Especially males are not always grayish or blackish. This male was amazingly colorful, looked freshly shed, and his skin displayed a pearlescent quality in bright sunlight.

Distribution and Habitat Utilization of *Ctenosaura bakeri* on Utila

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Photographs by the author except where indicated.

Abstract.—Ctenosaura bakeri, endemic to Utila (Honduran Bay Islands), is one of only two reptiles that are exclusive mangrove dwellers. With a total distribution of 1091 ha, the total size of the three mangrove areas on Utila, this species has the smallest range of any in the genus. Distribution of three species of mangroves is not homogenous in any of the three areas. Also, effects of tides and salt content vary substantially over place and time. I collected and marked 171 iguanas at three study sites. The most animals (107) were caught at the Iron Bound site, fewer than half that many (40) were caught at Big Bight Pond, and only 24 iguanas were caught at Blue Bayou. Adult iguanas totaled 125, 2.7 times the number of subadults (46). Population densities were 63 adults per ha or 103 iguanas (adults + subadults) per ha (Iron Bound), 37 adults or 39 iguanas per ha (Big Bight Pond), and 20 adults or 24 iguanas per ha (Blue Bayou). Recaptures of marked iguanas numbered from 1–14 and generated 123 distances moved involving 52 individuals (25 females and 27 males). Five animals were recaptured exclusively at initial capture sites and most (56 %) moved < 20 m from the site of initial capture. Distances moved were greater in males than females. Time between first capture and last recapture ranged from 10–323 days. Sex specific differences were not evident. The primary factor controlling population density was the abundance of tree hollows, used as retreats and found primarily in larger Black Mangroves (*Avicennia germinans*). These were inhabited for at least four years, regarded as territory year-round, and aggressively defended. Estimates, made using two different models, of total adult population size for the entire island were 21,820–73,097 and 38,185–85,098.

Key Words: *Ctenosaura bakeri*, Utila, Honduras, Bay Islands, Mangroves, Population size, Habitat association

The utilization of mangroves as preferred habitat has a certain exclusivity within the Iguanidae and also (as far as we know) within the class Reptilia. Certain reptiles appear frequently in mangrove habitat, but these are typically temporary visitors from marine (e.g., *Crocodylus acutus*) or terrestrial habitats (e.g., *Boa constrictor*). Even species often designated as mangrove specialists, such as the Mangrove Skink (*Emoia atrocostrata*), the Mangrove Monitor (*Varanus indicus*), and the Mangrove Snake (*Boiga dendrophila*), also inhabit terrestrial habitats such as rocky coastlines and tropical rainforest (Alcala 1986, Manthey and Grossmann 1997). In contrast, the Utila endemics *Ctenosaura bakeri* (commonly known as the "Swamper")and *Norops utilensis* are exclusively mangrove-dwelling lizards (Gutsche et al. 2004, Köhler 1996). From evolutionary and ecological perspectives, inhabiting mangroves entails some very specific adaptations of diet, behavior, and resource utilization.

Male *Ctenosaura bakeri* reach a total length of over 800 mm, snout-vent length (SVL) of 315 mm, and a weight around 900 g. Females are about 30% smaller. Adult males have a well-developed dewlap (up to 30 mm long) and a prominent dorsal crest consisting of up to 56 dorsal spines (each to 25 mm in height); both are less developed in females. Body coloration of adults varies from an inconspicuous grey-brown to bright turquoise blue. The body is generally patternless, and dark shading and dark lateral crossbands are only rarely distinguishable. In contrast, the tail has distinct dark crossbands. The dorsal crest of males consists of white and black spines arranged in alternating groups of two or three of the same color. Juvenile *C. bakeri* are uniformly blackish brown to grey-brown in color with dark brown crossbands on the dorsum and dorsal surface of the tail. This juvenile coloration varies notably from that of many other Spiny-tailed Iguana species, whose young display green or yellow-green pattern elements or are entirely green in color (Köhler 2002).

Isla de Utila belongs to the small Caribbean island group known as the Islas de la Bahia and lies in the Gulf of Honduras,

Swamper habitat in a Black Mangrove (*Avicennia germinans*) stand near Iron Bound Lake. Note the finger-like aerial roots emerging from the water in the foreground.

