lizards. Therefore, in order to exploit an herbivorous niche successfully, he hypothesized that lizards require some mechanism, such as a large body size, to reduce predation. He also noted that members of the genus *Uromastix* have spiny tails for defense while members of the genus *Enyaliosaurus* posses a similar tail used for blocking holes in trees used for refuge. The iguana, *I. iguana,* has a powerful tail for defense and also swims to escape predators. Due to the high temperature niche of *D. dorsalis,* it avoids many predators and competing lizard species, while insular species, such as *Amblyrhynchus cristatus* and *Conolophus subcristatus,* lack natural predators all together as adults.

Lastly, Iverson (1982) hypothesized that the most important determinants for herbivorous capabilities, as well as for body size, are the anatomical, physiological, and ecological characteristics of the gastrointestinal tract. This is due to the positive relationship of colic complexity (i.e. number of valves or folds) to body size observed in herbivorous lizards. Increased colon complexity is thought to allow for increased body size due to the ability to support an increased population of microbes. Refer to Partitioned Colon and Associated Symbionts section for further discussion of this relationship.

Dentition

Ostrom (1963) felt that the loss of the lower temporal arch in modern lizards and the resulting mobility of the quadrate bone prevented the evolution of an efficient plant-grinding mechanism. In the absence of a grinding mechanism, modification of the feeding apparatus of herbivorous lizards is related to the necessity to crop plant material (Throckmorton 1976). In conjunction with large body size for mechanical strength, the most distinctive modification to facilitate this task is the morphology of the marginal dentition.

Hotton (1955) showed that tooth morphology was related to diet in iguanid lizards. Herbivorous iguanines are characterized by an elevated degree of lateral compression and a blade-like multicuspid crown. Species that tend to be more obligatory plant feeders have cuspate teeth originating more anteriorly in the tooth row (Hotton 1955). Montanucci (1968) worked with the four iguanid genera and showed that dentition becomes highly modified as the amount of plant material in the diet increases. The iguana, *I. iguana,* the most herbivorous in the group, had all of its teeth cuspate and possessed the highest degree of lateral compression.

Throckmorton (1976) demonstrated that different dentitional modifications exist among herbivorous genera, but that the overall apparatus is modified to crop plant material. Herbivorous lizards have a shearing edge of the tooth expanded in the anterior and posterior directions, so that the space between adjacent teeth is reduced. This creates a nearly continuous cutting edge, not found in carnivorous lizards. Carnivorous lizards can only puncture their food. Because of the slanting orientation of the shearing crests relative to the long axis of the jaw, the anterior end of the perforation made by one tooth lies medial to the posterior end of the tooth preceding it. With a thin food item, the upper and lower dentitions will overlap, shearing the material in a scissors-like fashion. If the food item is thick, the perforations allow the food item to be torn with a quick movement of the head.

The applied upper and lower dentitions also produce an anterior force that tends to push the food out of the mouth. To cope with this, all herbivorous lizards possess some type of large, fleshy tongue to aid in food manipulation and stabilization. Additionally, Throckmorton (1976) has demonstrated that different restraining mechanisms are used in the genera *Iguana* and *Uromastix*. In *Iguana*, serrated and pterygoid teeth help stabilize the food, while in *Uromastix*, the retraction of the lower jaw acts to hold the food in position as the teeth shear through it.

Nasal Salt Glands

Several researchers have studied the nasal salt glands of several iguanine species (Schmidt-Nielsen *et al.* 1963; Norris and Dawson 1964; Templeton 1967). Schmidt-Nielson *et al.* (1963) postulated that the salt glands are a water conserving mechanism. Norris and Dawson (1964) reached similar conclusions while investigating the insular *Sauromalus hispidus*. Both studies reported the presence of potassium in the nasal secretions. Since *S. hispidus* is a desert island inhabitant that eats halophytes, Norris and Dawson believed that this was related to the excess of potassium in the diet. Additionally, nasal secretions of *I. iguana* were apparent so long as the animals received a primarily vegetable diet, even with free access to water (Schmidt-Nielson 1963). Consequently, Sokol (1967) suggested that a major function of these glands in the iguanines is to regulate the balance between sodium and potassium.

