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Contributions in Biology and Geology

Number 13
July 29, 1977

AGE AND SEX DIFFERENCES, REPRODUCTION
AND CONSERVATION OF *IGUANA IGUANA*

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Milwaukee Public Museum Press
Published by the Order of the Board of Trustees,
Milwaukee Public Museum
Accepted for publication April 28, 1977

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AND CONSERVATION OF *IGUANA IGUANA*

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Abstract

The iguana (*Iguana iguana*), formerly abundant in forest and stream-side habitats of the Neotropical region, is undergoing rapid reduction in numbers over much of its range as a result of overhunting. Sex ratio is approximately 1:1 in observed samples, but males are larger, 110% of female length. Average adult males, of those observed, weigh approximately 1.31 kg and females approximately 1.05 kg. Egg-laying extends over several weeks, with a peak in late February. There is a single annual clutch averaging 30.5 eggs ($n = 31$). Primiparous two-year-old females are about two-thirds the length of older adults and produce less than one-third as many eggs per clutch (13.4 vs. 44.5). Relative clutch weight increases from about 22% of body weight in primiparae to nearly 28% in old adults, in those sampled, and the eggs of primiparae are small, only 74 per cent of large adults' egg weights. As a result, there is a wide range in hatchling size, and the small hatchlings of primiparae are probably handicapped by their size. Eggs are laid in deep burrows in open places, often in sand of streambanks. Hatching occurs early in the rainy season, in April, May or June. Only adult iguanas are sold for food in city marketplaces. The sample of 343 measured seemed to fall in about five fairly well-defined size groups, representing discrete annual age groups of iguanas in their second to sixth year.

The thousands of iguanas captured by professional hunters and sold in city markets represent only a small part of the harvest; many more are hunted for the pot by campesinos who depend on them to supplement a meager subsistence. Gravid females are especially sought, as the eggs are considered delicacies and are preferred over the flesh. Much needless cruelty is involved in the iguana traffic, which involves prolonged deprivation from food and water, pulling out and tying tendons of toes, sewing shut mouths, cramming masses of trussed animals into crowded containers so that suffocation occurs, and leaving the immobilized animals lying in sunshine to die from overheating.

Education, indoctrination and legislation are needed to overcome traditional attitudes and customs of wanton exploitation. There must be sufficient protection of gravid females to assure that eggs will be laid to replace the iguanas harvested. Closed seasons and protected breeding areas are essential. Supplementing protection of natural populations, programs to "farm" iguanas in enclosures providing natural food and other essential resources, and/or to propagate them in confinement for large scale production of young to be used for restocking, have some promise.

* * *

The common, or green, iguana (*Iguana iguana*) is one of the most familiar and ubiquitous members of the Neotropical fauna. Its large size and its ecological role as a primary consumer of the dominant forest vegetation render it an important natural resource. Throughout much of its range it has been exploited for food. Local populations have been drastically reduced, and the species' future has become increasingly uncertain. Motivated by these considerations we undertook a study of the iguana's reproductive biology and its exploitation, centered in western Nicaragua.

Methods and Materials

Our field study in 1976 was concentrated on the stocks of iguanas offered for sale in mercados of Nicaraguan towns. From 30 January through 30 April we visited each mercado in Chinandega, León, Managua, Masaya, and Granada at frequent intervals and soon became familiar with the individual vendors who dealt in iguanas and the locations of their stalls. At each visit, if iguanas were on hand, we obtained permission to examine them, usually offering the vendor a small fee for the privilege. Measurements (snout-vent, tail, head) and weights were routinely recorded and measured as in Fitch and Henderson (1977). Selected specimens, especially gravid females, were purchased for dissection. Field observations on free-living iguanas were also made in a variety of habitats at many locations. In earlier field work we made more intensive studies of free living individuals in Costa Rica (Fitch, 1973; Fitch *et al*, 1971) and Belize (Henderson, 1974), and previously unpublished results of these studies are incorporated in the present report. Regressions were made using the least squares method. For those regressions in which the character was studied as a ratio of snout-vent length we first converted the data by arcsine transformations. Means are followed by \pm one standard deviation.

Results

Habitat. The iguana's habitat is lowland forest, often in the vicinity of streams and rivers. As habits are largely arboreal, it occurs only where trees are numerous and fairly large. Many kinds of leaves, flowers and fruits are eaten. Müller (1971) described a spectrum of habitats from mangrove swamp forest to xeric thorn scrub where the species thrives on the coast of northern Colombia. However, he emphasized the important effects of climate on the ecology. In xeric habitat growth is less rapid and maximum size is smaller than in the more humid banana zone only a few miles farther inland. During the dry season in xeric habitat, when trees are mostly bare and preferred foods are scarce, the lizards are forced to take foods they would not accept in time of plenty, such as coarse foliage or that high in alkaloid content. Under these conditions they lose weight.

Size and sexual dimorphism. Among 343 adult iguanas examined, S-V length ranged from 236 to 550 mm. Males ($n = 174$) averaged 361 (250 to 550) and females ($n = 169$) averaged 327 (236 to 411). Adult males averaged 1309 grams (500 to 2600+) and adult females averaged 1195 (400 to 2150, see Fig. 1). The female weights in this series were influenced by the fact that many of the lizards contained clutches of oviducal eggs adding about 10 per cent to mean weight of the entire group. A smaller number were spent and somewhat emaciated after recent oviposition. Exclusive of egg weights, females would have averaged approximately 1050 gm — about 88% of male weight. Several of the largest males that we examined were heavier than the 2500 gm

