

ular glands contained only round, membrane bound granules of alike or different sizes, whereas others had only aggregates of tiny acidophilic granules without membranes. However, in the majority of glands both forms of secretion were present (Fig. 1). Finally, in some glands we observed broken, empty membranes, imbedded into masses of tiny, acidophilic granules (Fig. 1). Our explanation is that small, round, membrane bound granules enlarge through accumulation until their membranes break and the tiny granules spill out as a finished secretory product.

Positive protein reaction of granular gland secretion (Table 1) for *H. nigrescens* and *O. japonicus* was the same as those reported by Dapson et al. (1974) in *R. pipiens* and by Pederzoli et al. (1990) in *B. variegata*. In hynobids the granular gland secretion is probably responsible for the noxious taste reported by Duellman and Trueb (1986) and by Daly et al. (1987). According to these authors noxious taste in various amphibians serves mainly as a defense function, causing them to be unsavory to certain predators. If here reported membrane bound granules in which the core stains stronger than the periphery and those which stain uniformly are two chemically different secretions and if their changes in staining properties represent different stages of their maturation cannot be decided by this study.

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### Body Size, Spatial Distribution, and Microhabitat Use in the Caimans, *Melanosuchus niger* and *Caiman crocodilus* in a Peruvian Lake

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Although the black caiman, *Melanosuchus niger*, and the spectacled caiman, *Caiman crocodilus*, have overlapping distributions throughout much of the Amazon basin, ecological relationships between these conspicuous top predators are poorly understood. Both species favor quiet waters, and they can be found together in rivers, lakes, and canals throughout Amazonia (Medem, 1971; Magnusson, 1985). Like other crocodylians, both *M. niger* and *C. crocodilus* are generalist carnivores. They eat terrestrial invertebrates when young, and switch to molluscs, fish, and some terrestrial vertebrates as they grow (Magnusson et al.,

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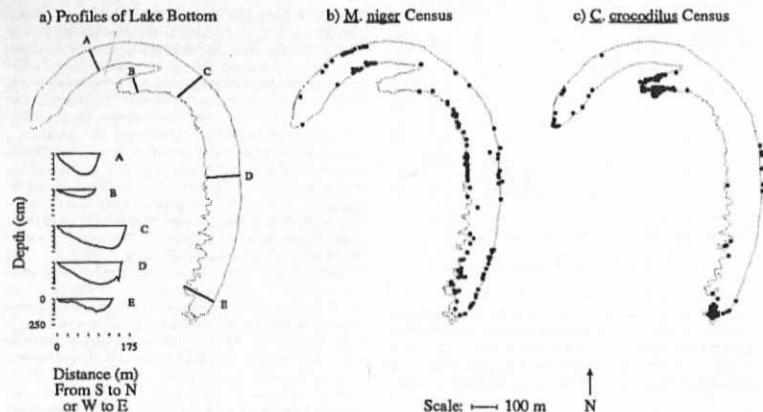


FIG. 1. a) Map of Cocha Cashu with water depth transects. I prepared this map by plotting the relative locations of 146 landmarks by compass triangulation and drawing the shoreline between them "by eye." For each transect, I stretched a rope across the lake and used a ruled pole to measure the water depth at 5 m intervals along the rope. b and c) Locations of *Melanosuchus niger* (N = 111) and *Caiman crocodilus* (N = 97) in Cocha Cashu during census on 16-18 October 1983. I mapped the locations of the caimans by ascertaining "by eye" their positions relative to the landmarks used in preparing the lake map.

1987). Despite these similarities, it is unknown whether and to what extent *M. niger* and *C. crocodilus* compete, and thereby affect each other's abundance and distribution. This paper documents ecological differences between the two caimans, as a step toward understanding the mechanisms through which they may interact.