The evolution of extrarenal nasal salt glands in herbivorous lizards would presumably reduce osmotic problems and simultaneously allow the lizards to utilize potassium rich plant parts without being susceptible to ionic problems (Iverson 1982). Templeton (1967) demonstrated that *Ctenosaura pectinata* have the ability to fluctuate the potassium/sodium ratio in the nasal fluid. The capacity of the nasal gland to alter this ratio through its secretion would be valuable in countering the dietary seasonal fluctuations in xeric environments. These factors suggest that the nasal glands may be regarded as an adaptation to herbivory (Sokol 1967).

Partitioned Colon and Associated Symbionts

While general external topography of the gastrointestinal tract of herbivorous iguanids is similar to most carnivorous lizards (Henke in Iverson, 1980), the large intestine is more extensive in herbivorous iguanids than in carnivorous iguanids and agamids (Iverson 1980). Different modifications of a specialized colon have been found in all herbivorous reptiles and are completely lacking in all carnivorous reptiles (Guard 1980). Specifically, all herbivorous lizards in the families *Agamidae*, *Iguanidae* and *Scincidae* possess an enlarged, specialized colon (Iverson 1982).

The marine iguana, *Amblyrhynchus cristatus*, possesses colic folds, the remaining iguanine lizards have from one (*D. dorsalis*) to eleven (*C. cornuta*) transverse valves in the proximal colon. Valves are either circular or semilunar and exhibit little intraspecific variation in the number and types of valves (Iverson 1980). Moreover, in the species that Iverson (1980) examined, he found colic valves to be present at hatching and showed no significant ontogenetic change in the number of valves. He felt that the number, type, and size of valves are so consistent within a given iguanine species, that it is an important taxonomic indicator. Colons of unknown origin can almost always be identified, at least to genus, based purely on morphological features of the organ (Iverson 1980).

Although not completely modified, Iverson (1982) discovered that the colon of *Uromastyx*, *Hydrosaurus* and *Corucia* are also partitioned. The partitions are less developed and consist of folds rather than valves. Nevertheless, this indicates that a partitioned colon has evolved independently at least three times (*Agamidae, Iguanidae, Scincidae*) in the Lacertilia (Iverson 1982).

The functional significance of a partitioned colon is still not clearly known. The partitioned colon most likely slows down the passage of plant material through the gut, thereby increasing time for digestion and absorption of nutrients to occur (Iverson 1980). The absorptive surface area for water and nutrients is also increased (Zimmerman and Tracy 1989). The most significant advantage that the partitions provide is that they offer important microhabitats for colic symbionts. Populations of worms are typical in herbivorous lizards, but are not found in omnivorous or carnivorous lizards (Bowie 1974). Large quantities of colic nematodes, from the families *Atractidae* and *Oxyuridae*, have been found in *C. carinata* (Iverson 1979), *C. nubila caymanensis* (Knapp, pers. obs.), and other iguanines (Iverson 1980). Nematodes have also been found in the large intestine and partitioned colon of *S. obesus* (Nagy 1977). Bacteria belonging to the genera *Clostridium* and *Leuconostoc*, exceeding 10^{10} bacterial clumps per gram of colic material, have been isolated from the hindgut in *I. iguana* (Troyer 1982). These cellulolytic bacteria are found in the hindguts of a variety of herbivorous reptiles, as well as in the rumen of cattle and sheep (Zimmerman and Tracy 1989).

Herbivorous mammals and reptiles typically obtain part of their energy from the fermentation of plant cell walls, or fibers, by symbiotic populations of microbes (McBee and McBee 1982). During hindgut fermentation in *Iguana*, protein and other digestible nutrients from plant cell contents are broken down and assimilated in the stomach and small intestine. Fiber components are then broken down and the products absorbed in the fermentative portions of the digestive tract (Troyer 1984).