Adult males are impressive. They can grow to a total length of 80 cm and weigh more than 900 g. Dorsal spines are not always held erect like those of Green Iguanas, but they can be erected for advertisement or aggressive displays.

about 30 km off the Honduran coast. The maximum length of the 41.4-km^2 island is 13 km, the maximum width is 4.6 km. Utila is of coralline origin and lies on a base of metamorphic rock. The island has very little relief, rising only slightly from west to east. Large portions of the island are flat and lie only a few meters (or in the case of the mangrove swamp areas, only a few centimeters) above sea level. The only two areas with more substantial topography are both in the eastern region. The remainder of the erstwhile volcanic crater, Pumpkin Hill, at 74 m above sea level, is the highest elevation on Utila, although it covers only a small area. The considerably larger area of the 51-m high Stuart Hill extends as a hilly landscape from the settlement at East Harbor (Utila Town) and runs about two kilometers to the north. Also significant to the makeup of the island is the canal, which was excavated in the 1950s as a connection between the south (Oyster Bed Lagoon) and north coasts (Rock Harbor) for small fishing boats and to provide easier access to the north side.

The climate of Utila has relatively constant temperatures throughout the year and distinct rainy and dry seasons. The rainy season begins around the end of August and extends to the end of February. The rainiest months are October and November, in which more than half (58%) of the annual precipitation falls. At this time, the northeast trade winds can form hurricanes over the central Caribbean, and these are known to pass over the island at irregular intervals (e.g., Hurricane Marco, November 1996; Hurricane Mitch, October 1998). The dry season, with monthly precipitation < 100 mm/m^2, starts in early March and lasts until the end of July, sometimes to mid-August. The months of March and April are driest.

The average monthly temperature is relatively constant with a mean annual temperature of 26.3 ± 1.9 °C. The lowest temperatures occur during the rainy season. The absolute daily temperatures during this period vary between 19 (night) and 29 °C (day). Starting in March, the weather conditions change. As the frequency of precipitation decreases, the mean daily temperature increases slightly, fluctuating between 23 and 32 °C, with the highest monthly mean in August (28.6 °C). The relative constancy of Utila temperatures can be attributed to its location in the tropics and the moderating effect of the surrounding Caribbean Sea.

Utila lies in the range of semi-evergreen, tropical tradewind forest. Leaf loss and blossoming of the uppermost canopy layers are tied to the summer dry season, whereas the lower levels remain largely evergreen (Walter and Breckle 1999). The vegetation of Utila is remarkably diverse, considering the small size of the island and the limited relief. Also notable is the clear separation of the various vegetative communities. Extensive transition zones are absent. The island can be divided roughly in two parts: The higher-lying eastern part with the remains of semi-evergreen tradewind forest and the larger, flatter western part, which is dominated by mangroves and wet savannah.

The mangroves on Utila make up one of the most important, but azonal (i.e., not linked to climate zones) vegetative communities (Walter and Breckle 1999). Their occurrence is much more strongly tied to the presence of salt and/or brackish water in the tidal zone. Strictly speaking, genuine mangrove habitat (Hogarth 1999) is characterized by the following criteria (Tomlinson 1986): (1) They are woody tree species, whose occurrence is restricted to mangrove habitat where they can form

These photographs of Iron Bound Lake during high and low tides demonstrate the extreme and dynamic nature of Swamper habitat.

stands; (2) Stands are periodically flooded by salt water; (3) The mangrove species have both physiological and morphological adaptations to their habitat, e.g., mechanisms for salt elimination and pneumatophores (erect roots that rise above the soil or water and promote gas exchange). Mangroves on Utila are surrounded in some areas by mangrove-accompanying flora, which has a transitional character between the genuine mangrove and the bordering vegetation. This flora includes species that are not found in pure mangrove habitat and have only limited tolerance for salt water and flooding. Adaptations, such as pneumatophores and salt glands, are lacking in these species.

Materials and Methods

Field studies occurred mainly in two phases, from 27 June 1999 until 17 July 2000 and 1 January to 31 December 2001, allowing examination of distribution, abundance, and population structures within a complete yearly cycle.

Due to the arboreal lifestyle of *C. bakeri* and the fact that the ground beneath the trees was usually submerged, trapping, as suggested for other large lizards (e.g., *Varanus niloticus* and *Iguana iguana*; Lenz 1995, van Marken Lichtenbelt and Alberts 1993), was not possible. In addition, traps would be in constant danger of plundering by poachers. Nighttime capture (as with *I. Iguana* and *Amblyrhynchus cristatus*; Boersma 1982, Harris 1982) is also not possible, because these lizards spend the night in largely inaccessible tree hollows. Consequently, animals were captured by hand with the aid of a noose. This was facilitated by a particular behavior of *C. bakeri*. Although many animals would flee at the approach of humans, some would remain motionless on their perches, bodies pressed against the branch.

