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An Isotopic Study of Diet and Muscles of the Green Iguana (*Iguana iguana*) in Puerto Rico

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ABSTRACT.—In Puerto Rico, the number of nonnative Green Iguana, *Iguana iguana*, has increased and the species has proliferated throughout the island. Reports on diet in the iguana's native range indicate exclusive herbivory, but observations in their nonnative range occasionally include animal materials. The aim of our study was to determine the diet and trophic level of *I. iguana* in Puerto Rico using gut content and stable isotopic analysis of muscle tissue (tongue and leg). We found significant differences in the isotopic signature between leg and tongue tissue, which may be related to differing strategies for allocating nutrients during muscle formation. The isotopic analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ showed little enrichment of both muscle tissues from that of their diet, demonstrating that *I. iguana* is primarily an herbivore. However, gut contents provided evidence for a first report of *I. iguana* eating crabs (*Uca* spp.). The gut contents consisted primarily of black mangrove leaves (*Avicennia germinans*), suggesting a higher impact of herbivory on this species of mangrove. Another plant species of interest found in the gut was Brazilian pepper, *Schinus terebinthifolius*. We suspect that *I. iguana* may be a disperser of this aggressive invasive plant in Puerto Rico. Our study indicates that *I. iguana* impacts the native flora and fauna in Puerto Rico, and that the ecological role of this species in introduced ranges warrants further investigation.

Over the past 15 yr, animal ecologists have increasingly applied stable isotope analysis to study diet and trophic level (Biasatti, 2004; Dalerum and Angerbjörn, 2005; Serrano et al., 2007). Diet can be assessed by the identification of fecal contents or stomach contents or by direct observations of feeding habits (Meckstroth et al., 2007); however, these techniques can underestimate the consumption of highly digestible materials (Stapp, 2002). Stable isotope techniques eliminate the bias associated with differential digestibility in traditional dietary studies (DeNiro and Epstein, 1978, 1981) and thereby provide a more accurate assessment of diet and trophic level (Eggers and Jones, 2000). The isotopic signatures of tissues generally reflect the diet over the period during which the tissue was synthesized (Hobson and Clark, 1992; Bearhop et al., 2002; Hatch, 2005). For example, liver and plasma will have high turnover rates that reflect recent diet, whereas tissues with slower turnover rates, such as blood cells and muscle, reflect diet over longer periods of time (Hobson and Clark, 1992).

The isotopic ratios of carbon ($^{12}\text{C}/^{13}\text{C}$) and nitrogen ($^{14}\text{N}/^{15}\text{N}$) of consumer and prey tissues are not identical due to selectivity for lighter isotopes during a consumer's metabolic processes (DeNiro and Epstein, 1978, 1981). The enrichment of lighter isotopes causes variation in isotopic signature among tissues and is very often between 0 to +1‰ for $\delta^{13}\text{C}$, and +3‰ to +5‰ for $\delta^{15}\text{N}$ per trophic level for soft tissues (DeNiro and Epstein, 1978, 1981). The relative abundance of carbon ($^{12}\text{C}/^{13}\text{C}$) more effectively describes different carbon sources (e.g., C_3 vs. C_4 plants), whereas the relative abundance of nitrogen ($^{14}\text{N}/^{15}\text{N}$) is especially useful for assessing trophic level (DeNiro and Epstein, 1978; Hobson and Clark, 1992; Kelly, 2000). The isotopic signature of muscles for animals higher in the food chain tend to be heavier (i.e., to have more positive $\delta^{15}\text{N}$ values) than that of animals lower in the food chain (Minagawa and Wada, 1984). The enrichment of $\delta^{15}\text{N}$ by 3‰ to 5‰ along each step in the food chain results in carnivores having higher $\delta^{15}\text{N}$ values than herbivores, which in turn have higher $\delta^{15}\text{N}$ values than plants. In reptiles, stable isotope analysis has been used primarily to determine trophic level in sea turtles (Godley et al., 1998; Hatase et al., 2002; Wallace et al., 2006; Seminoff et al.,

2007), and in lizards to a lesser extent (Magnusson et al., 2001; Struck et al., 2002).