Volatile fatty acids, the end products of anaerobic digestion of carbohydrates, have been demonstrated to appear in the hindgut of *Chelonia mydas* (Bjorndal 1979) and *I. iguana* (Troyer 1984) in quantities comparable to the rumens of mammals. The highest concentrations of the volatile fatty acids in the GI tract of *I. iguana* occur in the partitioned colon (Troyer 1984). Other studies conducted on *I. iguana* revealed that the animal receives energy, in the form of volatile fatty acids, from the hindgut at the rate of 30–40% of their requirements. These percentages are higher than any obtained from hindgut fermentation in birds or rodents (McBee and McBee 1982). Troyer (1984) states that the structure and function of the digestive organs of iguanas, and probably other reptilian herbivores, are similar to those of mammals. This suggests a certain amount of convergence in the possible adaptations for herbivory in vertebrate tetrapods.

Hypothesizing that colic compartmentalization permits the proliferation of nematodes and bacteria, Iverson (1982) compared the number of colic nematode species described from each lizard species (tabulated in Iverson, 1979) with the number of colic valves for the eleven best studied iguanine lizard species. He found a significant linear relationship between the two variables, indicating that increased colic partitioning permits and increases diversity of nematodes (Fig. 1).

Of the colic variations possessed by iguanids, there is a significant linear relationship between number of valves and mean body size for interspecific comparisons (Fig. 2). The larger the species, the more colic compartments are present (Iverson

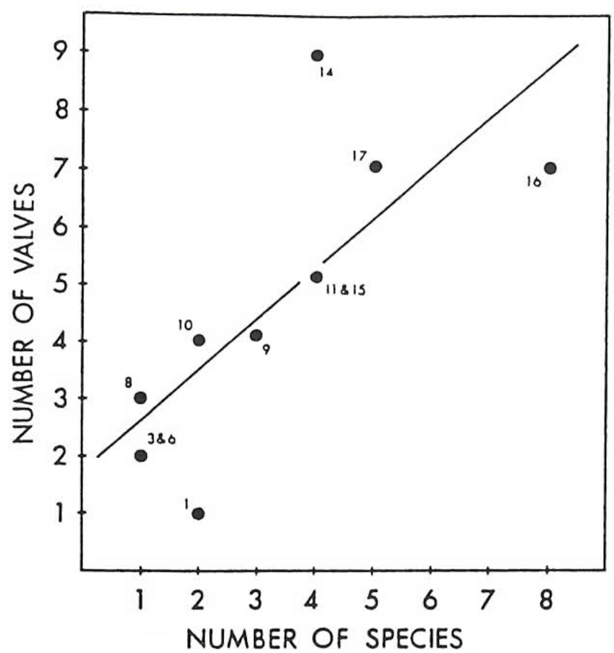

Figure 1. Intestinal nematode species richness versus colic modification for the 11 best-studied iguanine species. Species codes: *Dipsosaurus dorsalis* (1), *Ctenosaura defensor* (3), *Sauromalus obesus* (6), *Ctenosaura hemilopha* (8), *C. similis* (9), *C. pectinata* (10), *Cyclura carinata* (11), *C. cornuta* (14), *Conolophus subcristatus* (15), *Iguana iguana* (16) and *Cyclura nubila* (17). Least square regression is: y = 0.01895X – 0.6196; r = 0.908; p <<0.01. (Source: modified from Iverson 1982)

