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Habitat Selection, Parasites and Injuries in Amazonian Crocodilians

by

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Abstract

Caiman crocodilus is found most frequently in relatively warm, shallow or grassy areas in the larger rivers, lakes and canals of Amazonia. The habitats that it uses are increasing in area because of human activities. *Paleosuchus trigonatus* appears to be restricted to small forest streams in dense forest. Water temperatures are relatively low and constant in the streams and opportunities to bask are limited in the forest. *Paleosuchus palpebrosus* and *M. niger* are both found most commonly in the parts of major lakes, rivers and canals which have steep banks and little floating grass. To what extent the present distributions are influenced by intensive hunting of *M. niger* is unknown. Animals had similar injury rates in all habitats but in the Lago Amanã area individuals in the lake had higher leech, and lower nematode infestation than individuals in the surrounding canals. The giant rotifer *Limnias ceratophylli* is reported for the first time as an epizoic on the ventral surfaces of *M. niger*.

Keywords: **Crocodiles, Habitat selection, Parasites, Injuries, Amazon region.**

Resumo

Caiman crocodilus ocorre em maior frequência em áreas rasas ou em capinzais nos maiores rios, lagos e paranás da Amazônia. Os habitats usados por essa espécie estão aumentando em área por causa de atividades humanas. *Paleosuchus trigonatus* normalmente está restrito aos pequenos ribeirões da floresta densa. A temperatura da água nesses ribeirões é baixa e relativamente constante e oportunidades para insolação são escassas na floresta. *Paleosuchus palpebrosus* e *Melanosuchus niger* são encontrados principalmente nos lagos, rios e paranás grandes, que tem margens inclinadas e pouco capim flutuante. Os animais apresentavam incidência de ferimentos semelhantes em todos os habitats, mas na região do Lago Amanã, indivíduos tinham mais sangue-sugas e menos nematódeos do que os indivíduos nos paranás adjacentes. O rotífero gigante, *Limnias ceratophylli* é reportado pela primeira vez como um epizóico nas superfícies ventrais de *M. niger*.

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Introduction

The complex system of rivers, lakes and streams makes almost all of the Amazon Basin potential crocodilian habitat. However, the Basin is not uniform. The major river systems can be separated into three broad categories: (1) black water (low sediment loads, water stained brown by organic acids); (2) white water (high sediment loads, low levels of organic acids); (3) clear water (low sediment loads, low levels of organic acids). One might expect the four species of crocodilians inhabiting the basin (*Melanosuchus niger, Caiman crocodilus, Paleosuchus trigonatus* and *P. palpebrosus*) to separate into the major habitat categories, but all species can be found throughout the Basin (CARVALHO 1951). This is surprising as four species of crocodilians in apparent sympatry has not been reported for any other area.

Between 1979 and 1983 I surveyed the crocodilians in six widely dispersed areas within the central part of the Amazon basin. The primary purpose of the surveys was to establish the status of *M. niger* in those areas, but concurrently I recorded the distributions, habitat use, injury rates, and parasite loads of the three other species. *Melanosuchus niger* was rare in the areas studied (MAGNUSSON 1982), as it is throughout most of Brazil (REBÊLO & MAGNUSSON 1983), so most of the discussion relates to habitat selection by *C. crocodilus* and the two species of *Paleosuchus*.

Methods

Lago Amanã (lat. 2°30'S, long. 64°40'W) was surveyed between 24. Aug. 1979 and 29. Sept. 1979. It is a large, mainly "white-water" lake connected to the Rio Japurá near its confluence with the Rio Solimões (Amazon) by a complex network of paranás (natural canals). During the season of low water (aprox. Aug. - Dec.) the lake is shallow (< 1 m in most places) and the banks are generally shelving, with little vegetative cover. The paranás are often deeper (~2 m) during the season of low water and have both shelving and steep banks. At high water the lake and paranás have floating mats of grass along most of their banks. Water levels were relatively high at the start of the surveys but quickly dropped to the lowest levels for that year.

