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ABSTRACT: Adult male *Ctenosaura similis* are relatively large (females average 80% of their length and 55.6% of their weight) with relatively massive heads, bulging cheek muscles and elongated jaws, and a prominent middorsal crest of elongate spinelike scales. These differences are associated with polygyny and male aggression. The sexes are similar in color and pattern, but there is ontogenetic change from finely reticulate cryptic markings in the terrestrial and nomadic hatchling to bright green in the scansorial juvenile and finally to a dark-banded pattern in the relatively sedentary adult. Relative tail length is progressively reduced from more than 220% of snout-vent in hatchlings to 150% in old adults.

* * *

Intraspecific differences in behavior, morphology and size between sexes and between adults and young have been noted in various vertebrate species, and in recent years have aroused increasing interest as mechanisms for efficiently partitioning food, shelter and other resources. Mating systems and reproductive strategies (Tinkle et al., 1970; Pianka, 1970) contrasting selection for rapid population turnover vs. stability of population and increased survivorship have also proved to be fertile fields for study.

Such sexual and ontogenetic differences are prominent in *Ctenosaura similis*, a giant iguanid lizard common through much of Mexico and Central America. Noteworthy characteristics of the species are strong sexual dimorphism, with males much larger than females, their heads and jaws becoming progressively more massive with advancing age, and young from remarkably large egg clutches, hatched at a relatively smaller size (compared with adults) than any other American lizard, and differing greatly from adults in body proportions, color, pattern, and behavior.

Our objectives were to measure and define these differences and to correlate them with the ecology and habits of the species.

Methods and Materials

We have had opportunity to study ctenosaurs on several trips to Central America (Fitch, 1973; Henderson, 1973). In February and March 1976 we examined, weighed and measured approximately one thousand of these lizards, mostly live adults in the mercados of Nicaraguan towns. Also, a sizable sample which included young as well as adults was collected by shooting with a .22 rifle.

Measurements were made to the nearest millimeter. Regressions were made using the least squares method. For those regressions in which the character was studied as a ratio of snout-vent length (tail and jaw measurements, Figs. 2, 5) we first converted the data by arcsine transformations.

Results

Behavior — Hatchlings are highly active and terrestrial and they wander widely. Hatching occurs in May through the beginning of July, early in the rain season, after an almost rainless period of several months. The hatchlings usually inhabit extensive areas of bare soil. Approach of a person causes the lizard to flatten against the substrate where it may be overlooked because of the effectively cryptic pattern, but at a distance of 1-3 m an escape dash is triggered. The juvenile runs with speed and agility reminiscent of such cursorial lizards as *Callisaurus*, *Cophosaurus* and *Holbrookia*. The dash may cover many meters, with abrupt changes in direction on a course that passes through potential hiding places such as shrubs or grass tussocks, ending in a sudden stop. The effect is bewildering and the lizard is relocated only with difficulty. If it is followed and flushed more than once, the dashes increase in length, as does the distance at which flushing occurs. The hatchling is, of course, unfamiliar with its surroundings at first, and the observed behavior suggests that during this early terrestrial stage habits are nomadic with no special attachment to definite areas or objects. The young have insectivorous tendencies, and take a much higher proportion of animal food than do adults (Montanucci, 1968; Fitch and Henderson, ms). Within the first few weeks of life small scale population shifts occur, from the open places preferred earlier to places with dense vegetation, such as roadsides or stream banks. The young continue to change their habits and at an age of two months spend much of their time above ground, climbing in trees and bushes. Vegetation is lush and shelter is abundant at the height of the rainy season. In this scansorial stage the young become much more deliberate in their movements. At first they seem to have no regular retreats; they may run or leap to the ground when threatened, usually to dash to another tree, bush or thicket. Later they become attached to habitual retreats above ground, such as hollow limbs or fence posts.