The diet and trophic level of the Green Iguana (*Iguana iguana*) is of special conservation interest. Green Iguana can be found from Mexico to northern Argentina and in some South American coastal islands (Etheridge, 1982; Schwartz and Henderson, 1991), where native populations may be endangered. However, in the United States and Europe it is known primarily as a popular reptile pet (Meshaka et al., 2007). Since their introduction around the world as pets, some iguanas have escaped or been released, and new populations have become established in areas such as Florida, Hawaii, Puerto Rico, and other Caribbean islands (Rivero, 1998). The Global Invasive Species Specialist Group (2005) of the International Union for Conservation of Nature considers the Green Iguana an invasive species. Some of the reported impacts of this invasive species are the increase in delays for airport operations at the Luis Muñoz Marín International Airport in Puerto Rico (Engeman et al., 2005), the defoliation of mangroves (Carlo-Joglar and García-Quijano, 2008), and the consumption of bird eggs (Henderson and Powell, 2009).

The increasing numbers and population expansion of *I. iguana* farther inland in Puerto Rico raises conservation concern regarding the impact of this species on the native fauna and flora. Thus far, studies on gut contents in Puerto Rico show that *I. iguana* eats only plant matter (Guzmán-Ramírez, 2007; Carlo-Joglar and García-Quijano, 2008). Guzmán-Ramírez (2007) examined 52 stomachs from iguanas and found 19 identifiable plant species and Carlo-Joglar and García-Quijano (2008) found that *I. iguana* did not eat bird eggs in an experimental study. Even though no animal material has been reported in the gut contents of iguanas from Puerto Rico, there are frequent anecdotal sightings of iguanas feeding on wildlife such as bird eggs, lizards, small crabs, and carrion (community members around Pinoñes Forest, Department of Natural and Environmental Resources, pers. comm.).

The aim of this study was to determine the diet and trophic level of introduced *I. iguana* in Puerto Rico. We used stable isotope discrimination in muscle tissue (leg and tongue) to provide information on assimilated foods. We used muscles because they do not reflect changes in diet instantaneously but gradually incorporate nutrients from the animal's diet; thus

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reflecting a span of dietary history (DeNiro and Epstein, 1978; Hobson and Clark, 1992; Kelly, 2000).

MATERIALS AND METHODS

Study Sites.—We sampled two sites, a natural and a managed forest, along the northeast coast of Puerto Rico (Fig. 1). The Pinoñes Forest was a natural site consisting of the largest remaining stands of mangrove forest in Puerto Rico with at least 46 species of birds, some of which are rare and endangered (Pinoñes Forest Manager, Department of Natural and Environmental Resources, pers. comm.). In contrast, the Villa Bahia Golf Course was an intensively managed site composed of a mosaic of habitats including open areas, bare ground, ponds, streams, and mangrove forest.

Sampling.—Forty-two iguanas (16 females, 25 males) were captured by hand or using a 0.22 caliber rifle during daylight hours in two sampling periods, April–November 2008 and April–June 2010, in the Pinoñes State Forest ($n = 36$) and Vista Bahia Golf Course ($n = 6$), Rio Grande. For each iguana, we collected data on mass, snout–vent length (SVL), tail length, and sex. During our first sampling period we collected 19 tongue (without stripping outer layer) tissue samples and in our second sampling, we collected both tongue and muscle tissue from 22 individuals, and from one individual we collected only tongue tissue. The entire digestive system was collected from all iguanas and inspected microscopically in the laboratory. We collected and analyzed the C and N isotopes of leaves and muscles of crabs identified from gut contents. Muscle tissues of iguanas, muscles of crabs, and leaves were dried for 72 h in a Shel Lab Oven at 60°C. Samples were finely ground using a Retsch M200 frequency grinder. A sample of 0.9 to 1.3 mg was placed in 5 × 8–mm tin cups (Elementar, Hanau, Germany), compressed to a small sphere and analyzed at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems (University of Miami).