Lago Calado (lat. 3°15'S, long. 60°40'W) is a "white-water" lake connected to the Rio Solimões about 20 km upstream of its confluence with the Rio Negro. The lake is superficially similar to Lago Amanã, except that the paraná that connects it to the Rio Solimões is short. The banks of much of the lake have been deforested for cattle raising and shifting agriculture. However, one branch of the lake retains fairly extensive stands of regrowth forest. During low water the banks of most of the lake are shelving and muddy. During high water the banks are covered by floating grass mats, except for the narrower upstream parts of the forested branch which are lined by igapó (flooded forest). Lago Calado was surveyed between 23 and 27 March 1982.

In the Manaus (lat. 3°05'S, long. 60°00'W) area surveys were carried out in Lago dos Reis, a large "white-water" lake on an island in the middle of the Rio Amazonas, and the many small forest streams that run through the "terra-firme" (unflooded) forest which is typical of the greater part of the Basin. The lake is superficially similar to Lago Calado but lacks a narrow forested branch. The small forest streams are 0.1 - 2 m deep and are completely shaded by the forest canopy. Very little vegetation grows in the streams. Although heavy rainfall, which raises the level of water in the streams, is more common during the wet season (aprox. Nov. - April), the streams rarely overflow their banks, and they return to normal level within 24h of the rain stopping. During the wet season the streams are "black-water", but during the dry season they become clear. Lago dos Reis was surveyed 28 February 1982 and the small forest streams were surveyed at irregular intervals between 1979 and 1983.

Curuá-una is a small hydroelectric dam on the Rio Curuá-una (lat. 2°45'S, long. 55°20'W). The river was originally "black-water", but eutrophication caused by decomposition of the forest that was inundated when the dam was constructed, resulted in extensive areas of floating grass mats. At the time of the survey (30 May to 27 June 1980) there were areas of the original banks, that had deep water and were free of grass mats, interspersed along the length of the dam.

The Parque Nacional da Amazônia (lat. 4°30'S, long. 56°30'W) encompasses a variety of habitats including small forest streams similar to those near Manaus, a large "clear-water" river (Rio Tapajós), many small oxbow lakes near the river, and shallow artificial lakes caused by the construction of the Transamazon Highway. Those habitats have been described in more detail by MAGNUSSON (1982). The park was surveyed at the end of the season of low water (24 Oct. to 3 Nov. 1979).

The Archipelago Anavilhanas (lat. 2°30'S, long. 61°00'W) consists of many islands in the Rio Negro upstream of its junction with the Rio Amazonas. During the period of low water (aprox. Aug. - Dec.) the islands are surrounded by sand beaches. At the time of the survey (5 May 1982) most of the islands were submerged and they were marked only by the protruding trees which secured floating grass mats. The Rio Negro is a "black-water" river.

Representative sections of most areas were surveyed at night using a canoe and a spotlight. Small forest streams were surveyed on foot with a forehead-mounted flashlight. For each crocodilian I noted the species, an estimate of its size and the type of bank it was near. The species are easily differentiated in the field at distances less than 8 m. Bank type was characterized as steep (> 30 cm deep at 1 m from the water line), shelving (< 30 cm deep at 1 m from the water line), or covered by floating grass mats. Size estimates were corrected by equations based on a sample of the animals that were captured subsequent to the size estimate being made (MAGNUSSON 1983). The equation for *P. trigonatus* given in that paper is in error and should read : $y = -0.88 + 1.25x$. The statistics and discussion relating to the original equation are correct. My size estimates of *P. palpebrosus* are not sufficiently accurate to construct size distributions (MAGNUSSON 1983).

Animals caught in the Lago Amanã area and the Parque Nacional da Amazônia were examined for leeches, and stomach contents, removed by the method of TAYLOR et al. (1978), were checked for the prescence of parasitic nematodes. Although the actual infection rates are not known, the proportion of animals from which nematodes were retrieved gives a useful index of population stomach-parasite loads without necessitating killing the animals. Not all nematodes were identified to species but all of the nematodes collected from 12 of the *C. crocodilus* from the Lago Amanã area were *Multicaecum acuticauda.* That is a common nematode parasite of Amazonian crocodilians and it is likely that it was the predominant species in all the stomach contents.