At an age of six months young have generally grown to more than 20 times their original weight (3+ grams to 80+ grams) and 2.5 times their original length (57 to 141 mm). They have come to resemble adults in habits and may frequent the same situations, often perching on logs, walls, or fence posts. Adults occasionally climb on trees, rocks, walls, or buildings, but spend most of their time on the ground, and generally retreat into underground burrows for periods of inactivity. Though mating may be somewhat promiscuous, there seems to be a tendency toward a polygynous social system, as large old males control their chosen areas, dominate or displace smaller males, and monopolize breeding females that are present. In an undisturbed colony of 49 ctenosaurs in the Belize City cemetery in March 1976 there were 5 large males and 14 adult females. In the week covered by our observations each male was closely associated with a particular female, but there were indications that these associations were temporary, and that each male shifted from time to time, to a different area and different female. No fighting was observed between the well-spaced males of this group, but when Henderson (1973) introduced and tethered a new male in an area, this male was immediately attacked by a resident male and violent and prolonged fighting ensued.

Body Size — Mean S-V length for 610 adult males (of S-V lengths greater than 200 mm) was 345 mm, contrasted with 276 mm for females (n = 283). Maximum measurements were 489 (male) and 347 (female). Forty percent of the males were larger than the largest female. Mean weight was 1034 g in males (n = 524) and 651 g in females (n = 263). Many females were carrying oviducal eggs or ovarian follicles, constituting an estimated 11.7% of overall female weight. Exclusive of egg-weight females average 575 grams — 55.6% of male weight (see Fig. 1).

Presumably hatchlings of both sexes are approximately the same size. Perhaps the sex ratio is biased at hatching; our collecting during February, March and April revealed an unbalanced ratio of first-year young: 32 males (135-220 mm) to 50 females (127-200 mm). For females the main division between first-year immatures and second-year adolescents is approximately 200 mm (S-V) with some overlapping. The smallest egg-bearing females are of about this size, and most that are larger produce eggs.

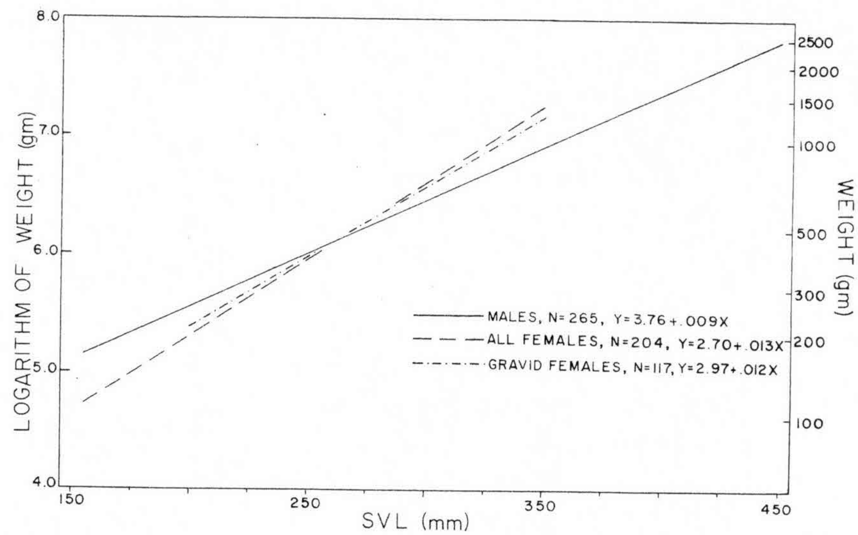

FIGURE 1. Regression of body weight as a function of length in *Ctenosaura similis*; males, females (all) and gravid females shown separately. Differences between the three classes are not significant ($p > .05$).

The ctenosaurs offered for sale in mercados have been subjected to various sorts of selection, and the population samples obtained from them are probably somewhat biased. For instance, few individuals smaller than 250 mm are to be found, hence first-year young and most second-year adolescents or small adults are excluded. Females, being smaller than males, may be passed up more often by the hunters, resulting in biased sex ratios in our samples; we recorded more than twice as many males as females. Probably this bias also involved selection for larger females, so that mean adult female size in the *mercado* samples was larger than in a natural population, causing the sex difference in size to seem less than it really is. Our field work did not support the data obtained from *mercado* samples as we obtained more adult females than males, but most of these females (25 of 41) were less than 250 mm S-V.

Dorsal crest — In adult males the enlarged erect middorsal scales of the neck and body form a comblike crest of flat spines which is the basis for the generic name. The longest spines are approximately 12 mm high, but in adult females these middorsal scales are low (2 to 3 mm) and flattened. The middorsal scales in young are also low and inconspicuous, but in second-year males they become prominent. The degree of development of the crest provides a basis for separating first- and second-year males, which overlap in size because of the great amount of individual variation in growth. In the field the crest on body and neck of adult males provides the best means of distinguishing between sexes.