Isotopic Analysis.—Small tin spheres containing samples were placed in an automated elemental analyzer (Eurovector, Milan, Italy) and pyrolyzed. The gases from the pyrolysis were led into a mass spectrometer (Isoprime, Elementar) and analyzed for ^{13}C and ^{15}N abundance. Carbon and nitrogen isotope ratios are expressed as

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 10^3$$

respectively, where R_{sample} and R_{standard} represent the molar ratio of the heavier (^{13}C and ^{15}N) to lighter isotope (^{12}C and ^{14}N) in the sample and standard, respectively. The standards are belemnite from the PeeDee formation in South Carolina and atmospheric nitrogen, for carbon and nitrogen isotope ratios, respectively.

Statistical Analysis.—We ran an analysis of variance (ANOVA) to determine differences in individual attributes (SVL, tail length, and mass) between the sexes. We ran a Spearman's correlation analysis to determine the relationship between isotopic signature and individual attributes. To compare the isotopic signature between tongue muscle and leg muscle we used a paired t -test for $\delta^{13}\text{C}$ and because the data for $\delta^{15}\text{N}$ were nonnormal, we used the Wilcoxon signed-rank test. To determine differences in isotopic signature between iguana muscles, leaves of plants, and crab muscles, we ran a Kruskal-Wallis analysis for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. To determine the enrichment of isotopic signature of *I. iguana* muscle to the food items eaten, we used the average of the combined isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for leg muscle ($n = 22$), tongue ($n = 41$), plant material ($n = 8$), and muscles of crabs ($n = 9$).

RESULTS

We found significant differences between the sexes for mass (ANOVA: $F = 10.26$, $df = 39$, $P = 0.003$) and SVL (ANOVA: $F = 4.37$, $df = 39$, $P = 0.0358$) with males being larger than females (Table 1). We found no significant differences between sexes for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values; therefore we pooled the results. We also found no correlation between iguana size (mass, SVL) and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Gut contents for all animals revealed that *I. iguana* ate mostly leaves; however, in one individual we found an insect (coleopteran), in two individuals we found intertidal crabs, one individual had four crabs (*Uca* spp.) in the foregut, and four individuals had snail shells in the hindgut. The plants that we identified from the gut included both native (*Rhizophora mangle*, *Avicennia germinans*) and nonnative species (*Terminalia catappa*, *Schinus terebinthifolius*, *Pithecellobium dulce*, *Heliconia* sp.) (Fig. 2).

We found no significant difference in the $\delta^{13}\text{C}$ isotopic signatures between tongue and leg muscle (paired t -test: $df = 21$, $P = 0.180$). We did however find a significant difference in the $\delta^{15}\text{N}$ isotopic signature between tongue and leg muscle (Wilcoxon signed-rank test: $T = -3.60$, $df = 22$, $P = 0.016$) (Fig. 2). We found significant differences in $\delta^{15}\text{N}$ between muscles of crabs and muscles of *I. iguana* (Kruskal-Wallis: $\chi^2 = 23.96$, $df = 3$, $P < 0.001$) (Fig. 3) and significant differences in the $\delta^{13}\text{C}$ isotopic signature between the muscles of crabs and leg muscles of *I. iguana* (Kruskal-Wallis: $\chi^2 = 27.47$, $df = 3$, $P < 0.001$) (Fig. 3). The greatest difference in mean for $\delta^{13}\text{C}$ was between tongue muscle and crab muscle (4.5‰) and for $\delta^{15}\text{N}$ was between the tongue and plant tissue (3.4‰).

TABLE 1. Demographic measurements (average \pm SD) of male and female *Iguana iguana* captured in Puerto Rico. (SVL = Snout–vent length, TL = tail length.)

Sex	n	SVL (cm)	TL (cm)	Mass (kg)
Female	16	34.5 \pm 7.2	80.2 \pm 21.2	1.61 \pm 0.9
Male	25	40.4 \pm 9.0	87.9 \pm 26.9	2.8 \pm 1.2