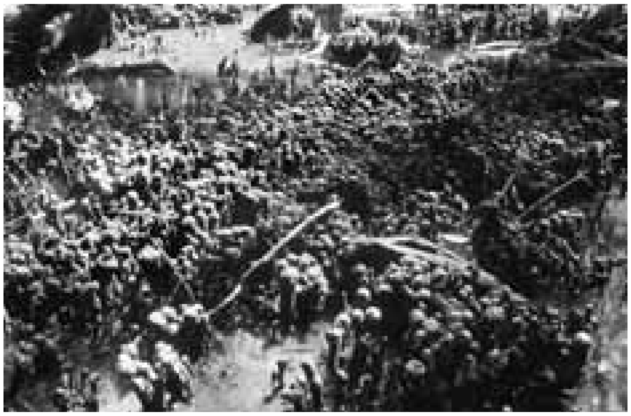
I climbed trees to 17 m in height, using a 3-m-long catchpole equipped with a self-closing noose. I used 2–3 mm strong, smooth cord for adult iguanas and waxed dental floss for lighter juveniles. Once noosed, a secure grip behind the head would calm the animal, which was then transferred into a sturdy cloth bag and passed to a second person on the ground. Handling time between capture and removing the noose was generally less than one minute.

Following capture, I examined, measured, and marked each iguana. This task was facilitated by the lethargic behavior individuals generally began to exhibit once caught. I recorded biometric data, sex, any special characteristics, cloacal and ambient temperatures, and the identification code. Two types of marking were used; a permanent code by removing some dorsal spines, and a temporary lateral color code for distance recognition. I also noted the exact circumstances of capture, such as the location and time, tree criteria (e.g., the presence of a hollow retreat or basking perch), exact position of capture, and the current weather conditions. Data collection and marking required about 15 min. Subsequently, each iguana was released in the tree from which it was taken.

Results

Ctenosaura bakeri exclusively inhabits the genuine mangrove swamps and iguanas occurred in all areas with mangrove stands. Individuals might inhabit an appropriate tree in mangrove-bordering vegetation, which would only occasionally be influenced by tides; however, this tree would always be within a few meters of true mangrove habitat. Because the mangrove areas are clearly differentiated from the bordering vegetative communities and transition zones rarely extended more than a few meters, the habitat of *C. bakeri* was essentially congruent with areas covered by mangrove.

The brackish mangrove swamps form a permanent part of Utila's wetland and cover about 30% of the island. Large portions of Utila's west side are covered with the non-permanent wet savannah, a unique and fascinating landscape rarely seen on the mainland because of deforestation and draining of land. The wet savannah is covered with up to 30 cm of fresh water during rainy seasons and completely dry during dry seasons. The primary vegetation is reed grass, small palm trees, and shrubs; carnivorous plants are common in some spots.



Knob-like aerial roots of the White Mangrove (*Laguncularia racemosa*). The most striking feature of mangrove trees is the aerial roots, which are essential for the trees to breathe in the saturated soil.

ALEXANDER ARZT

To catch the Swamper, the author had to climb as high as 15 m into the trees with his catchpole and noose loop.

The total distribution area of *C. bakeri* consisted of three separate mangrove areas not connected by corridors of mangrove or mangrove-bordering vegetation. The smallest of these areas (115 ha) is on the eastern part of the island. It extends around Big Bight Pond between the settlement at Utila Town and Utila's eastern coast. Another area lies in the central part of the island and extends from the northern coast of Utila at Rock Harbor and Iron Bound along the canal to Oyster Bed Lagoon in the south and from there first to the west and then north to Turtle Harbor Pond. With a total area of 612 ha, this is the largest stretch of habitat. The third area is in western Utila and has an area of 364 ha. It extends from the southern coast at Aliah Channel in a northeasterly direction as far as the north coast at Turtle Harbor, where it splits into two small stretches, one east along the coast at Turtle Harbor and the other west as far as Don Quickset Bay. The total size of the three mangrove areas is 1091 ha or 10.91 km^2 and comprises 26.6 % of Utila's total land area.