All statistics reported in this paper are Chi-Squared analyses of contingency tables or Fisher exact tests. Significance levels for tests were 0.05, but categories were not considered similar enough to be combined unless probabilities were greater than 0.1. Animals less than 20 cm S - V length were not included in analyses as they were always encountered in groups (pods) and so cannot be regarded as independent observations.

Results

Size distributions

The distributions of estimated sizes differed among species (Fig. 1), but there were no significant differences between the estimated sizes of individuals of each species in the populations and the samples collected for analyses of parasites and injuries. Size distributions differed among habitats only for *Caiman crocodilus* ($X^2_4 = 14.313$, $P < 0.05$). However, when animals from the Parque Nacional da Amazônia were deleted from the analysis there was no significant difference among the remaining habits (Lago Amanã, paranás of Lago Amanã, Curuá-una, and Anavilhanas) ($X^2_3 = 4.622$, $P > 0.25$). There were more animals in the larger size classes in the Parque Nacional da Amazônia (Fig. 1). The smallest size class shown in figure 1 was not included in the analysis as it included hatchlings from only 4 pods.

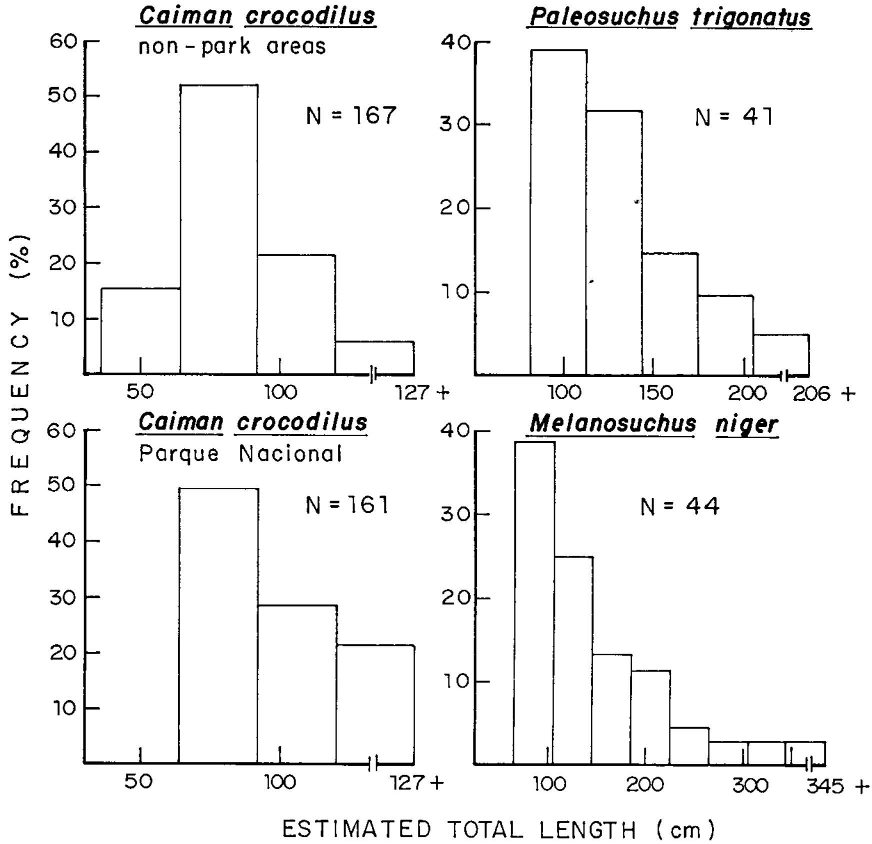

Figure 1:
Size distributions of *Paleosuchus trigonatus, Melanosuchus niger* and *Caiman crocodilus* in the areas surveyed. Original estimates were in feet. Intervals represent one foot (30.5 cm).