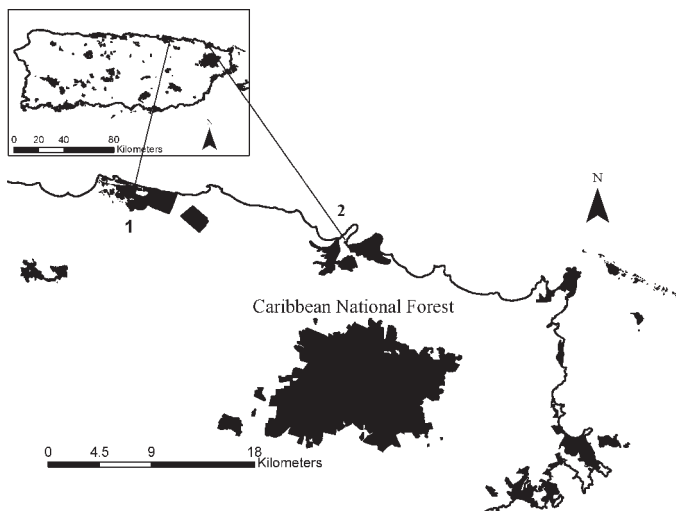


FIG. 1. Capture sites of *Iguana iguana* in (1) Pinoñes mangrove forest and (2) Vista Bahia Golf Course, Rio Grande; inset Puerto Rico.

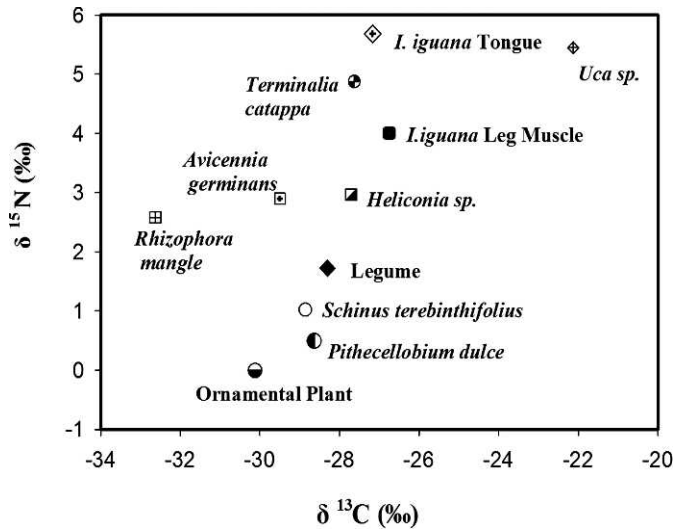


FIG. 2. Isotopic signature of muscles of *Iguana iguana* when compared to the leaves of plants and muscles of crabs identified in gut contents.

DISCUSSION

The gut content analysis indicates that *I. iguana* is an opportunistic omnivore; however, $\delta^{15}\text{N}$ isotopic values establish a strong herbivore signature for *I. iguana* in coastal areas of Puerto Rico. It is generally accepted that normal enrichment of muscles from the animal's diet is approximately 0 to +1‰ for $\delta^{13}\text{C}$, and +3‰ to +5‰ for $\delta^{15}\text{N}$ (DeNiro and Epstein, 1978, 1981; Herrera et al., 2002). Although we found significant differences for the $\delta^{15}\text{N}$ signature between both muscles and food items eaten (Fig. 3), the isotopic enrichment falls within the normal range of enrichment that occurs during incorporation of nutrients into the muscles (Herrera et al., 2002). Therefore we conclude *I. iguana* is primarily an herbivore.

The differences in $\delta^{15}\text{N}$ isotopic signature between the leg muscle and tongue can be attributed to two factors. First, isotope ratios of different tissues are not equally representative of diet (DeNiro and Epstein, 1978; Hatch et al., 2002). The physical and chemical processes involved in the synthesis and construction of the tissue causes fractionation of isotopes to vary in different muscle tissues (Tieszen et al., 1983; Hatch et al., 2002). Second, the higher, more variable $\delta^{15}\text{N}$ values in the tongue may be explained by the presence of other organisms such as bacteria and saliva found on this muscle. These significant differences warrant further experimental investigation to understand fractionation values between leg and tongue muscle tissue.