Color and pattern — The hatchling is pale grayish brown dorsally with a reticulum of darker brown markings that is effectively cryptic in the open, terrestrial habitat. By the time the young ctenosaur is two months old, the original juvenile pattern has faded, and the color has turned partly or entirely green, blending with the lush vegetation that prevails in the rainy season. At an age of six months the lizard is losing the green color and beginning to assume the adult pattern. This pattern is variable; essentially it consists of broad dark bands on a paler tan ground color. There are four main bands on the body, extending onto the ventral surface. The limbs and toes are similarly banded. The tail is dull tan. The subocular and loreal area is pale tan tinged with ocherous or orange. Pale areas between bands of the dorsal surface are heavily speckled with dark pigment. The dark bands on the body tend to be split middorsally by lighter areas. Dull red or orange spots in varying amounts may be present on the dorsal surface.

Length of tail — There is a striking progression from the remarkably long, attenuate tails in the hatchlings and small juveniles to relatively short-stubby, blunt-ended tails in old adults (Fig. 2).

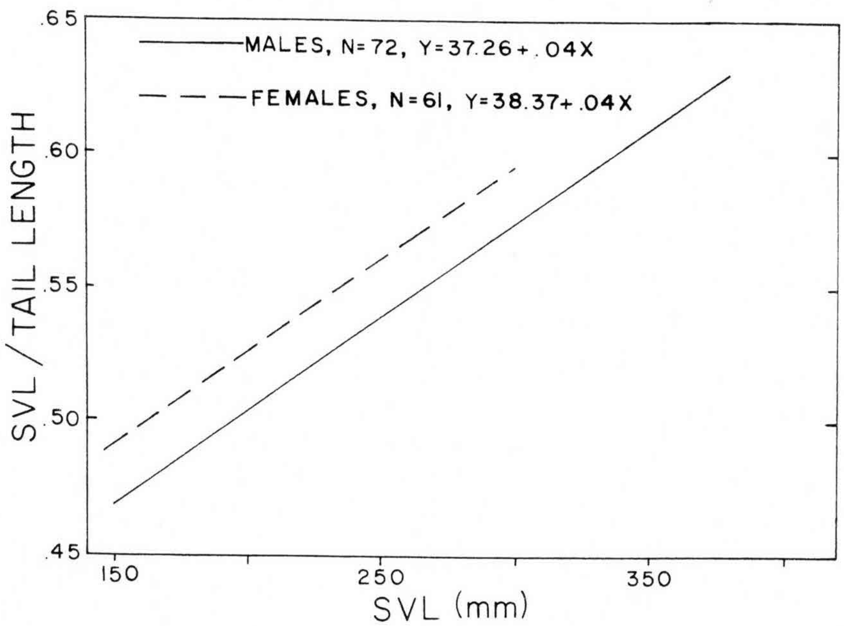

FIGURE 2. Regression of tail length as a function of snout-vent length in *Ctenosaura similis*; relative tail length decreases with increasing size, and female tails average shorter than in similar sized males. Difference between regressions is not significant ($p > .05$).

This reflects an ontogenetic change in the function of the tail: in the scansorial juveniles the long tail is mainly an organ for balance, whereas in the terrestrial adults the tail assumes an essentially defensive function. Tail-length averages a little more than 220 percent of snout-vent in hatchlings and is reduced to approximately 150 percent in old males. Partly grown males, and adult males have slightly longer tails than females of the same size. The tail-length-body size regression seems to be a straight line. Deviations may result from inadequately small samples, and perhaps from occasional individuals with well regenerated tails that were erroneously included. Most adult ctenosaurs (61% in a sample of 100) had had their tails broken and regenerated one or more times. Of 16 small adults that were judged to be in their second year, 50% had regenerated tails, but in a sample of 74 first year young only 34% had regenerated tails. For adults with regenerated tails, mean tail-length was 135 $\pm$ 0.58% of snout-vent length ($n = 28$), and for first year young with regenerated tails mean tail-length was 169 $\pm$ 0.30%. Hence in these immatures even individuals with regenerated tails had a relatively greater tail length than old adults with intact tails.