Magnusson (1985) found that sympatric *M. niger* and *C. crocodilus* occupied different microhabitats. *Melanosuchus niger* occurred most commonly near steep banks with little floating grass, while *C. crocodilus* occurred most frequently in shallow or grassy areas. Because *M. niger* were rare in the areas Magnusson surveyed, the generality of this observation is difficult to assess. Unfortunately, *M. niger* are rare or locally extinct throughout most of their original range, largely because they have been hunted for several decades for their hides (Groombridge, 1982; Magnusson, 1982a; Plotkin et al., 1983; Rebelo and Magnusson, 1983). This reduction of the *M. niger* population has severely limited opportunities to study the comparative ecology of *M. niger* and *C. crocodilus*. The data I present here suggest that Magnusson's (1985) observations of microhabitat differences between *M. niger* and *C. crocodilus* are indeed general. I studied *M. niger* and *C. crocodilus* in Cocha Cashu, a small lake in Peru's Manu National Park. Manu Park is among the few areas where *M. niger* remains abundant (Plotkin et al., 1983; Jahoda, 1990), and where the comparative ecology of *M. niger* and *C. crocodilus* can be studied in an approximately pristine state.

Cocha Cashu (Fig. 1a), an oxbow formed by the Manu River, is located at 11°51'S, 71°19'W in the Am-

azon drainage of SE Peru. The lake covers approximately 20 ha and has about 4000 m of shoreline. The northern and eastern edges of the lake have steeply sloped bottoms, and are shaded by tall vegetation which grows on the bank and overhangs the water. The southern and western edges have gradually sloped bottoms, and are covered with grass and low vegetation growing on the bank and in the water. The three ends of the lake are shallow and marsh-like, with grass growing on the bank and in the water.

Although Cocha Cashu is about 400 m from the Manu River, the caimans in the lake belong to larger Manu basin populations. Large caimans may travel between the lake and the river via the stream beds that run from the ends of the lake to the river. Even small individuals probably can enter and leave the lake during periods of high water. In October 1982, for example, the entire Manu meander belt flooded, and Cocha Cashu temporarily ceased to exist separate from the river.

I worked at Cocha Cashu from June through November 1983 and from May through August 1984. The lake and surrounding forest have been protected since 1970 and have been part of Manu National Park since its establishment in 1973 (Terborgh, 1983). Some caiman hunting, selective tree cutting, and rubber trapping occurred before 1970 (Rios et al., 1986), but the region is essentially pristine.

I censused caimans in Cocha Cashu by direct night counts from a hand-paddled kayak, using binoculars and a headlamp to spot animals (Woodward and Marlon, 1979; Magnusson, 1982b). When viewed as they float in the water, *M. niger* appear to have boxy heads,

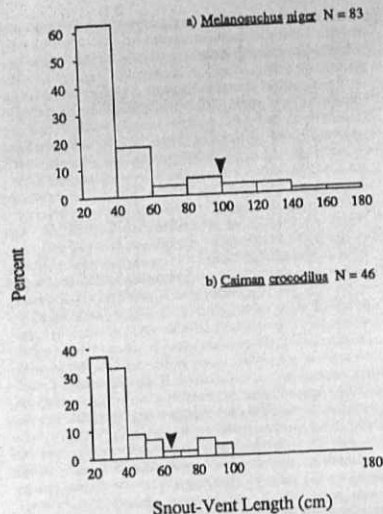


Fig. 2. Size frequency histograms for (a) *Melanosuchus niger* and (b) *Caiman crocodilus* captured in Cocha Cashu from June 1983 to August 1984. The black arrowheads indicate the sizes at which *M. niger* and *C. crocodilus* are thought to mature (Brazaitis, 1973; Staton and Dixon, 1977).

flat eyelids, and shorter snouts with smaller and less elevated nostrils, while *C. crocodilus* have sloped heads, pointed eyelids, and longer snouts with larger and more elevated nostrils. Using these differences I was able to identify to species approximately 95% of the caimans I sighted. I conducted censuses on 6–8 October 1983, 16–18 October 1983, and 24–28 August 1984.

Each census included more than one night. *Caiman crocodilus* and small *M. niger* (snout-vent length < 80 cm) appeared to be site faithful enough that I could census sections of the lake on different nights without recounting individuals. By the end of my study this impression had been confirmed by more than 400 sightings and recaptures of 47 marked *M. niger* and 17 marked *C. crocodilus*. Large *M. niger* can be quite mobile, so when counting them I covered the entire lake in one night. The number of crocodilians counted in a census varies with water level, temperature, and other factors (Woodward and Marion, 1979), so I regard my counts as minimum estimates of the population sizes.