Three mangrove species occur on Utila: Black Mangrove (*Avicennia germinans*, Verbenaceae), White Mangrove (*Laguncularia racemosa*, Combretaceae), and Red Mangrove (*Rhizophora mangle*, Rhizophoraceae). The three mangrove species display no particular distribution pattern on Utila, across the island and within individual stands. In principal, the following formations could be identified. A large portion of mangrove stands was composed of a mix of the three species with mean tree height of 8–10 m. The mixture of mangrove species was not homogeneous, instead *R. mangle* predominated and small groups of the other two species were interspersed in a mosaic pattern. One other formation was characterized by the clear dominance of one of the three species, with the non-dominant species scattered individually. Tree height was highly variable. For example, in the area of Oyster Bed Lagoon, stands were dominated by *R. mangle* with a mean height of 3 m, whereas the two interspersed species reached heights to 6 m. In contrast, stands in the area around Iron Bound Lake were dominated by *A. germinans* that reached heights to 12 m, whereas the interspersed species reached only 3–5 m. Stands consisting of only one of the three mangrove species were both rare and small. Trees within these stands were mostly very old, massive, and tall. Examples include *A. germinans* west of Oyster Bed Lagoon (to 17 m), *R. mangle* on the banks of Turtle Harbor Pond (to 15 m), and *L. racemosa* north of Aliah Channel (to 20 m). Several mangrove lakes, such as Iron Bound Lake, occurred in all areas. These are open basins with isolated mangrove islands and often only temporary drainage. Noteworthy was a high proportion of dead mangroves inside of the lakes.

The periodic flooding (tide) of the mangroves on Utila occurs over lagoons (e.g., Oyster Bed Lagoon) and canals as well as over the coralline, highly porous ground, which is filled with an extensive network of cavities (J. Grant, USAID, pers. comm., 2001). According to my measurements, the normal tidal rise along the coast was about 300 mm, in the mangrove areas in the interior of the island only 30–50 mm. Only mangrove areas close to the shore are subjected to periodic tides throughout the year. Areas far from shore were extremely dependant on precipitation-related flooding. During the rainy season, these areas, depending on relief, would be covered by up to 800 mm of floodwater. During the dry season, water levels would be

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One of the essential requirements for Swampers is a refugium. Tree hollows are necessary for mangrove dwellers unable to dig holes in the ground. Older Black Mangroves (more often than the other mangrove species) offer hollow trunks and branches. From our studies, we were able to conclude that a high incidence of older Black Mangroves (with the Swamper's preferred tree hollows) correlated with higher population densities of Swampers. Without a compelling reason to seek a new home (outgrowing a current one or destruction of a tree by a hurricane or poachers), Swampers may stay in the same tree for years.

Swamper habitat in a White Mangrove stand near Iron Bound Lake. "Mangrove" is a generic name for an intertidal forest.

reduced to a few centimeters or nothing. Occasionally even the flatter mangrove lakes would be completely dry for long periods of time. When the spring tides came, the tidal rise along the coast measured about 600 mm. Mangrove areas that had dried up completely were flooded within a few hours without any precipitation.

Salt content of the mangrove areas varied considerably and was inversely proportional to the yearly distribution of precipitation. During the winter rainy season, brackish water in the mangroves is diluted by precipitation. Beginning at the onset of the dry season, the salt content increased over the course of the summer, sometimes substantially exceeding that of the ocean. Also, heavy rains spontaneously decreased concentrations.

Capture-recapture Study.—The following data pertain largely to adults. Wherever relevant, data from juvenile animals is included, although detailed conclusions were not possible due to the nature of the data. Animals with an SVL > 150 mm were designated as adults and smaller animals as subadults.

I collected and marked 171 iguanas at three study sites, each about one ha in size, over a period of 11 months. The most animals (107) were caught at the Iron Bound site, fewer than half that many (40) were caught at Big Bight Pond, and only 24 iguanas were caught at Blue Bayou. Adult iguanas totaled 125 individuals (73.1 %), 2.7 times the number of subadults (46 individuals, 26.9 %). Similar adult-biased ratios occurred at all three study sites: 1.00:0.20 (Blue Bayou), 1.00:0.05 (Big Bight Pond), and 1.00:0.60 (Iron Bound). Population densities were 63 adults per ha or 103 iguanas (adults + subadults) per ha (Iron Bound), 37 adults or 39 iguanas per ha (Big Bight Pond), and 20 adults or 24 iguanas per ha (Blue Bayou).