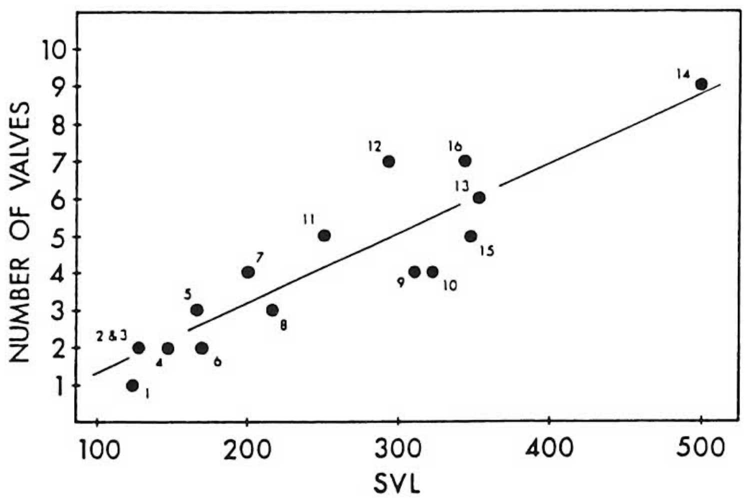

Figure 2. Relationship between modal number of colic valves and body size (mm snout-vent length) for the following iguanine species. Species codes: *Dipsosaurus dorsalis* (1), *Ctenosaura defensor* (2), *C. quinquecarinatus* (3), *C. clarki* (4), *C. palearis* (5), *Sauromalus obesus* (6), *Brachylophus fasciatus* (7), *Ctenosaura hemilopha* (8), *C. similis* (9), *C. pectinata* (10), *Cyclura carinata* (11), *C. cychlura* (12), *C. ricordi* (13), *C. cornuta* (14), *Conolophus subcristatus* (15), *Iguana iguana* (16). Least square regression is: $y = 0.01895X - 0.6196$; $r = 0.908$; $p << 0.01$. (Source: modified from Iverson 1982)

1982). This relationship may have allowed larger body sizes in herbivorous lizards. Previous studies on both lizards (Case 1976) and turtles (Parmenter 1978) have shown that body size may be significantly related to resource availability. Analogously, Iverson (1982) felt that the evolutionary advancement in colon complexity increased resource utilization, not necessarily availability, and thereby energetically permitted increased body size. By modifying their colons, and thus diversifying and augmenting intestinal symbionts, he hypothesized that these herbivores were able to grow to larger sizes, and therefore more fully gain other selected advantages, such as reduced predation, as well as metabolic (Pough 1973), and thermoregulatory (Ellis and Ross 1978) benefits.

Summary and Conclusions

Relatively few lizard species have been able to efficiently exploit a vegetative food source. This is most likely due to the difficulty of digesting plant material and its lower energy derivatives compared to animal tissue. Lizards utilizing plant material share multiple characters such as large body size, modified dentition, nasal glands and a partitioned colon with associated symbionts.

Advantages for a large body include protection from predators and increased mechanical strength for reducing vegetation. A large body size provides a stable internal thermal environment, thereby increasing digestion efficiency. Also, colic complexity and number of gut symbionts increases with larger size. A modified scissors-like dentition allows cropping of vegetation. Nasal salt glands help alleviate an increased potassium load. A partitioned colon slows movement of digesta, allowing more time for digestion or absorption. Colon valves also provide microhabitats for gut symbionts, which assist in food assimilation.

With exception of Iverson's (1980) colon comparison study (51 species, 7 families) and Montanucci's (1968) dentition comparison (4 species, 1 family), the remaining herbivorous lizard studies that I could identify concentrated on one or two species encompassing no more than two families. Detailed comparative studies similar to Iverson (1980), encompassing multiple genera and species, would be useful in discovering exceptions to the general herbivore characteristics. Comparing diets to number of colic valves and species of symbionts would be of interest in order to determine if a correlation exists between specific diet, valve type and number and diversity of microbes. For example, why does *A. cristatus* possess only colic folds, while its closest relative, *C. subcristatus* possesses valves? Are marine algae easier to assimilate, thereby negating the need for colic valves? Additionally, due to its marine existence and algae diet, does *A. cristatus* posses gut symbiont species that differ from those in terrestrial iguanas?

An interesting theory is the speculation (Iverson 1982) that the causal evolutionary factor for large size is the correlation between increased body size and number of colic valves. This leads to the question, what came first, large body size or a partitioned colon? Perhaps the question could be answered by modifying the dentition of a herbivorous lizard. Would it be able to crop vegetation as efficiently? If the lizards failed to effectively feed, thereby decreasing energy input, perhaps a modified dentition is an evolutionary response for increased body size.

Nevertheless, adaptation to herbivory is an interesting and complex subject, which was overlooked until the late 1970's. In the 1960's, reptilian herbivores were considered primitive. However, recent insights have demonstrated that this is not the case. Hopefully, future investigations will answer additional questions concerning herbivory in lizards.