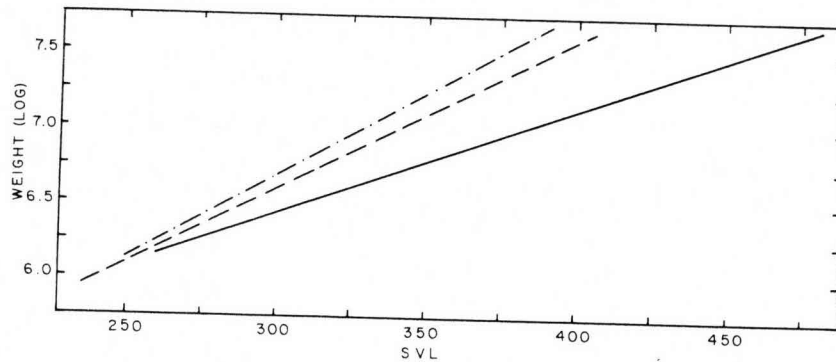


FIGURE 1. Regression of body weight (natural logarithm) as a function of length (mm) in *I. iguana*. Solid line = males ($N = 92$), $Y = 0.007x + 4.331$; dashed line = all females ($N = 105$), $Y = 0.010x + 3.588$; dash-dot line = gravid females ($N = 28$), $Y = 0.011x + 3.384$.

capacity of our scales. There is little published information on iguana weights. Swanson (1950) mentioned one from Panamá that weighed 13.25 pounds (6040 gm), but probably this figure was erroneous, as it was much heavier than any examined in the course of our study, although the length of 515 mm (S-V) was exceeded by several.

Besides the length and weight differences indicated above, sexual differences include those of color and pattern, relative tail length (Fig. 2), proportions of the head (Figs. 3, 4 and 5), size of the dewlap, and length of the spines in the dorsal crest. Adult females remain predominantly green but are much duller colored than juveniles. In old males the green coloring is largely lost, and golden tan color predominates. Relative tail length is greatest in hatchlings and decreases gradually throughout life, but decreases more slowly in males than in females. In 11 live juveniles tail length averaged $252.36 \pm 3.67\%$ of SVL, while in adult males and females corresponding figures were 251.0% and 242.33% respectively (Fig. 2). In both sexes larger and older adults tended to have slightly shorter tails, relatively, than younger and smaller ones but with the small series available significant differences could not be demonstrated.

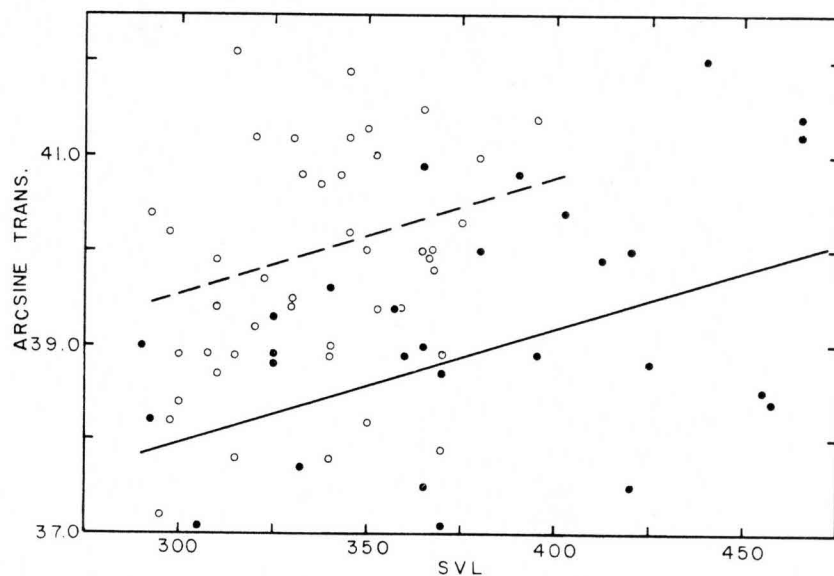


FIGURE 2. Regression of tail length as a function of SVL (mm) in *I. iguana*. Solid line and solid dots = males (N = 28), $Y = 0.012X + 34.384$; dashed line and open circles = females (N = 39), $Y = 0.012x + 35.96$.

In adult males the head and jaw become massive, with swollen temporal muscles. With increasing size and advancing age, these tendencies become more prominent but in females relative size of head may decrease slightly. The following series of mean measurements, with male first in each instance, contrast the head proportions as a percentage of S-V length in adults.

Head width 11.4% (n = 37) and 10.3% (n = 19)

Head circumference 42.1% (n = 36) and 36.6% (n = 17)

Jaw length 16.2% (n = 36) and 14.7% (n = 18)

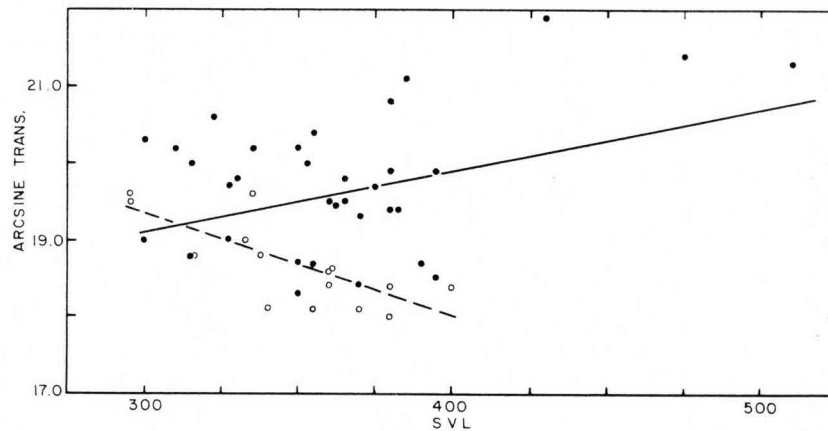


FIGURE 3. Head width as a function of SVL (mm) in *I. iguana*. Solid line and solid dots = males (N = 34), $Y = 0.008x + 16.701$; dashed line and open circles = females (N = 15), $Y = 23.244 - 0.013x$.