Sex ratios

Sex ratios of captured animals differed significantly from 1:1 for *C. crocodilus* (X_1^2 = 28.93, $P < 0.001$) and *P. palpebrosus* (X_1^2 = 6.722, $P < 0.01$) but not for *M. niger* (X_1^2 = 0, $P > 0.95$) or *P. trigonatus* (X_1^2 = 2.083, $P > 0.1$). The small sample sizes may be responsible for the lack of significance for one or both of the latter two species, as the sex ratio of *P. trigonatus* (9:3) was strongly skewed towards males as for *C. crocodilus* and *P. palpebrosus.*

There was no significant difference in sex ratio among size classes of *P. trigonatus, P. palpebrosus* or *M. niger* (Fisher's Exact Test, $P > 0.5$ in each case). However, the sex ratio of *C. crocodilus* varied significantly among size classes (X_1^2 = 6.72, $P < 0.01$). The sex ratio of animals less than 50 cm S - V length was not significantly different from 1:1 ($X_1^2 = 0.291$, $P > 0.5$), but the sex ratio of animals larger than 50 cm S - V length was significantly skewed towards males ($X_1^2 = 12.12$, $P < 0.001$). Neither the proportion of male *C. crocodilus* in each size class ($X_1^2 = 1.023$, $P > 0.5$) nor the proportion of female *C. crocodilus* in each size class ($X_1^2 = 0.023$, $P > 0.98$) differed between Lago Amanã and the paranás of Lago Amanã. Too few individuals were collected to test for differences between other habitats or within other species.

Habitat utilization

Most (80 %) *P. trigonatus* seen in surveys were in small forest streams (Table 1). As surveying small forest streams is much more difficult and time consuming than surveying other habitats this probably greatly underestimates the proportion of the *P. trigonatus* population that inhabits small forest streams. The other species were all found in large numbers in lakes, rivers and paranás, but their distributions within those areas differed according to characteristics associated with the banks. In the Lago Amanã area, where the three species were surveyed during low water, there was a significant difference between the species in the proportions of individuals adjacent to steep and shelving banks ($X_1^2 = 81.334$, $P < 0.001$). However, there was no significant difference between *P. palpebrosus* and *M. niger* (Fisher's Exact Test, $P = 0.881$) when *C. crocodilus* was dropped from the analysis. In that area, at that season, *C. crocodilus* is more likely to be found adjacent to shelving banks than the other two species.

Table 1: Numbers of crocodilians seen in each habitat.

	Species	Steep banks	Shelving banks	Grass mats	Forest streams
Lago Amanã	C. c.	1	43	4	NS
(low water)	P. p.	4	5	0	NS
	M. n.	4	1	0	NS
Paranás of	C. c.	22	42	1	–
Lago Amanã	P. p.	55	6	1	–
(low water)	M. n.	3	1	1	–
Lago Calado	C. c.	4	0	32	0
(high water)	P. p.	11	0	1	2
	M. n.	0	0	1	0
Manaus area	C. c.	–	–	38	0
(high water)	P. t.	–	–	0	32
	M. n.	–	–	0	0
Curuá-una	C. c.	0	–	8	0
(high water)	P. t.	7	–	0	2
	M. n.	0	–	0	0
Parque Nacional	C. c.	85	43	–	1
da Amazônia	P. t.	7	3	–	30
(low water)	M. n.	25	0	–	0
Anavilhanas	C. c.	–	–	28	–
(high water)	P. sp.	–	–	0	–
	M. n.	–	–	0	–

NS = habitat not surveyed; – = habitat not present in that area, at that season;
C. c. = *Caiman crocodilus;* P. p. = *Paleosuchus palpebrosus*; P. t. = *P. trigonatus*;
M. n. = *Melanosuchus niger*; P. sp. = *Paleosuchus* species

The distributions of bank types are generally clustered such that the overall distribution of crocodilians relative to bank type could be caused by some factor other than preference for bank type. A more sensitive test for differences in preferences for bank type between *P. palpebrosus* and *C. crocodilus* can be made using only data from the Paraná de Castanha, which has deep and shelving banks interdigitated at intervals of 100 m or less. Animals living in that area could chose to forage in either habitat without moving far from any important seasonal resource such as nest sites. Twelve of 13 *P. palpebrosus* were adjacent to steep banks but only 7 of 25 *C. crocodilus* were adjacent to steep banks (X^2_1 = 18.6, $P < 0.001$). Therefore, bank-type selection was not caused by differences in availability of banks.