Variation in population density was closely correlated with the abundance of appropriate tree hollows that were used by iguanas as retreats for sleeping and hiding. Blue Bayou exhibited a comparatively small number of iguanas and a comparably small number of retreats, whereas Iron Bound had both a high density of iguanas and a greater number of retreats. Even on a small scale within study sites the distribution of tree retreats is heterogeneous. For example, in one of two 300-m^2 areas at Iron Bound, two retreats exist and were used by two adults. In the other area, of 12 retreats, only nine had adult inhabitants, while the other two were unoccupied.

The abundance of tree retreats depended largely on the presence of particular mangrove species. Within the three study sites, 31 of 945 mapped mangrove trees contained retreats. Of these, 27 (87.1 %) retreats were in Black Mangroves, four (12.9 %) in White Mangroves, and none in Red Mangroves. In relation to the number of trees of each species, 14.8 % of Black Mangroves (n = 182), 10.8 % of White Mangroves (n = 37), and none of the

Surrealistic view of a mangrove lake during low tide. Open places like this, with dead remnants of mangrove trees, are common components of Utila's swamp vegetation. The genesis of Utila's mangrove lakes is not precisely clear; they nevertheless create a fascinating landscape.

Red Mangroves (n = 726) contained retreats. The proportion of mangrove species varied among study sites. Blue Bayou was dominated by Red Mangroves with few retreats and a limited number of iguanas. Iron Bound, with a smaller percentage of Red Mangroves and an increase in Black Mangroves, had a greater abundance of iguanas (Table 1).

Space and Time Constancy.—The greater the spatial and the longer the temporal constancy of the animals locally, the more precise the estimates of population size and structure (White 1982). The measure used to determine spatial constancy for *C. bakeri* was the distance between capture and recapture location, and for temporal constancy, the time span between first and last capture or sighting. To calculate the distance covered by the iguanas, all adult iguanas with at least one recapture were considered.

The number of recaptures ranged from 1–14 and generated 123 distances involving 52 individuals (25 females and 27 males). Five animals, three females and two males, were recaptured exclusively at initial capture sites. Extreme values occurred at Iron Bound, where one male was recaptured 14 times at his original capture site and another male was recaptured twice with displacement distances of 77 and 89 m. Of the 123 distances, 50 (42.3 %, 30 females and 20 males) fell within 5 m of their first capture site. The number of recaptured animals diminished with increasing distance. Only 22 (44.0 %) captures involved distances > 20 m from the site of initial capture.

Mean distance covered, as well as the minimum and maximum values for males at both Big Bight Pond and Iron Bound were higher than for females. At Blue Bayou, no females were recaptured. Altogether, the mean distance covered by females was 8.8 m and the greatest recorded distance for any female was 36 m. With a mean of 19.6 m, the mean distance for males was 2.2 times greater than that of females. The individual time differences between first capture and last recapture for the 52 iguanas ranged from 10–323 days. Seven (13.5 %) animals were recaptured within one month, 29 (55.8 %) animals within to six months, and 16 (30.8 %) animals within 7–11 months after initial capture. Sex specific differences were not evident.

Population sizes.—I selected two models to calculate adult population sizes at each of the three study sites (Table 2). Both models are extrapolations using proven statistical methods. Based on recapture data, the population numbers calculated for each of the individual study sites varied from 35–78 individuals per hectare using the first model and from 72–114 individuals per hectare for the second model. The lowest values were for Blue Bayou, the highest for Iron Bound. Based on the reality that the total distribution is small and of known size, adult iguanas display site fidelity over several years, and individual activity radii are small, I calculated an estimated total adult population size for the entire island (Table 3) as 21,820–68,733 based on actual capture data, 38,185–81,825 (model 1) and 78,552–120,010 (model 2).

Discussion

The habitat of *Ctenosaura bakeri* is limited exclusively to three disjunct mangrove areas of Utila with a total area of 1091 ha. I could not determine whether the surviving remnant mangrove areas were once contiguous. Such a scenario is quite possible given the flat topography of Utila and the variable water levels evident in the region's geological history (Perfit and Heezen 1987, Pregill and Olson 1981). Larger anthropogenic influences on the extent of the mangroves, at least in modern times, can be ruled out. Older local people claim that the current extent is the same as it was about 30–40 years ago (J. Gabourel, S. McNab, BICA-Utila, pers. comm., 2000). However, clearing and draining of small sections of mangrove around Utila Town occurred at the end of the 19th Century (Rose 1904).