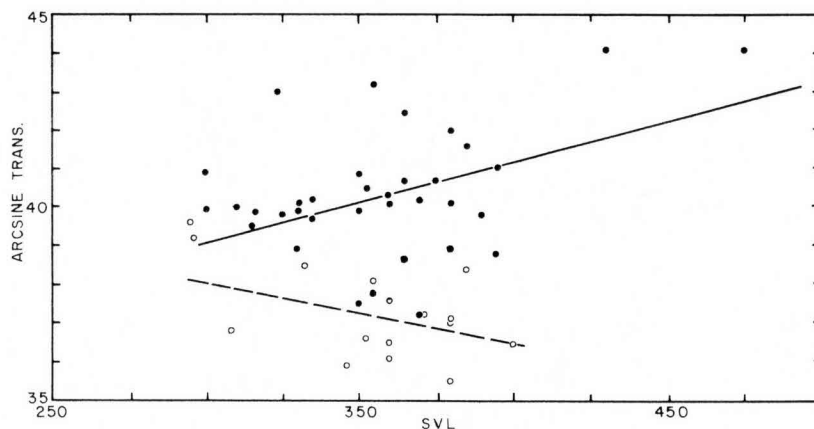


FIGURE 4. Head circumference as a function of SVL (mm) in *I. iguana*. Solid line and solid dots = males (N = 35), $Y = 0.021x + 32.708$; dashed line and open dots = females (N = 16), $Y = 42.829 - 0.016x$.

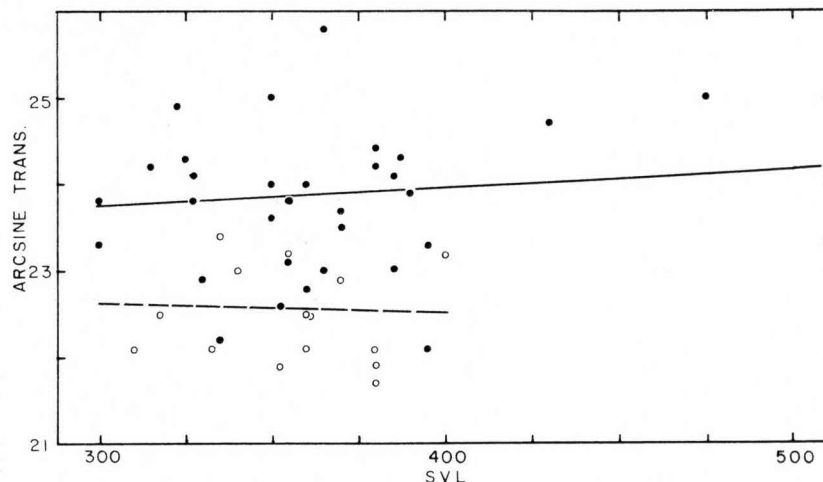


FIGURE 5. Jaw length as a function of SVL (mm) in *I. iguana*. Solid line and solid dots = males (N = 32), $Y = 0.002x + 23.166$; dashed line and open dots = females (N = 15), $Y = 22.915 - 0.001x$.

Reproduction. The iguana is oviparous, and, unlike most tropical lizards that live in wet climates, it produces a single clutch of eggs annually. Most females mature and breed in the second year and most produce a clutch annually thereafter. Timing of the breeding cycle is influenced by the diverse climatic conditions where iguanas occur. Beebe (1944) reported the finding of nests with eggs in British Guiana (= Guyana) on 26 September and 3 October. However, these two nests had abnormally small clutches of only four and seven eggs that averaged 58.3 gm, more than five times the mass of the eggs examined in this study. We suspect that they were misidentified, and actually were eggs of a large snake or turtle.

In Central America and northern South America iguanas apparently breed toward the end of the calendar year; egg laying occurs from late January into April, and hatching occurs mainly in April, May and June. Table 1 shows the months and specific dates reported by various observers for different events in the breeding cycle. The reproductive conditions of our mercado samples from western Nicaragua are shown in Table 2.

In a sample of 31 gravid females examined from 30 January to 31 March 1976, clutches ranged from 11 to 54 eggs and averaged 30.5 ± 2.1 . Number of eggs per clutch was found to be highly correlated ($r = .892$) with size of female (Fig. 6); the largest adult

TABLE 1: Phenology of Reproduction in *Iguana iguana* in Different Parts of Its Range

	Breeding	Digging Nests	Egglaying	Finding of Nests	Appearance of Hatchlings
Belize			late Mar-early Apr ⁵		April ⁹
S. Chiapas	between Oct and Dec ¹ 14 Feb ³		Mar-Apr ¹		
Nicaragua		6 Feb ³		14 April ³ 4 April ³	18 May ³ 1 & 2 June ³
Costa Rica		17-18 Jan 11, 15, 17 Feb ²	Mar, early Apr ⁶		6 April ² early to mid-June (Tortuguero) ⁶ 6 June
Panama			Feb ¹⁰	24 Feb ⁴ early Feb-Mar ¹¹	early May ¹⁰
Colombia	Dec ⁸		Mar ⁸		late May to early June ⁸
Surinam					February ⁷

Alvarez del Toro, 1960¹; Fitch, 1973²; Fitch and Henderson field notes³; Hallinan, 1920⁴; Henderson, 1974⁵; Hirth, 1963⁶; Hoogmoed, 1973⁷; Müller, 1968⁸; Neill and Allen, 1959⁹; Rand, 1968¹⁰; Swanson, 1950¹¹.

TABLE 2: Percentages of Female Iguanas in Different Stages of Reproductive Cycles
In Mercados of Western Nicaragua, February-March 1976

		Dissected Sample				Externally Examined Sample		
		Yolked follicles	Uterine eggs	Non-reproductive	N	Gravid	Spent	N
∞	31 Jan to 10 Feb	16.7	66.6	16.7	30	100	0	37
	21-27 Mar	20.0	80.0	—	5	55.5	44.5	36
	2-9 Mar	—	—	—	—	80.0	20.0	70
	12-21 Mar	—	—	—	—	80.5	19.5	51
	31 Mar	—	100.0	—	1			

females produce up to three times as many eggs as the smallest. Divided into size classes that possibly correspond with age cohorts, the sampled females showed the following average clutch sizes:

- \bar{x} 13.4 ± 0.65 (11-15) in 5 females 250-279 mm
S-V (probable 2nd year primiparae)
- \bar{x} 23.14 ± 0.49 (20-29) in 7 females 280-319 mm
S-V possible 3rd year
- \bar{x} 32.50 ± 3.10 (26-42) in 4 females 320-335 mm
S-V possible 4th year
- \bar{x} 34.2 ± 2.26 (28-48) in 8 females 336-367 mm
S-V possible 5th year
- \bar{x} 44.4 ± 2.14 (37-54) in 7 females 368-400 mm
S-V probably 6th year or older