Shape of head — Complex allometric changes in head shape occur. Like other infant animals the hatchling has relatively large head and eyes with a blunt snout and short jaws. In early growth the head increases in size less rapidly than the body, but at adolescence the sexes follow different trends. The male's head grows faster than the body in some of its proportions, becoming widened posteriorly with bulging jowls resulting from the enlarged masseter muscles, and the rostrum and jaw are lengthened. From dorsal view the head is triangular. The larger the individual, the more pronounced is the head shape characteristic of its sex (see Figs. 3 and 4).

Three head measurements were taken: greatest circumference (midway between eye and ear opening), greatest width (on the same part of the head from dorsal view), and jaw-length from the corner of the mouth to the tip of the snout. Figures 5, 6 and 7 show the trends of these measurements. In females circumference of head relative to body length steadily declines from juvenile to adult. The same measurement remains fairly constant in large young and small adult males, but increases steeply in males larger than average adult size. Relative jaw-length changes little in females; in males the ratio is already higher than that of females in half-grown young, remaining fairly constant until adolescence, and then increasing steadily. Relative head width decreases steadily in females as growth proceeds; in males it remains fairly constant in large young and small adults, then increases abruptly in large adults.

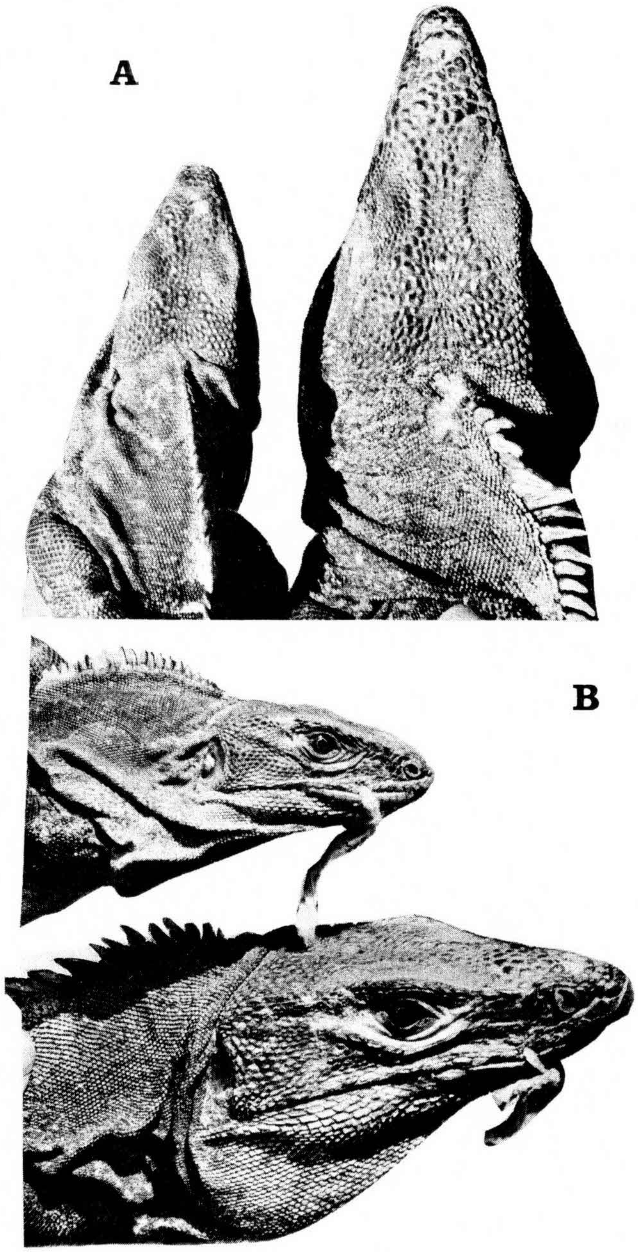

FIGURE 3. (a) Heads and necks of adult female (left) and male *Ctenosaura similis* from dorsal view, showing relatively large size, elongate rostrum, massive jaw muscles and prominent dorsal crest in the male. (b) Same from lateral view, female above.