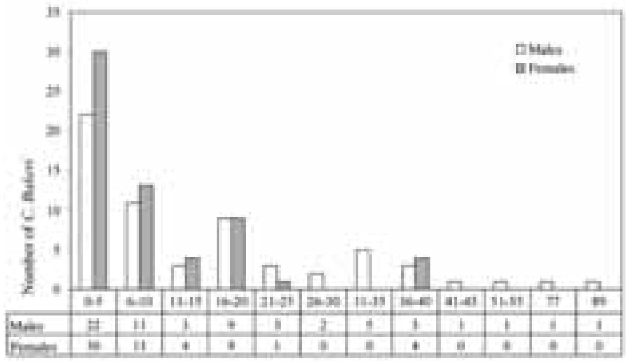
With a total distribution of 1091 ha, *Ctenosaura bakeri* has the smallest range of any species in the genus *Ctenosaura* (Köhler 2002). Only *C. nolascensis*, with a range of barely 1500 ha (Grismer 1999), comes close. Consequently, *C. bakeri* was recently upgraded to the status of "Critically Endangered" by the IUCN (Zoerner and Köhler 2004).

Habitat association.—Based on both biotic and abiotic factors, the habitat of *Ctenosaura bakeri* can be characterized as extreme. The mangroves of Utila correspond to a type of basin or inland mangrove (Hogarth 1999). Limited tidal influence and the accumulation of nutrients and sediment are typical for this type, as is the influence of local conditions such as precipitation, evap-

Table 1. Characterization of habitat relative to the abundance of *Ctenosaura bakeri* in three study sites on Utila.

High Abundance (Iron Bound)	Dominance of Black Mangrove (> 60 %) or pure stands, predominantly medium to larger sized trees (6–12 m), other species interspersed.
Medium Abundance (Big Bight Pond)	Slight dominance of Red Mangrove (ca. 50–60 %), predominantly of medium height (6–8 m), other species in small areas or interspersed in a mosaic pattern.
Low Abundance (Blue Bayou)	Strong dominance of Red Mangrove (> 80 %), predominantly of low to medium height (3–6 m), other species isolated or scattered throughout.

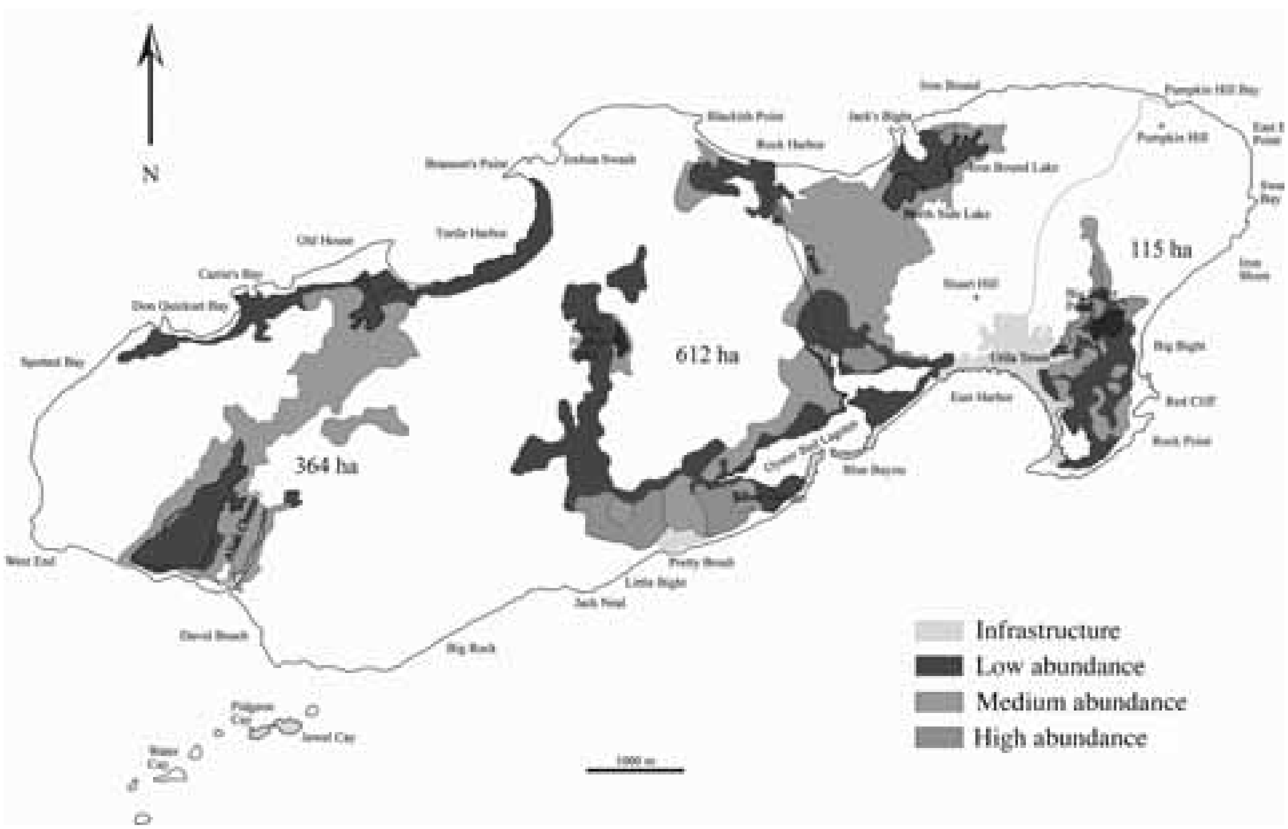
Resting volunteers in Swamper habitat in a pure Red Mangrove (*Rhizophora mangle*) stand. Surveying the Swamper population is a difficult job involving a great deal of climbing.