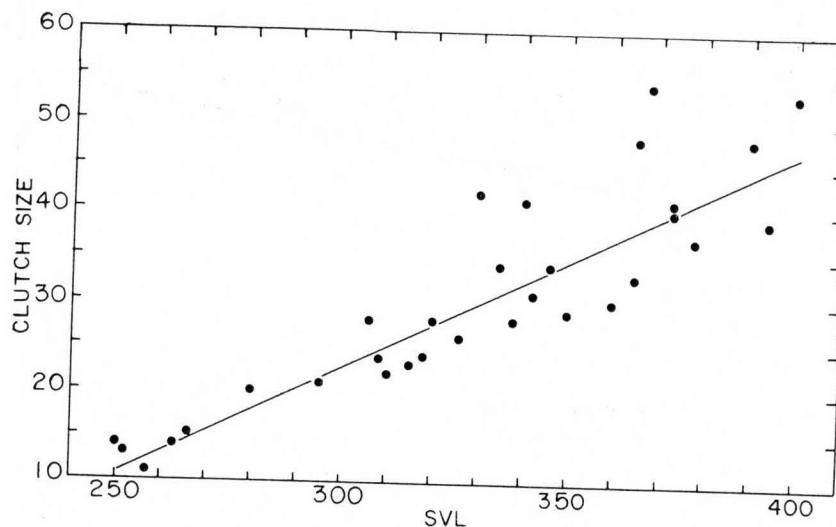


FIGURE 6. Relationship of clutch size to SVL (mm) in *I. iguana* (N = 31), $r = 0.892$, $Y = 0.24x - 49.62$.

The 31 oviducal clutches averaged 323 (92-724) gm; those in the largest females (S-V more than 360 mm) averaged more than four times as heavy as in the smallest group. Clutch weight increases relatively with body size, from 21.8% of body weight in the smallest ovigerous females to 27.6% in the largest (Fig. 7). Egg size also increases from an average of 8.96 gm in the smallest females to 12.16 in the largest. Overall average for oviducal eggs was 10.28 gm. Hence, reproductive effort of primiparous females, still only about two-thirds average adult length, is considerably

less than that of full adults: their small clutches comprise a smaller percentage of body weight, and individual eggs are less than three-fourths the weights of those laid by large adults. The presumably smaller hatchlings of primiparous mothers consequently begin life with a handicap, and their chances of survival would seem poor as compared with larger young. Individually the primiparae contribute little to the next generation, but they comprise the largest cohort of reproductive females and their collective contribution is important. Large clutches of eggs and attainment of sexual maturity while still far short of average adult size exemplify *r*-selected traits in the iguana which in other respects (single clutch, longevity to more than 10 years) is *K*-selected.

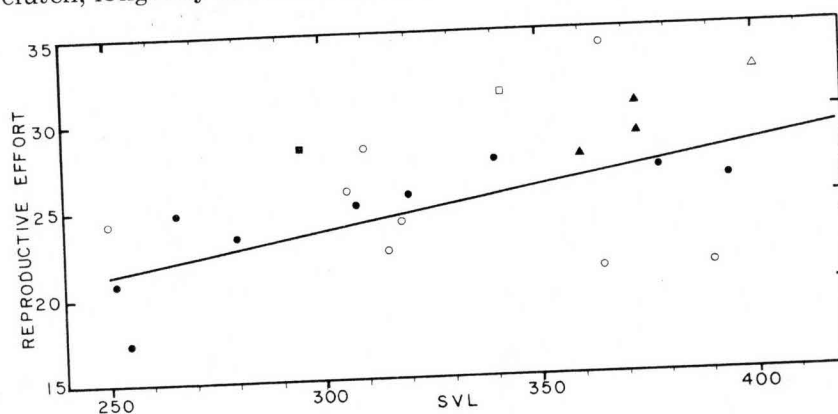


FIGURE 7. Reproductive effort (% clutch weight to body weight) as a function of SVL (mm) in *I. iguana*. Open circles = February 1; solid dots = February 8; solid triangles = February 21; solid square = February 26; open square = March 24; and open triangle = March 31. The regression line is fitted only for the February 8 records ($N = 9$); $r = 0.745$, $Y = 0.046x + 9.791$.

At Tortuguero, Costa Rica, Hirth (1963) found an average of 35 eggs in females of 34 to 38 cm S-V. He stated that these females were probably producing their first clutches, and that much larger females reported as formerly nesting in the area, had been eliminated by relentless persecution. Actually, all but the largest of Hirth's seven females fall in the size group that we tentatively identify as the fifth-year class, and their average clutch size is nearly three times that of primiparae. In 1976 the first spent female was noted on 24 February and the latest ovigerous female was noted on 31 March. These records indicate that egg-laying extended over approximately five weeks, including the last part of February and all of March. A hatchling (KU 42170) was collected near Managua on 18 May 1956 and 11 others from the same lo-

cality were collected on 1 and 2 June. An incubation period of approximately 2½ months is suggested, and this conforms with the findings of previous investigators (73 days, Licht and Moberly, 1965). In the course of field work in Costa Rica in 1968 hatchlings were first found on 6 April (at Boca de Barranca, Puntarenas Province) and this observation bears out the impression gained from egg-laying as early as January that the phenology in northwestern Costa Rica is somewhat advanced over that of Nicaragua and more northern areas, and much advanced over that of the Caribbean coast to the east.