For statistical evaluation of spatial segregation of the two caiman species I recorded nearest-neighbor relationships during the census on 16–18 October 1983 and the census on 24–28 October 1984. As I scouted the perimeter of the lake counting caimans, I scored each one as either a focal individual or as the nearest

neighbor of the previously scored focal. I scored each caiman only once. I included all individuals I spotted, except those I could not identify to species and those that were so far from the nearest unscored animal that several already scored individuals were closer. I used G tests to determine whether the species of a focal individual was associated with the species of its nearest neighbor.

During the 1984 census I noted vegetation types near each caiman sighted. I classified habitats by eight categories (open water, bare bank, overhanging trees and bushes, trees and bushes in the water, *Heliconia*, grass, *Ficus* roots, treefall), and used a Chi-square test to determine whether species were associated with particular vegetation.

I captured caimans at night by spotlighting and noosing (Chabreck, 1965; Jones, 1966) and with baited set-snare (Murphy and Fendley, 1973; Herron, 1985). I measured snout-vent lengths (SVL, tip of snout to anterior edge of cloaca) to the nearest 0.5 cm with a flexible tape. For subsequent identification I marked all caimans captured with tail tags and scute cuts (Herron, 1985, 1991).

Noosing worked well for caimans under 60 cm SVL, while set-snare were effective for caimans over 80 cm SVL. Thus, caimans between 60 and 80 cm SVL may be underrepresented in my sample. However, observations during censuses suggest that the size distributions of captured individuals (Fig. 2) are reasonable estimates of the population size distributions. For one *M. niger* I estimated SVL from weight because the SVL I recorded in the field was obviously incorrect.

I obtained an index for the steepness of the lake bottom by using a ruled pole to measure the water depth (cm) 7.5 meters from shore at intervals of approximately 25 meters around the lake. I assigned to each caiman I captured the steepness value measured nearest to the site of capture. For caimans captured equidistant from two measurement points I used the mean of the two measurements.

I used linear regression to analyze inter- and intraspecific patterns in the steepness of the lake bottom vs. body size. I used ANCOVA to show that the regression lines for bottom steepness vs. SVL for *M. niger* and *C. crocodilus* differ significantly in intercept, after first establishing that the lines did not differ significantly in slope (Kleinbaum and Kupper, 1978). I dropped four *M. niger* from the data set because I did not record their capture sites, and a fifth because its field-recorded SVL was incorrect (see above). Because the data appear to violate the assumptions of linear regression analysis (the residuals are not normally distributed and the variances are heteroscedastic) I repeated the significance tests non-parametrically using bootstrap resampling. I created 1000 replicate data sets, each time sampling with replacement 78 *M. niger* and 46 *C. crocodilus* from the original data, then performed the regressions mentioned above on each of the replicate sets.

*Melanosuchus niger* and *C. crocodilus* were abundant and present in roughly equal numbers. I found the greatest numbers of both species during the census on 16–18 October 1983, in which I counted 111 *M. niger*, 97 *C. crocodilus*, and 9 individuals whose species I was unable to determine.

*Melanosuchus niger* and *C. crocodilus* were both re-

producing at Cocha Cashu. In 1983 females of both species nested near the lake (Herron et al., 1990), and the 1984 census included 24 *M. niger* and 17 *C. crocodilus* small enough to be identified as young of the year. Juveniles were numerically dominant in both *M. niger* and *C. crocodilus*, but several adults of both species were present (Fig. 2).

Although *M. niger* and *C. crocodilus* coexisted in Cocha Cashu, I found that the two species segregated spatially (Fig. 1). *Caiman crocodilus* tended to be found in the ends of the lake, whereas *M. niger* tended to occur in the areas between. This pattern of spatial separation held in both October 1983 and August 1984.