Distances between initial capture and recapture sites for *C. bakeri* in the three study areas. The x-axis is distance (m).

oration, and the flow of ground water, which collectively result in enormous fluctuations of salt content. Such abiotic conditions have a crucial influence on the distribution of individual mangrove species (Hogarth 1999, Tomlinson 1986) and may be responsible for the heterogeneous composition of Utila's mangroves.

The reasons for *Ctenosaura bakeri* adapting to specialized mangrove habitats on Utila are unclear. The species probably evolved from mainland-based ancestors. Potential ancestors may include the same ancestors as for *C. melanosterna* and *C. palearis*. *Ctenosaura similis*, which also occurs on Utila, belongs to a different subgenus (Buckley and Axtell 1990, Köhler et al. 2000, Köhler 2002). Access to the island may have involved over-water dispersal during hurricanes, as is known for *I. iguana* in the Lesser Antilles (Censky et al. 1998), or a landbridge to the mainland during the last ice age (Perfit and Heezen 1987, Pregill and Olson 1981). Two possible explanations for the habitat associa-



Hypothetical abundance of *C. bakeri* on Utila.

Table 2. Hypothetical total population of adult *Ctenosaura bakeri* on Utila. Calculations reflect extrapolations from actual capture data and from models 1 and 2.

Study Site	#/ha (capture data)	#/ha (model 1)	#/ha (model 2)	Total Population Estimates (1091 ha)
Blue Bayou	20	35	72	21,820 / 38,185 / 78,552
Big Bight Pond	37	43	70	40,367 / 46,913 / 76,370
Iron Bound	63	75	110	68,733 / 81,825 / 120,010

Table 3. Population density estimates of adult *Ctenosaura bakeri* in the individual study sites based on recaptures of marked animals. Data are from two different models. Each value is presented ± one standard error (SE), followed by the 95 % confidence interval in parentheses.

Study Site	Model 1	Model 2
Blue Bayou	35 ± 9 (26–65)	72 ± 20 (45–129)
Big Bight Pond	44 ± 3 (41–55)	72 ± 15 (53–117)
Iron Bound	78 ± 5 (73–91)	114 ± 16 (93–155)

tion include forced adaptation, since mangrove swamps largely covered Utila at the time of speciation, or, more likely, ecological exclusion from other habitats that had been successfully colonized by *C. similis* and *Iguana iguana*. Niche partitioning would account for the coexistence of three species of large iguanas in a limited area, a situation unique to Utila, the only known location with more than two sympatric, naturally-occurring species of iguanas.