Nest burrows. Ovigerous females resort to open, barren places, preferably sand banks, to dig nest burrows for their large clutches. In Nicaragua in 1976, open, recently dug burrows were found at Laguna de Asososca, León Province, 6 February, and at Río Fonseca, Boaco Province 16 March. In Costa Rica, Fitch (1973, and unpublished field notes) observed nesting activity as follows: Río Congo 11 Feb. 1970, females excavating burrows at several places along streambank; four flushed from their unfinished burrows within a space of 9 m. Río Higuerón, Finca Taboga 11 Feb. 1973, female caught by the tail, protruding as she was digging inside burrow. Río Congo, 14 Feb. 1973, 13 open burrows counted along sandy streambank. Playas del Coco, 15 Feb. 1970, female much distended with eggs flushed from nest site on gully bank. Río Higuerón, Finca Taboga, 17 Feb. 1970, many open burrows in sandbanks, as many as four females flushed simultaneously from burrow areas. Río Congo, 25 March 1973, digging of burrows still in progress; Richard K. LaVal noted four open burrows at the base of a sandbank, and tail of the digging female protruded from one.

The streamside sandbanks where nest burrows were found in Costa Rica were at sites that were sometimes flooded in the rainy season, but incubation took place mainly in the dry season (February, March, early April) when flooding was not a threat.

Female iguanas sometimes are solitary in their nesting, or several or many may congregate at a favorable site, especially if nesting places are few. Rand (1968) found 150-200 females congregating each year on the open beach of an islet (Slothia) at Barro Colorado, Panama Canal Zone. Four that were trailed by radiotelemetry on their post-nesting dispersal averaged 1600 m (approximately one mile), perhaps returning to established home ranges (Montgomery, Rand and Sunquist, 1973). Rand (1968) found that nesting takes several days, sometimes as much as two weeks after a female arrives at the nesting area. In an initial exploratory phase the female digs briefly at many potential sites,

abandoning them even though they appear suitable. Later, she concentrates her efforts at one site and digs with increasing perseverance until the burrow is completed after several hours of work. The final phase, following egg laying is the filling in and covering of the burrow. In completing this process, the female throws earth over the entrance, digs and scratches over an area of several meters in radius, and gradually shifts her activities away from the actual burrow entrance, which is well disguised by the disturbed surroundings.

Nest burrows slope downward, often at an angle of about 30 degrees. One excavated by C. W. Myers was 2 m in length, with the nest cavity about 0.65 m deep (Rand 1968). Some of those observed by us were probed with poles, and seemed to have similar dimensions. On the Caribbean coast of Costa Rica at Tortuguero, Hirth (1963) found destroyed nests, dug out by dogs, from depths of about 1 m.

Hatchlings. Young iguanas near hatching size, and probably not more than a few days old, were found at Boca de Barranca, Guanacaste Province, Costa Rica, on 6 April 1968 (73 mm SVL) and 13 April 1968 (74 and 76 mm SVL). Müller (1971) mentioned hatchling lengths of 65-67 mm SVL and weights averaging 10.25 gm (7.8-11.6). These weights approximate the weights of oviducal eggs that we obtained (both in average and extremes) but the lengths of 65-67 mm S-V seem to be near the minimum.

Burghardt *et al.* (1977) studied the behavior of hatchlings where nests were extremely concentrated on the islet of Slothia, Barro Colorado, Panama Canal Zone. They found that the hatchlings, after digging escape holes from the nests, would spend hours inside the entrances alertly observing their surroundings. When one finally emerged, others from the same burrow and adjacent burrows often would follow almost immediately. The small group would travel as a unit to the shoreline, along it to a reed bed, and finally, by swimming, cross a narrow channel to the main island.

Various observers have noted that hatchling and juvenile iguanas were found on the ground or in low vegetation (Swanson, 1950; Lazell, 1973; Henderson, 1974). Our observations in Costa Rica and Belize bear out the supposition that young are less scansorial than adults. Henderson (1974) found that height of perch tended to be proportional to size of the iguana.

Most accounts of iguana ecology reiterate the statement that juveniles are largely insectivorous, but Hirth (1963), Müller (1968), and Henderson (1974) found only plant material in stomachs examined. In other instances observers have recorded juveniles

eating large insects such as butterflies and grasshoppers (Hirth, 1963, Müller, 1968) but adults too are known to take animal food — beetles, moths and frogs (Alvarez del Toro, 1960), carrion (Loftin and Tyson, 1965) and birds' eggs (Lazell, 1973). Whether there is a major ontogenetic shift in diet from animal to plant food remains to be demonstrated.

Composition of the population. The iguanas that we found in mercados had doubtless already been subjected to various sorts of selection by the hunters who captured them, the vendors, and the buyers. Because the unlaidd eggs are much preferred over the flesh, hunters concentrated their efforts on catching gravid females, which were most readily sold by the vendors. The smallest iguanas found in the mercados were approximately 250 mm S-V (one only 236). Of the 25 that were less than 270 mm S-V, 80% were females and nearly all of these were gravid. Seemingly the hunters spare first-year young and sometimes spare the smaller second-year adolescents, but take any female that is obviously gravid, small size notwithstanding. Such selection introduces bias in the true ratio of the sexes and of the various age classes.

The selection that occurs causes second-year adolescents to be represented in less than their true ratio to adults. It may also cause the female-to-male ratio to appear a little higher than it otherwise would be, and may cause the ratio of gravid to spent females to seem higher than it should be late in the season.

Despite these sources of bias, the samples reveal certain population parameters. For each sex the snout-vent measurements tend to cluster in certain size ranges that apparently represent discrete annual age-groups. For females these concentrations are at approximately 27, 31, 34, 37 and 40 cm and are tentatively interpreted as representing classes that are second-year to sixth-year (and older). For males the corresponding age classes are a little larger: 29, 34, 37, 40, 43 and 47 cm. In the entire sample there were 169 females and 174 males, suggesting a 1:1 sex ratio.

At Santa Marta, Colombia, Müller (1968) found that juveniles and second-year young combined made up about half of the population, and individuals in their third to sixth years made up most of the remainder, while those older than six years made up only a small percentage. Müller stated that the largest iguanas in the area of his study attained a total length of 1.5 m and were probably more than 10 years old. He expressed doubt that any attained an age over 20 years.