In both nearest neighbor censuses, significantly more focal individuals had nearest neighbors of the same species than had nearest neighbors of different species, confirming that *M. niger* and *C. crocodilus* were spatially segregated. On 16–18 October 1983, 47 *M. niger* focals and 36 *C. crocodilus* focals had 39 conspecific vs. 8 heterospecific, and 29 conspecific vs. 7 heterospecific nearest neighbors, respectively ( $G = 35.73$ ;  $P < 0.001$ ). On 24–28 August 1984, 45 *M. niger* and 23 *C. crocodilus* focals had 39 conspecific vs. 6 heterospecific, and 19 conspecific vs. 4 heterospecific nearest neighbors, respectively ( $G = 32.85$ ;  $P < 0.001$ ).

*Melanosuchus niger* and *C. crocodilus* occupied the same regions of the lake in both October 1983 and August 1984. No pattern appeared in the species of a caiman vs. the vegetation at the water's edge nearby. In the 1984 census, the frequency distribution of 105 *M. niger* and 54 *C. crocodilus* across habitat types (see above) was not significantly associated with species ( $\chi^2 = 12.45$ ;  $df = 7$ ;  $P = 0.09$ ).

The slope of the lake bottom, however, yielded significant patterns both within and between species (Fig. 3). In general, I caught small (SVL < 40 cm) and medium (40 < SVL < 80 cm) *M. niger* in a variety of locations where the slope of the lake bottom ranged from gentle to moderate (steepness index 20–80), including the northern forks, the central western shore, and the southern end of the lake (Fig. 1). I caught large *M. niger* (SVL > 80 cm) almost exclusively along the eastern shore where the slope is steepest (steepness index > 80). I captured small *C. crocodilus* in the southern upper fork where the slope of the bottom is gentle, medium *C. crocodilus* along the central western shore where the slope is gentle to moderate, and large *C. crocodilus* in a variety of locations, including the steep-bottomed eastern shore. The regression lines for bottom steepness vs. SVL for the two species do not differ significantly in slope ( $F = 0.017$ ;  $df = 1,120$ ;  $P > 0.05$ ). Repeating this test by bootstrap resampling supported this conclusion: mean  $\pm$  SD of the difference in slope in 1000 bootstrap replications =  $-0.045 \pm 0.290$ , suggesting that the difference in slope is not significantly different from 0. When assumed to be parallel, the regression lines differ significantly in intercept (ANCOVA;  $F = 12.747$ ;  $df = 1,121$ ;  $P < 0.001$ ). As before, repeating this test by bootstrap resampling supported this conclusion: mean  $\pm$  SD of the difference in intercept ( $M. niger - C. crocodilus$ ) in 1000 bootstrap replications =  $-15.47 \pm 4.198$ , suggesting that the difference in intercept is significantly less than 0.

The observations reported here document coexistence of *M. niger* and *C. crocodilus* even when both are locally abundant (Figs. 1 and 2). In accord with Magnusson's (1985) observations, although they live to-

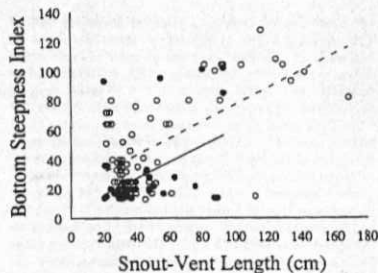


Fig. 3. Plot of the steepness of the bottom where caimans were captured vs. SVL for *Melanosuchus niger* (open circles and dashed line;  $N = 78$ ; regression line:  $y = 20.23 + 0.57x$ ) and *Caiman crocodilus* (solid circles and solid line;  $N = 46$ ; regression line:  $y = 5.70 + 0.55x$ ). Bottom steepness index is the water depth (cm) 7.5 m from shore.

gether in a small lake the *M. niger* and *C. crocodilus* in Cocha Cashu segregate spatially (Fig. 1). The spatial segregation is associated with body size and at least one component of microhabitat (Fig. 3). In both species larger individuals occur in areas where the lake bottom is more steeply sloped, but *M. niger* are found at steeper bottoms for their size than *C. crocodilus*.

The spatial segregation between *M. niger* and *C. crocodilus* in Cocha Cashu could reflect either (1) the exclusion of one species by the other from microhabitats preferred by both, or (2) an interspecific difference in microhabitat preference.