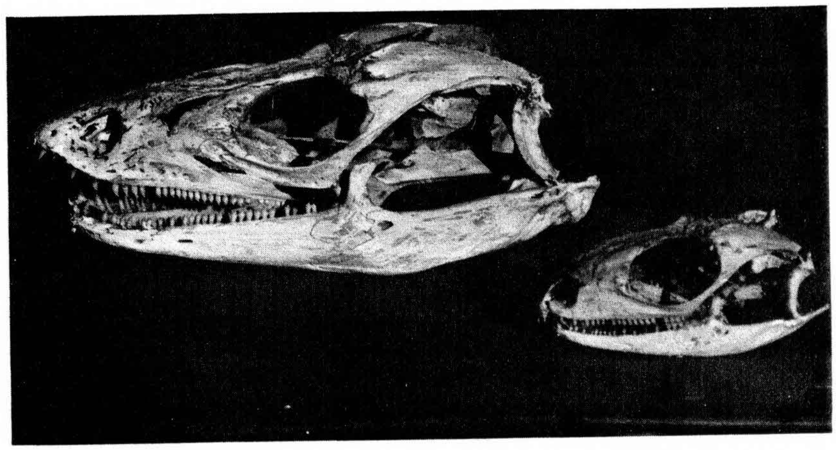

FIGURE 4. Skull of large adult male *Ctenosaura similis* (left) and adolescent female (right) showing relatively massive bones, elongate jaw and enlarged front teeth in the male.

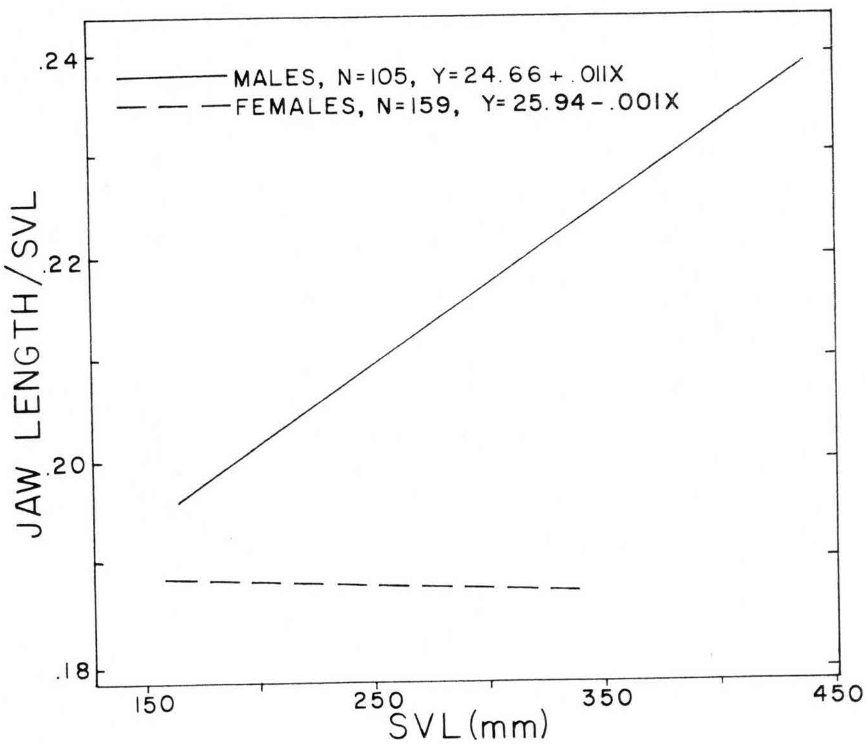

FIGURE 5. Jaw length as a function of snout-vent length in male and female *Ctenosaura similis*; in males relative jaw length increases with larger size, whereas in females overall length increases a little more rapidly than jaw length. Difference between the regressions is highly significant ($p < .001$).

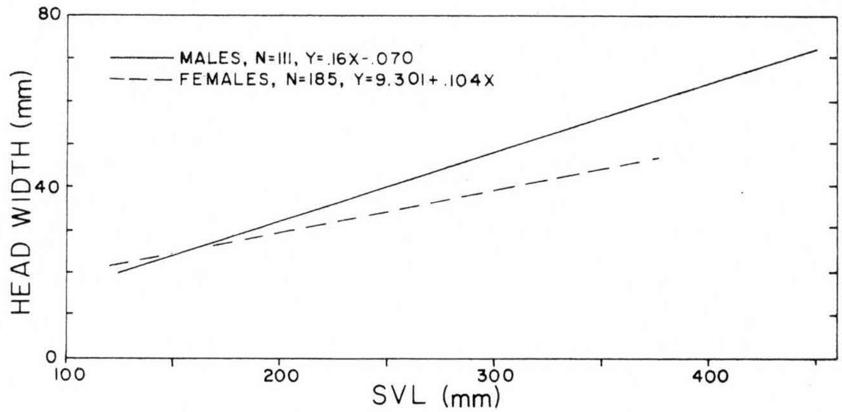

FIGURE 6. Head width as a function of snout-vent length in male and female ctenosaurs; it increases more rapidly in the males. Difference between the regressions is highly significant (p < .001).