If the estimates of longevity suggested by Müller (1968) and implied by the size groups that we recognized are valid, the popu-

lation might be expected to sustain approximately 40% annual loss. At that rate an original cohort of 100 animals would be reduced to a single survivor in the 10th year. In a population of adolescents and adults such as we examined at the mercados, the older age groups would comprise successively smaller percentages. In our samples there were fewer iguanas in the supposed second-year and third-year classes than there were in the supposed fourth-year class, presumably because of selection by the hunters, rejecting small animals. The fifth- and sixth-year classes were represented by dwindling numbers, about as expected.

Exploitation. Throughout its wide range in México, Central and South America, and the West Indies, the iguana is esteemed as food for humans. It has been hunted since pre-Columbian time without regard for the preservation of adequate breeding stock. However, the iguana's high reproductive potential and adaptability, and the partial or local elimination of many of its natural enemies have favored its survival. Nevertheless, in recent decades rapid increase and proliferation of human populations, destruction of natural habitats, and widespread acquisition of firearms have tipped the scales against the iguana so decisively that it is rapidly disappearing or becoming scarce in areas where it formerly abounded.

In towns of western Nicaragua in February and March 1976 we regularly found live iguanas offered for sale in mercados. Usually there were several vendors in each mercado, each having from one to more than 100 iguanas on hand. The vendors usually replenished their stocks once or twice weekly, from middlemen who in turn obtained the animals from professional hunters. Main suppliers of the city markets are the villages of Palo Grande, Somotillo and Villa Nueva in northwestern Nicaragua near the Honduran border, San Francisco de Carnicera on the northeastern shore of Lago de Managua and San Carlos at the southeastern end and outlet of Lago de Nicaragua. The latter two villages are collecting points for iguanas captured in more remote areas.

Dealers usually had mixed lots of iguanas and ctenosaurs (*Ctenosaura similis*) with a ratio of one iguana to about 2.5 ctenosaurs, reflecting the greater abundance of the latter species in the xeric habitats that prevail in western Nicaragua. In that country at least, the ctenosaur is preferred as food over the iguana. However, the iguana averages slightly larger and the two kinds command equivalent prices. The cost varies somewhat according to the size and condition of the animal (gravid females command the highest price), and there is even greater variation in price from one part of the country to another. The lowest prices prevail in the villages

of northwestern Nicaragua, where the hunters receive from 1.5 to 2.5 cordobas (1 cordoba = \$0.14 U.S.) per animal and sell them in dozen lots. Prices were highest (usually 8-12, but up to 15 cordobas) in mercados of Masaya and Granada.

The thousands of iguanas and ctenosaurs that are sold annually at city mercados, and on a smaller scale in outlying villages, are estimated to be only a small percentage of the total harvest; larger numbers are taken for family consumption. Hunting iguanas is a popular form of outdoor recreation and the flesh is an important protein source in diets that tend to be meager in quantity and high in starch content.

Several dozen country people were interviewed at random concerning their use of iguanas at scattered points in western Nicaragua. Most of these persons said that they ate iguana flesh regularly or occasionally, or had done so in the past. Nearly all agreed that within their memories both iguanas and ctenosaurs had dwindled rapidly in numbers, sometimes to the point that hunting them was no longer rewarding.

Published reports from studies of iguanas in other parts of the range indicate that the trends we noted in Nicaragua — increasing hunting pressure and rapidly dwindling populations — are widespread or universal. Swanson (1950) described the great abundance of iguanas in Panamá and noted that in the Panamá City market dozens could be seen at one time lying in the street, but Tovar (1969) noted that they had largely disappeared and that a closed season had been imposed. Knight (1968) related that on San José, an uninhabited island in the Gulf of Panamá, iguana hunters annually burned off a 20-acre savanna, and this open area attracted ovigerous females searching for nesting sites. The iguanas captured in this relatively remote area were destined for the Panamá City marketplace where they brought \$2 to \$4 apiece. Alvarez del Toro (1960) noted that formerly iguanas had been excessively abundant in the mangrove swamps of the south coast of Chiapas, México, near Arriaga, but that they had become scarce as a result of overhunting. Hirth (1963) related that in one season at Tortuguero 40 gravid iguanas were taken by local residents along a 4-mile stretch of beach, and at least 7 nests were destroyed by dogs and he concluded that "... the numbers of iguanas are diminishing rapidly" despite the remoteness of the locale and the sparseness of the human population. Between 20 March and 16 April 1971 at Belize City, Henderson (1976) counted approximately 300 ovigerous females in the main market place (most shipped from the western part of the country near the Guatemalan border as they were scarce at Belize City) but in 1976, 2-9

March there were none in the marketplace, although local residents stated that small shipments were received from time to time. In Nicaragua, Ramirez (1968) deplored the mass shipments of iguanas to El Salvador where they were already depleted, and Villa (1968) estimated that 150,000 iguanas and ctenosaurs, mostly gravid females, were eaten annually, causing both species to be threatened with early extinction. By 1976 both species still remained abundant in some localities but were scarce or absent in other areas where they had been abundant formerly. It seemed that fulfillment of Villa's pessimistic predictions had been delayed by the uneven distribution of the animals and the inaccessibility of some populations to the hunters. In March and April 1976 the Nicaraguan Government banned sale of the animals in parts of the country. Effectiveness of the ban was problematical. The lizards were no longer on display in the mercados, but we were told that many vendors kept them concealed in bags and boxes and continued to make sales. Some professional hunters turned to other means of livelihood. One hunter told us that eight dozen ctenosaurs and iguanas that he had captured all died eventually when he was unable to sell them.

On the Caribbean coast of Colombia, where the flesh is not eaten, Müller (1971) found that the sex ratio was much weighted in favor of males because of intensive hunting of gravid females for the sake of their eggs.