*Caiman crocodilus* appears to be an opportunistic species: it can maintain populations in disturbed habitats and areas into which it has been introduced, and may replace *M. niger* in habitats from which *M. niger* has been eradicated (Medem, 1971; Ellis, 1980; Magnusson, 1982a, 1985). Such observations suggest that *C. crocodilus* may be an ecological generalist that is excluded from some desirable habitats by a more specialized *M. niger*. *Melanosuchus niger* would seem capable of evicting *C. crocodilus* from contested areas; with a maximum size of 5 m or more, *M. niger* grows to roughly twice the length of *C. crocodilus* (Brazaitis, 1973; Medem, 1981). If *M. niger* excludes *C. crocodilus* from mutually desirable habitats in Cocha Cashu, however, direct aggression seems an unlikely mechanism. I frequently found small, and sometimes even large *M. niger* and *C. crocodilus* within a few meters of each other, but only once observed an aggressive encounter (on the night of 27 October 1983 a marked female *M. niger* [SVL = 134 cm] chased a marked female *C. crocodilus* [SVL = 75.5] out of the water at a run). Furthermore, the *C. crocodilus* at Cocha Cashu concentrate in habitats apparently similar to those in which the species concentrates even when *M. niger* are rare or absent (Magnusson, 1985; Ouboter and Nanho, 1988).

A difference in the microhabitats preferred by the two caimans is also plausible. In addition to their large difference in maximum size, *M. niger* and *C. crocodilus*

have heads of distinctly different shape. *Melanosuchus niger* has a short, broad, deep snout like the American alligator, *Alligator mississippiensis*, whereas *C. crocodilus* has a longer, narrower, shallower snout like the American crocodile, *Crocodylus acutus*. Pooley and Gans (1976) and Magnusson et al. (1987) suggested that different head shapes, which have been a recurrent theme in crocodylian evolution (Buffetaut, 1979) and are common when two species co-occur (Dodson, 1975), are adaptive for different foraging modes. Magnusson et al. (1987) hypothesized that *M. niger* and *C. crocodilus* use different foraging strategies that vary in effectiveness depending on microhabitat. At present this hypothesis cannot be evaluated because too little is known about the foraging strategies of *M. niger* and *C. crocodilus*, and about the biomechanics of crocodylian movement and feeding.

In contrast to Magnusson (1985), who found no intraspecific patterns in microhabitat use, I found that larger individuals of both species occur near steeper lake bottoms. The ecological significance of this pattern is also unclear. The habitats used by individuals of different size may reflect the relative abundances of the different prey these individuals eat. Alternatively, individual habitat preferences may be dictated by the availability of vegetative cover at the water's edge. Jaguar, *Panthera onca*, and giant otters, *Pteronura brasiliensis*, frequent Cocha Cashu and can catch large caimans (M. Brecht, pers. comm.; L. Emmons, pers. comm.). The safest place to hide from these predators may be at the water's edge under cover of vegetation, exactly where the caimans in Cocha Cashu spend most of their time. The larger the caiman, the steeper the lake bottom must be for the caiman to be both submerged in the water and hidden by the vegetation at the shore.

The comparative ecology of *M. niger* and *C. crocodilus* deserves further study. Knowledge of the ecological interactions between the two caimans has become increasingly important during recent decades as humans have altered the abundance and distribution of both species. *Melanosuchus niger* has suffered intense and widespread hide hunting, reducing it to about 1% of its abundance 100 years ago and putting it in danger of extinction (Groombridge, 1982; Magnusson, 1982a; Plotkin et al., 1983; Rebêlo and Magnusson, 1983). Although *C. crocodilus* is now hunted for its hide and is considered vulnerable to extinction, it appears to be maintaining its numbers more effectively than *M. niger* (Groombridge, 1982; Magnusson, 1982a; Rebêlo and Magnusson, 1983; Herron, 1991). The extent to which *C. crocodilus* can functionally replace *M. niger* in ecosystems from which *M. niger* has been eliminated is unclear. Also unknown is how interactions between the two species may affect *M. niger*'s ability to recover from depletion.