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Feeding Behavior of a Free-Ranging *Iguana iguana* in the Lower Florida Keys

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Finca Cyclura Reserve, Big Pine Key, Florida

In January 1993, a friend working at the Dreher Park Zoo in Palm Beach, Florida brought us an unsolicited young female green iguana. She had been quarantined at the zoo for three months and appeared to be about six months old. Here at Finca Cyclura, she was housed on a 16 x 3.3 ft. screened balcony (328 sq. ft.). She fed voraciously and grew rapidly, sunning herself in the shifting patches of sunlight and thermoregulated by reclining on a 60 watt incandescent light fixture on a 40 gallon aquarium which housed two hatchling *Cyclura cornuta*. By early summer, I was anxious to find alternate housing for her, as she had grown substantially and was becoming more difficult to clean up after. She had also started exploring the house and causing minor problems before returning to her porch territory. On 22 June, 1993 during one of her explorations she exited the building by way of an open sliding glass door. She was recovered the following day from vegetation next to the house and returned to the balcony.

Mikey, as this iguana was called, was not a pet. She did not tolerate being touched or approached, and would whip her tail at the offender at the slightest provocation. She exhibited no fear of humans, but clearly associated them with food. If someone showed too much interest toward her, she simply moved away.

On 3 July the iguana left the building on her third adventure, while I was out feeding other iguanas. When I noticed she was missing I made no attempt to locate her, as I felt strongly that she would remain in the vicinity. She was easily located the following day, but not approached. She was sighted four of the next five days in the vegetation surrounding the house. On 10 July a paper plate of food was left on the center deck of the house adjacent to the door she had exited. The procedure was repeated the next day and within two

Free-ranging *Iguana iguana* eats food from a paper plate. 1994 (left). 1996 (above). This iguana consistently fed 30% of the days per year for a 4½ year period. *Photograph: R.W. Ehrig*

Iguana iguana leaves feeding station by way of stairs.
Photograph: R.W. Ehrig

hours the iguana walked up the stairs, consumed the food in less than ten minutes, then departed.

During the next four and a half years the iguana would feed between 103 and 112 days per year. Over 90% of the time she would feed between 0900 and 1400 hrs. On the days when she would arrive before her plate of food was prepared, she would wait at the spot where her food was normally left. She entered mostly from above, climbing down a blackbead tree from the steel roof or from a large mahogany on the north side of the building. Often she would eat most of her meal, climb down the stairs to defecate in the understory vegetation at the base of the stairway, then return to finish her meal, climb the railing, and exit through the trees. Guests were most amazed at this routine.

The iguana would sometimes enter the house, walk around for ten minutes and leave. She returned to her balcony on at least seven occasions. If food preparation was slow she sometimes would enter the house and wait in the kitchen.

The food offered consisted primarily of collards, mustards, spinach, mixed vegetables, squash, broccoli, bananas, grapes, and other greens and vegetables. She was observed eating *Ipomea*, *Tabebuia*, *Lysiloma*, and *Ficus* in the area around the house. The diet items we provided made up the majority of her caloric consumption. Her feeding was much reduced in late December, January, and February. These are the coldest months of the year in the Lower Florida Keys with night time temperatures often reaching the low and mid 60's.

Mikey occasionally encountered feral green iguanas, which have become increasingly common in the Florida Keys in the last decade. She seemed to avoid her own species, and on two occasions we watched male iguanas pursue her through the tree canopy. She preferred a solitary existence.