The traditional methods of transporting and keeping iguanas that prevail throughout Latin America involve much cruelty. Those brought to marketplaces are kept alive, because they survive a long time without food or water, whereas the flesh would deteriorate rapidly in the heat. The animal is immobilized by tying the fore- and hind limbs behind the back. Sometimes the tendon is drawn out from the end of a toe and used to tie the limb to that of the opposite side. In Nicaraguan marketplaces the limbs were more often tied with thongs, but in some instances the tightly bound limb was malodorous and gangrenous. Swanson (1950) noted that in Venezuela the animals awaiting sale were immobilized by breaking their backs instead of tying the limbs. In ctenosaurs and occasionally male iguanas, which are inclined to defend themselves by biting, mouths are sewn shut. A special heavy, flattened and curved needle is used to pierce the lips. Ovigerous females are often slit open as soon as captured, to remove the eggs, and then left alive. In some instances the incision in the belly is crudely sutured, in the belief that the female will recover and produce more eggs.

Usually when large batches of iguanas were on display in mercados, a few were dead. Mortality often resulted from overheating in immobilized animals lying in direct sunlight. In other instances deaths probably resulted from suffocation in those at the bottom of a pile, as several dozen might be stuffed into a large gunny sack.

Conservation. If present trends continue, it can be predicted that *Iguana iguana* as a species will survive for a long time, but in low densities and remote places, losing its importance as a food source because of rapidly declining numbers. This loss, if it occurs, will be especially regrettable because it involves the developing countries of Latin America where expanding human populations require ever-increasing supplies of protein food in order to improve or maintain present standards of living or even to exist.

As a primary consumer, converting foliage to flesh suitable for human food, the iguana has potentialities for development as a renewable resource. It can be saved and restored to abundance by the simple expedient of sparing enough breeding females each year to permit a new generation to develop. There is general recognition by the people who hunt iguanas that overhunting is rapidly leading to scarcity and local extinction. Governmental authorities also are aware of the problem in many instances, and legislation has been passed to afford protection. However, even where the needed legislation exists, the protection afforded has been inadequate. Campesinos, often living on a marginal subsistence in remote areas where law enforcement is minimal, continue to kill and eat iguanas at every opportunity.

Education and indoctrination of the general public, through the media and the schools, would seem to be an important part of any conservation program. Strong public sentiment in favor of conservation must replace the traditional attitude of wanton exploitation of nature if protective legislation is to be effective.

Improving the iguana's status as wild game and as a marketable resource will require legislation that is adapted to local conditions. It will need to include imposition of closed seasons, establishment of reserves where the animals are not hunted, and protection of gravid females, at least at certain times and places. Needless to say, protection of juveniles is also necessary. However, immature iguanas are rarely if ever hunted for food by people, and most juvenile mortality is a result of natural predation.

An additional approach to the problem of iguana conservation was suggested by Villa (1968) — farming the species. On relatively small areas of a few hectares, with natural stands of trees, water, and suitable nesting sites, enclosures could be installed to contain

the iguanas and exclude human hunters and some natural predators. The two-year period required for the animals to reach maturity would be largely compensated for by the high reproductive potential and the small amount of care required. An efficient system of farming would probably need to include supplemental feeding, measures to control disease, parasites and natural enemies, and other refinements. Through artificial selection the breeding stock doubtless could be rapidly altered in ways that would render the iguana better suited to pen rearing — large size, rapid growth, prolonged breeding season, and docile disposition. Maintaining large numbers of iguanas in artificially high densities probably would be feasible, because at times large numbers congregate in the same tree under natural conditions (Fitch, 1973) and there is a high degree of intraspecific tolerance although it varies seasonally. Large, dominant males are polygynous and territorial and fight fiercely during the mating season in December (Müller, 1971). Alvarez del Toro (1960) described violent territorial fights, beginning in trees and ending on the ground, with the loser so badly injured as to be immobilized, perhaps dying. At times of year other than the breeding season some fighting occurs but it is ritualized and relatively mild (Peracca, 1891). In view of the polygynous and territorial habits of males, it would seem desirable to harvest most of them as soon as they attain maturity, late in the second year.

A third approach to efficient utilization of the iguana as a natural resource would combine the methods indicated in the last two paragraphs, keeping large numbers of adults confined in semi-domestication for propagation, but distributing the hatchlings from their eggs to restock available habitats. The effectiveness of such an operation would depend largely on local mortality factors that might eliminate some or most of the young before they reached harvestable size. Obviously under natural conditions high juvenile mortality is normal. Reducing this mortality is a key to successful management. It might include local control measures against certain natural predators, and especially against domestic or feral dogs and cats.

Resumen

La iguana verde común (*Iguana iguana*), que abundaba en las selvas y orillas de ríos y arroyos de la región neotropical, está sufriendo una reducción numérica alarmante debido a una caza excesiva. La proporción sexual es aproximadamente de 1:1, siendo los machos más grandes que las hembras en una proporción de 110% sobre el largo de la hembra. Los machos adultos pesan aproxima-

damente 1.31 kg y las hembras 1.05 kg. La oviparición se extiende por varias semanas, alcanzando su máximo a finales de febrero. Las iguanas sólo ponen una vez al año, con un promedio de 30.5 huevos ($n = 31$). Las hembras fecundadas por primera vez miden aproximadamente $2/3$ del largo de las otras hembras adultas y producen menos de $1/3$ de huevos (13.4 vs. 44.5). El peso relativo de la nidada equivale aproximadamente al 22% del peso del cuerpo en las primerizas, e incrementa hasta casi 28% en iguanas viejas; los huevos de las primerizas también son mas pequeños, teniendo solamente un 74% del peso de huevos producidos por hembras adultas. Como resultado, existe una gran variedad en el tamaño de las crías donde la supervivencia probablemente es más difícil para las de las primerizas pues son más pequeñas. Los huevos son puestos en cavidades profundadas en lugares abiertos libres de vegetación, muchas veces en la arena de los arroyos y ríos. La eclosión ocurre temprano durante la temporada de las lluvias, en abril, mayo o junio. El grupo analizado fue de 343 donde encontraron agrupaciones bastante bien definidas de tamaños; éstas representaron cinco grupos discretos de iguanas según su edad desde los 2 hasta los 6 años.