The $\delta^{13}\text{C}$ signature of both muscles also reflects enrichment of carbon between muscle and food items that is within the normal range for an herbivore (Fig. 3). The isotopic $\delta^{13}\text{C}$ signature for the iguana muscles is indicative of a dietary source of carbon that is composed mainly of C_3 plants, for which the isotopic signature ranges from 27‰ to 32‰ (Gannes et al., 1997) (Fig. 3). Most of the C_3 plant species found in the gut of captured iguanas in this study confirm the findings of other studies in Puerto Rico (Guzmán-Ramírez, 2007; Carlo-Joglar and García-Quijano, 2008). An interesting observation in our data was the presence of Brazilian pepper fruits, *Schinus terebinthifolius*, in the gut. Brazilian pepper is a highly aggressive invasive plant found in disturbed areas (Ewe and da Sternberg, 2002). The proliferation of *I. iguana* in coastal areas and its migration inland is of concern as it may constitute a potential disperser of this plant invader.

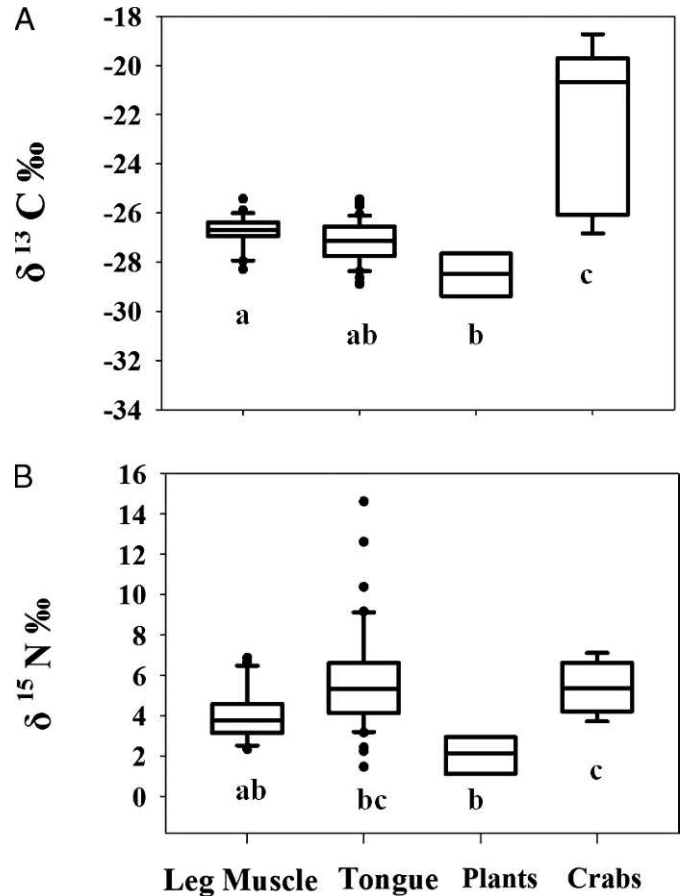


FIG. 3. Isotopic signature of *Iguana iguana* tongue and leg muscle when compared to food items. (A) $\delta^{13}\text{C}$ (median \pm SD) and (B) $\delta^{15}\text{N}$ (median \pm SD). Nonoverlapping letters indicates a significant difference among sample compositions.

The gut contents revealed that although *I. iguana* consumed different plant species, there was a predominance of black mangrove leaves (*Avicennia germinans*), suggesting a higher risk of defoliation for this species. We also found seeds, fruits, and flowers of *A. germinans* within the gut, confirming the higher incidence of herbivory or the greater availability of this species, and the greater potential for structural damage reported for this plant species by Carlo-Joglar and García-Quijano (2008) who found more severely damaged and dead trees in sites with higher iguana density. Therefore, on a long-term basis, *I. iguana* may influence the structure of mangrove forests in their newly invaded range (e.g., Meshaka et al., 2007).

Although crab remains were found in three iguana guts, the isotopic signatures of muscles were consistent with herbivory, suggesting that crab-eating is occasional or restricted to the study population (Gannes et al., 1997). Why *I. iguana* eats nonvegetarian food items, how much of nonvegetarian food items are eaten, and the protein quantity and quality of nonvegetarian food items warrant further experimental investigation. This is the first study to document evidence of *I. iguana* eating crabs (*Uca* spp.) in coastal areas in Puerto Rico and reflects novel community-level dynamics. The species' ecological role and potential impacts on other wildlife warrants further investigation.

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