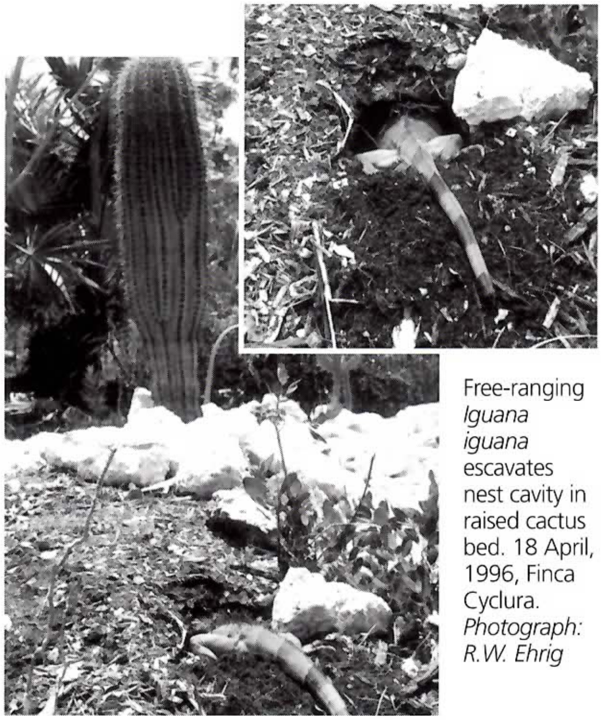
1993	JUL	AUG	SEP	OCT	NOV	DEC
01		■	■			
02		■				■
03			■			
04		■	■			
05			■			
06		■	■			
07		■	■			
08		■	■			■
09			■			■
10			■			■
11	■		■			■
12			■			
13			■		■	
14			■	■	■	
15	■			■	■	
16	■				■	
17			■		■	
18					■	
19	■				■	
20			■		■	
21					■	
22	■		■		■	
23	■		■		■	
24	■	■	■		■	
25					■	
26	■	■			■	
27	■	■			■	
28	■				■	
29						
30	■					
31						
TOTAL DAYS	**11 DAYS**	**9 DAYS**	**18 DAYS**	**2 DAYS**	**16 DAYS**	**5 DAYS**

Total days fed in 6 months: 61

In early April, 1996 Mikey fell 25 feet out of a tree and lost one third of her tail. During this same period she was gravid and her condition probably made climbing more awkward. On 16 April, 1996 she entered the house and spent two hours searching around and under furniture in the living room, kitchen, and office before leaving. On 18 April, 1996 she laid a large clutch of infertile eggs in a raised planting bed for cacti about 300 feet from the house (see photos). She had found the most suitable nesting area on her own.

My experience with this iguana over the last half decade has convinced me of the potential of iguanas as free-ranging livestock. The iguana is still not fully understood or appreciated and is certainly much more efficient than most of the other species that humans have chosen to domesticate.

A special thank you to John Bendon for collating the data from field notes.



Free-ranging *Iguana iguana* escavates nest cavity in raised cactus bed. 18 April, 1996, Finca Cyclura. *Photograph: R.W. Ehrig*

1994	**JAN**	**FEB**	**MAR**	**APR**	**MAY**	**JUN**	**JUL**	**AUG**	**SEP**	**OCT**	**NOV**	**DEC**
01					■	■		■			■	
02					■	■		■		■		
03					■			■		■	■	■
04					■	■		■		■	■	
05					■	■		■	■			■
06						■			■			
07					■	■			■		■	■
08						■					■	
09					■	■			■		■	■
10					■	■		■				
11				■	■							■
12				■					■		■	
13				■		■						■
14				■	■	■		■				
15					■			■	■		■	
16					■	■		■	■			
17					■	■			■		■	
18				■		■		■	■			
19				■	■	■		■	■			
20				■		■		■				
21				■	■	■		■			■	
22				■		■					■	
23					■	■		■				
24					■	■						
25				■		■						
26						■						
27			■	■	■	■					■	
28			■		■							
29			■	■	■	■						
30				■	■	■		■		■		■
31			■		■							■
TOTAL DAYS	**0 DAYS**	**0 DAYS**	**4 DAYS**	**13 DAYS**	**22 DAYS**	**24 DAYS**	**0 DAYS**	**15 DAYS**	**10 DAYS**	**4 DAYS**	**12 DAYS**	**8 DAYS**

Total days fed in 12 months: 112

1995 **(Data unavailable)**

Total days fed in 12 months: 112

1996	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
01			■	■		■	■		■			
02					■			■				
03							■					
04							■	■			■	
05					■	■	■	■			■	■
06			■		■	■			■			
07						■	■	■	■		■	■
08						■	■					
09					■	■	■	■			■	
10				■	■		■					
11						■	■	■				■
12						■			■			■
13				■		■						■
14					■	■	■	■	■			
15			■		■	■	■	■				
16					■	■			■			
17			■			■	■		■		■	
18								■	■			
19				■	■		■	■	■			
20			■				■		■			
21				■								
22												
23								■				
24			■		■				■		■	
25			■		■		■			■		
26		■		■	■		■			■		
27					■		■	■	■			
28		■		■	■						■	
29			■					■	■			■
30			■	■	■			■			■	
31								■		■		
TOTAL DAYS	**0 DAYS**	**2 DAYS**	**9 DAYS**	**9 DAYS**	**15 DAYS**	**13 DAYS**	**17 DAYS**	**14 DAYS**	**14 DAYS**	**3 DAYS**	**9 DAYS**	**6 DAYS**