Solamente las iguanas adultas son vendidas como alimento en los mercados de las villas y ciudades. Los miles de iguanas capturadas por cazadores profesionales y vendidas en los mercados representan solamente una pequeña parte del total capturado, pues muchas más son atrapadas por los campesinos que dependen de su carne para suplementar su alimentación cotidiana, la cual es bastante pobre. Las iguanas hembras fecundadas son las más apetecidas, ya que los huevos son considerados como un manjar delicado y se los prefiere a la carne. Innecesaria crueldad existe en el comercio a que son sometidas las iguanas, falta de agua y alimento, quijadas suturadas, con los desgarrar tendones de las extremidades. Almacenamiento en receptáculos y con la siguiente asfixia; otras mueren de insolación.

Programas educativos así como una legislación encaminada a eliminar los hechos citados anteriormente se hacen extremadamente necesaria. Debe haber suficiente protección para las hembras fecundadas de manera que se asegure el reemplazo de las iguanas cazadas. Veda y áreas de protección donde se efectúa la oviparación son esenciales. Medidas extras de protección de las poblaciones naturales, como programas de crianza en "granjas" naturales y su propagación en criaderos para obtener grandes producciones de juvenes, son algunas ideas que tienen asidero.

Acknowledgments

We are greatly indebted to Sr. Jaime Villa of Managua, Nicaragua, for much material aid and advice at the outset, and throughout our field study; also to Mr. Allen Porter, who as a U.S. Peace Corps Volunteer assisted us in the field, and in late March and April 1976, after our departures, carried on with the field work. Thanks are also due to the Managua Banco Central, and to Dr. Jaime Incer and Sr. Roberto Incer of that institution for the funding of our field study. The Nicaraguan government, through *Catastro*, made available a jeep and driver for the field work during part of our sojourn. Drs. W. Auffenberg, J. Iverson and M. A. Nickerson offered many helpful comments to improve our efforts. Vivian Corres and Jaime Pefaur prepared the resumen.

Literature Cited

- Alvarez del Toro, M. 1960. Reptiles de Chiapas. Inst. Zool. del Estado Tuxtla Gutierrez, Chiapas. 204 pp.
- Beebe, W. 1944. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 2. Iguanidae. *Zoologica* 29(4):195-216.
- Burghardt, G. M., H. W. Greene and A. S. Rand. 1977. Social behavior in hatchling green iguanas: life at a reptile rookery. *Science* 195:689-691.
- Evans, H. E. 1947. Notes on Panamanian reptiles and amphibians. *Copeia*, 1947(3):166-170.
- Fitch, H. S. 1973. A field study of Costa Rican lizards. *Univ. Kansas Sci. Bull.*, 50(2):39-126.
- Fitch, H. S., A. V. Fitch and C. W. Fitch. 1971. Ecological notes on some common lizards of southwestern Mexico and Central America. *Southwestern Naturalist*, 15(3):397-399.
- Fitch, H. S. and R. W. Henderson. 1977. Age and sex differences in the ctenosaur (*Ctenosaura similis*). *Milwaukee Public Mus. Contr. Biol. Geol.* 11:1-11.
- Hallinan, T. 1920. Notes on lizards of the Canal Zone, Isthmus of Panama. *Copeia* (83):45-49.
- Henderson, R. W. 1974. Aspects of the ecology of the juvenile common iguana (*Iguana iguana*). *Herpetologica*, 30:327-332.
- Henderson, R. W. 1976. Notes on reptiles in the Belize City, Belize area. *J. Herpetol.* 10(2):143-146.
- Hirth, H. F. 1963. Some aspects of the natural history of *Iguana iguana* on a tropical strand. *Ecology*, 44:613-615.

- Hoogmoed, M. S. 1973. Notes on the herpetofauna of Surinam. IV. The lizards and amphisbaenians of Surinam. W. Junk, The Hague. i-ix + 419 pp.
- Knight, D. H. 1968. Ecology of a tropical savanna burned annually by iguana hunters. Jour. Colorado-Wyoming Acad. Sci., 61(1):50.
- Lazell, J. D., Jr. 1973. The lizard genus *Iguana* in the Lesser Antilles. Bull. Mus. Comp. Zool., 145(1):1-28.
- Licht, P. and W. R. Moberly. 1965. Requirements for embryonic development in the tropical lizard, *Iguana iguana*. Copeia, 1965:515-517.
- Loftin, H. and E. L. Tyson. 1965. Iguanas as carrion eaters. Copeia, 1965:515.
- McGinnis, S. M. and C. M. Brown. 1966. Thermal behavior of the green iguana, *Iguana iguana*. Herpetologica, 22:188-189.
- Montgomery, G. G., A. S. Rand and M. E. Sunquist. 1973. Post-nesting movements of iguanas from a nesting aggregation. Copeia, 1973:620-622.
- Müller, H. 1968. Untersuchungen über Wachstum und Altersverteilung einer Population des Grünen Leguans, *Iguana iguana* L (Reptilia: Iguanidae). Mitt. Inst. Colombo-Aleman Invest. Cient., 2:57-65.
- Müller, H. 1971. Ökologische und ethologische Studien an *Iguana iguana* L. (Reptilia: Iguanidae) in Kolumbien. Abteilung Physiologie und Ökologie des Zoologischen Instituts der Universität Münster. 109-131.
- Neill, W. T. and R. Allen. 1959. Studies on the amphibians and reptiles of British Honduras. Publ. Research Div. Ross Allen Reptile Inst. Inc. 2:1-76.
- Peracca, M. G. 1891. Osservazioni sulla riproduzione della *Iguana tuberculata* Laur. Boll. Musei Zool. Anat. Comp. R. Univ. Torino, 110:1-8.
- Ramirez, D. 1968. Iguanas y Garrobo Nicas a El Salvador. La Prensa, 27 Febrero 1968.
- Rand, A. S. 1968. A nesting aggregation of iguanas. Copeia, 1968:552-561.
- Swanson, P. L. 1950. The Iguana, *Iguana iguana* (L). Herpetologica, 6(7):187-193.
- Tovar, A., Dario. 1969. Man's effect on natural fauna. The Florida Naturalist. March 9-13, 1969:20.
- Villa, J. 1968. Explotación Irreflexiva de Nuestras Iguanas. El Pensamiento Nacional, 17 Febrero 1968:2-3.