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### Efficiencies of Digestion and Assimilation in the Gecko *Hemidactylus turcicus*

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The gekkonid lizard *Hemidactylus turcicus* is a widespread and highly successful exotic in the United States, often occurring at high densities (e.g., Rose and Barbour, 1968). Various aspects of the ecology of these populations have been studied (King, 1958; Rose and Barbour, 1968; Trauth, 1985; Selcer, 1986, 1987; Paulissen and Buchanan, 1991), but little information relative to energetics (Selcer, 1987) is available. Here we report on efficiencies of digestion and assimilation in *H. turcicus* and compare them to those reported for various insectivorous non-gekkonid lizards.

Adult *H. turcicus* were captured 15 September 1992

in Baton Rouge, Louisiana. Geckos ranged from 45-54 cm snout-vent length (SVL) and 2.2-3.9 g body mass. Geckos were housed individually in glass jars (25 cm height × 15 cm diameter) containing wooden shelter boxes (9 × 5 × 18 cm). Water was provided ad libitum. Jars containing geckos were maintained in an environmental chamber at 27°C on a 12L:12D photoperiod. After measuring SVL and mass, geckos were starved for 3 wk and then checked for gut clearance by palpation. Each gecko was then fed one pre-weighed 3-6 wk old cricket (*Acheta domestica*) every 3 d for 70 d. All geckos fed regularly and maintained or gained body mass during the experiment (mean mass gain = 10.6%, SD = 7.2). Crickets were fed poultry pellets dusted with vitamins. Water content of crickets was determined by drying samples of at least 10 crickets each for 24 h at 60°C and subtracting the resulting mass from wet mass. Feces and solid urinary wastes of geckos were collected and pooled for each individual gecko after each feeding. Urinary wastes were manually separated from feces, and each was frozen separately until processed. Processing involved drying at 60°C for 24 h, grinding into homogenous mixtures, pressing into pellets, weighing, and then bombing the pellets in a PARR Semimicro Oxygen Bomb Calorimeter (PARR Instrument Co., Moline, Illinois). Crickets were processed likewise to determine caloric content. Dry masses of crickets, feces, and urinary wastes were corrected for ash content determined by weighing the residue remaining after bombing each sample (Smith, 1976).

Efficiencies of digestion and assimilation were calculated using the equations of Kitchell and Windell (1972) as modified by Johnson and Lillywhite (1979). Digestive efficiency (DE) is the percent of calories absorbed through the gut and is calculated as  $(C - F)/C \times 100$ , where C = calories consumed and F = calories of fecal waste. Assimilation efficiency (AE) is the percent of useable calories retained by the animal and is calculated as  $(C - (F + U))/C \times 100$ , where C = calories consumed, F = calories of fecal waste, and U = calories of urinary waste.

For crickets, mean water content was 76.7% (SD = 0.91, N = 5), mean ash content was 4.2% (SD = 1.04, N = 3), and mean caloric content was 5298 cal/g (SD = 103.6, N = 3). For 13 geckos, mean mass of crickets consumed was 1.07 g (SD = 0.070), mean mass of feces was 0.22 g (SD = 0.043), mean caloric content of feces was 3377 cal/g (SD = 203.9), mean mass of urinary wastes was 0.34 g (SD = 0.027), and mean caloric content of urinary wastes was 2470 cal/g (SD = 26.1). Mean digestive efficiency was 87.0% (SD = 2.27, range = 83.2-90.3, N = 13) and mean assimilation efficiency was 72.4% (SD = 2.13, range = 69.0-74.8, N = 13).

Efficiencies of digestion and assimilation in *H. turcicus* are similar to those reported for various other insectivorous and omnivorous lizards fed insects, including angnids, iguanids, lacertids, teiids, and xantusids (DE = 80-90%; AE = 70-80%; Waldschmidt et al., 1987). Such efficiencies in lizards may vary according to kind of food and body temperature (Harwood, 1979; Waldschmidt et al., 1987). Because our geckos could not choose either their food or body temperature as do free-living *Hemidactylus* spp. (Marcellini, 1976; Avery, 1981), the significance of our laboratory results relative to the biology of *H. turcicus* under natural field conditions is unknown.