Population density.—The high population densities within my three study sites (24, 39, 103 individuals/ha) was comparable to findings from three other sites where Kuttler (2000) found densities of 27, 39, and 50 individuals/ha. In contrast, studies of other large iguana species in areas not threatened by hunting often found lower population densities, e.g., 5.1 individuals/ha for *Ctenosaura similis* (Case 1982, Fitch and Henderson 1978), 1.5–17.7 individuals/ha for *Iguana iguana* (Muñoz et al. 2003, Van Devender 1982), and 12.4 individuals/ha for *Sauromalus varius* (Case 1982). High population densities seem to correlate with a high proportion of juveniles, mainly because adults are territorial and usually protect large individual territories (Fitch 1973, Fitch and Henderson 1978). This would account for isolated high population densities of *C. similis* (139.2 individuals/ha) and *I. iguana* (100.5 individuals/ha), where the proportion of adults was only 10 % (Van Devender 1982).

In contrast, the average proportion of adult *Ctenosaura bakeri* in all six study sites (this study and that of Kuttler 2000) was 77.6 ± 11.3 % (62.6–95 %) and all available personal observations indicate that the animals are territorial throughout the year. An explanation for the high density of individuals would be the favorable distribution of limited resources, e.g., suitable retreats for hiding and sleeping (Duellman and Duellman 1959, Fitch and Henderson 1978, Köhler 2002). Where retreats were abundant locally, high concentrations of individuals were observed, e.g., for *C. similis* (Fitch and Henderson 1978). Similar correlations seem to exist for *C. bakeri*, as the number of tree-hole retreats corresponds to abundance. The behavior of *C. bakeri* confirms the significance of suitable retreats. Retreats were inhabited exclusively for at least four years, regarded as territory year-round, and aggressively defended. Retreats were found predominantly in *Avicennia germinans*, usually in older trees. This is due to core rot, which begins in early stages of growth. The correlation between the number of retreats and iguanas and the obvious significance of suitable retreats thus appears relevant for extrapolating the total distribution area of *C. bakeri*.

During the capture-recapture study, adults displayed site-fidelity and remained predominantly within a radius of about

Typical view of a Swamper, high in a tree, difficult to see, and almost impossible to reach. When it is too late for them to hide in holes (as in this picture), they rely on crypsis by pressing their bodies against a branch and remaining motionless.

In the face of any threat (in this case, the author), Swampers move behind branches and carefully assess the risk while relying on crypsis and lack of motion to prevent detection. Such "squirreling" behavior is not uncommon among iguanian lizards..

Another avenue of escape is to jump from a tree and dive or swim away from the threat. In this case, the male jumped from about 10 m when the author tried to catch it, but Iron Bound Lake was too shallow and it could not escape.

20 m from their home tree. Suitable retreats continued to be inhabited even past the 11-month study period. Of 29 animals recaptured in Iron Bound during the course of the study, 17 were recaptured at the same home tree in later control captures after periods of 410–1305 days. Behavioral observations in 2001 (in Iron Bound) additionally showed that individuals not recaptured during the study (1999/2000) continued to inhabit their home trees. With animals situated permanently, the basic conditions for the most precise possible calculation of the population size are satisfied (Begon 1979, White 1982). The estimated population size of 21,820–73,097 adults, in comparison to earlier population estimates of only a few hundred individuals (Köhler 1998) was surprising, although similarly high numbers (21,000–24,000) were estimated by Kuttler (2000). The earlier lower estimate was attributable to a lack of sufficient data.

Maximum densities in the study sites had not yet been reached. New captures originated predominantly from animals that were present within the study area. This resulted in observations of individuals living in the study sites but not yet captured, as well as studies of flight behavior. When approached, over 90 % of iguanas fled into retreats. Only a few animals would remain in place with bodies held tightly against the branch and could be captured or identified. This was further verified by the low number of iguanas sighted per catch day, which ranged from 5–19 % of the total number of animals captured and the number of animals actually proven to be in the areas.

New captures were distributed over the entire catch period, so that the probability of capture was not based on time-dependant criteria. The total recapture rate (41.6 %) would have been lower if capture and marking had substantially influenced behavior. Many marked animals were recaptured during the next catch day. Personal observations indicated that some iguanas would leave their retreats within 30 min of being marked. The recapture rate of males was higher than that of females. This is probably attributable to more aggressive territorial behavior in males, and is similar to observation of male *C. similis* and *C. pectinata* (Evans 1951, Fitch and Henderson 1978).

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