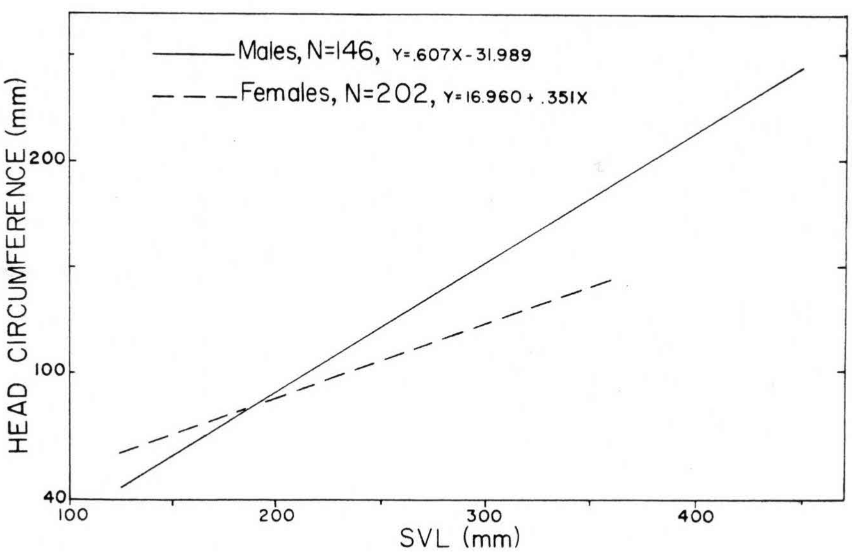

FIGURE 7. Head circumference as a function of snout-vent length in male and female ctenosaurs; like other head measurements, it increases more rapidly in the males. Difference between the regressions is highly significant (p < .001).

Discussion

As a member of the abundant lizard fauna of Central America, *Ctenosaura similis* is outstanding in several respects: giant size, relatively small hatchling size, marked size difference between adult male and female, large clutch size and limitation of reproduction to a brief breeding season. All these traits are interrelated in the intraspecific diversity that our study has revealed.

The short breeding season is adaptive in the strongly seasonal climate with a long dry season, where *C. similis* occurs. The ctenocaur's annual cycle is attuned to community phenology. Sexual size difference, with large, powerful males is correlated with a short and concentrated breeding season. For instance, the large iguanid genus *Anolis* consistently shows marked sexual size difference in those kinds that live in regions subject to seasonal drought, but in species subject to relatively aseasonal climates of rain forests and cloud forests, females approximate male size, or are markedly larger than males (Fitch, 1976). Stress involved in establishing and maintaining territory and acquiring mates in a concentrated breeding season selects for large and aggressive males. The male-female length ratio of 125% in *C. similis* is exceeded among Central American lizards only by *Basiliscus basiliscus.* Egg-laying of *C. similis* is concentrated in March (mainly the latter half) and early April. Hatchlings appear early in the rainy season, chiefly in June, when insects and succulent vegetation provide abundant food sources. The hatchling-to-female length ratio of 20.6% (57-276) is lower than in any other Central American lizard (25-45% in most). Small size of hatchling is correlated with the large number of eggs per clutch (mean 43.4, n = 69) more perhaps than in any other New World lizard.

In its large clutch and small hatchlings *C. similis* is "*r*-selected", but in delayed maturity (second year), limitation to one clutch per year, and survival for several years as an adult, it is "*K*-selected". As in the horned lizards, *Phrynosoma*, (Pianka and Parker, 1975) reproductive strategy is a mixture of *r*-selected and *K*-selected traits. Because of its "*r*-selected" traits the species is remarkably resistant to exploitation by humans. Despite relentless hunting it is the chief surviving game animal in some parts of Nicaragua, but in recent years its populations have undergone drastic reduction. Conservation measures are much needed.

Acknowledgments

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