Total days fed in 12 months: 111

1997	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
01					■	■		■				■
02							■	■	■			
03							■	■				
04							■	■		■		
05	■			■		■		■				
06							■	■				■
07						■	■	■				
08						■	■					
09	■		■				■	■		■		■
10					■			■				■
11			■			■	■	■				
12				■	■		■	■	■		■	■
13		■		■		■		■				
14					■	■	■	■	■		■	
15	■				■	■						
16						■		■				
17						■	■					
18	■					■		■				
19						■	■	■				
20					■	■	■				■	
21						■						
22			■		■	■	■	■	■			
23						■						
24			■				■	■				
25							■	■			■	
26			■				■					
27				■	■		■	■	■		■	
28			■				■					
29					■			■			■	
30							■	■				
31					■							
TOTAL DAYS	**2 DAYS**	**3 DAYS**	**6 DAYS**	**4 DAYS**	**10 DAYS**	**18 DAYS**	**20 DAYS**	**21 DAYS**	**6 DAYS**	**2 DAYS**	**6 DAYS**	**5 DAYS**

Total days fed in 12 months: 103

I.I.S. Bookstore

Photograph courtesy of Jayme Gordon

As a service to our members, a limited number of publications will be distributed through the I.I.S. Bookstore. The following publications are now available:

Green Iguana, The Ultimate Owner's Manual, *by James W. Hatfield.* 1996. **$28.00** (including postage); **$35.00** (nonmembers). Covers just about everything from birth to death of an iguana. 600+ pp. Limitied quantities.

The Green Iguana Manual, *by Philippe de Vosjoli.* 1992. **$7.00** (including postage); **$8.75** (nonmembers).

Guide to the Identification of the Amphibians and Reptiles of the West Indies (Exclusive of Hispaniola), *by Albert Schwartz and Robert Henderson.* 1985. **$19.00** (including postage); **$27.00** (nonmembers).

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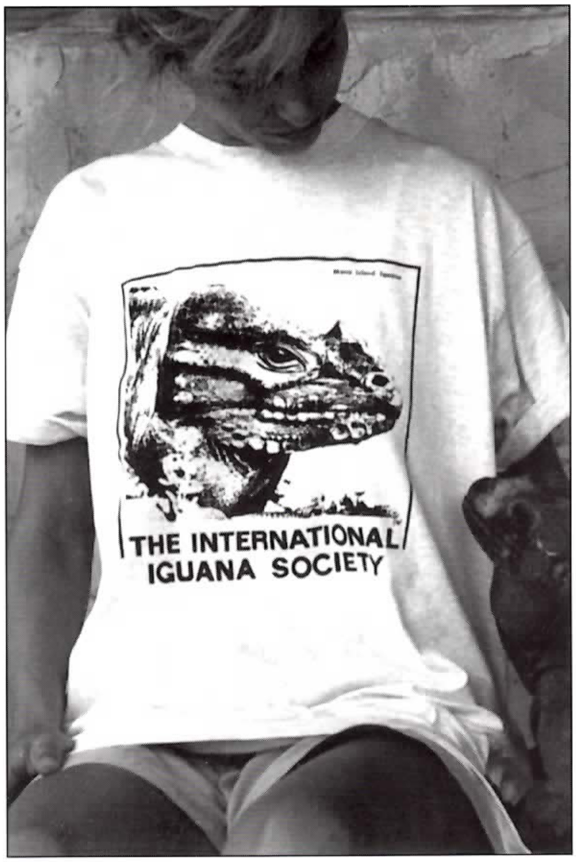

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Free-ranging green iguana, *Iguana iguana*, finishing food from a paper plate.
Photograph: R.W. Ehrig