Except for small forest streams, the banks of areas surveyed near Manaus and the Anavilhanas were completly covered by grass mats. Only *C. crocodilus* was seen in the grassy areas. *Caiman crocodilus* and *P. palpebrosus* were present in Lago Calado and *C. crocodilus* and *P. trigonatus* were present in Curuá-una. Both *P. palpebrosus* and *P. trigonatus* were found significantly more often adjacent to steep banks than *C. crocodilus* (X^2_1 = 20.8, $P < 0.001$; Fisher's Exact test, P = 0.0001, respectively), which was most common among the grass mats (Table 1). Steep banked and grassy areas were well separated in Lago Calado, but steep banked and grassy areas were so closely interdigitated in Curuá-una that individuals could easily have moved to another bank type if they wished.

Injuries

The most common major injuries were missing tails and legs (Fig. 2d), though some animals had major scarring on the trunk (Fig. 2b). There were no significant differences between size classes within species, between species, or between habitats in injury rates ($P < 0.1$ in each case).

Parasites

The proportion of individuals from which nematodes were retrieved differed between *C. crocodilus* and *P. palpebrosus* (X^2_1 = 9.88, $P < 0.005$). However, the proportion of *C. crocodilus* from which worms were retrieved differed between the lake and paraná habitats in the Lago Amanã area (X^2_1 = 9.236, $P < 0.005$). The difference between the species in apparent infection rates was much less, but still significant when only animals caught in paranás were considered (X^2_1 = 5.886, $P < 0.025$). As the growth rates of the species in the wild are not known it cannot be discounted that this is an age effect. Insufficient *P. palpebrosus* were caught to compare between habitats (Table 2).

There was a large, but not statistically significant, difference between the proportion of *C. crocodilus* with leeches and the proportion of *P. palpebrosus* with leeches (Table 2). This probably results from the significant difference in the proportions of each species in each habitat (X^2_1 = 4.3, $P < 0.05$). Significantly more *C. crocodilus* were infested with leeches in the lake than in the paranás (X^2_1 = 6.58, $P < 0.025$). Insufficient *P. palpebrosus* were collected in the lake to test for differences between habitats for that species. The analysis given above does not include hatchlings, although hatchling *C. crocodilus* were common in the lake and 2 of 11 collected had leeches. The leeches had no obvious effect on the larger animals, but the large size of the leeches relative to the hatchlings, and the fact that they generally attached to the umbilicus, delaying healing (Fig. 2c) indicates that they may affect the health of hatchlings.

Table 2: Parasite loads and injuries of crocodilians in different areas.

	Species	Leeches		Nematodes		Injuries		
		with	without	with	without	missing members	large scars	none
Lago Amanã	C. c.	8	12	1	18	5	0	22
	P. p.	1	2	0	3	0	0	3
	M. n.	1	0	0	1	0	0	1
Paranás of Lago Amanã	C. c.	2	23	11	12	9	5	28
	P. p.	0	15	13	2	4	0	15
	M. n.	0	3	3	0	0	0	3
Parque Nacional da Amazônia	C. c.	1	8	1	8	3	0	6
	P. t.	12	0	4	8	3	0	9
	M. n.	1	5	0	6	1	0	5

C. c. = *Caiman crocodilus*; P. p. = *Paleosuchus palpebrosus*; P. t. = *P. trigonatus*; M. n. = *Melanosuchus niger*.
The number of animals from which nematodes were retreived is an index, rather than an indication of absolute infection rates.

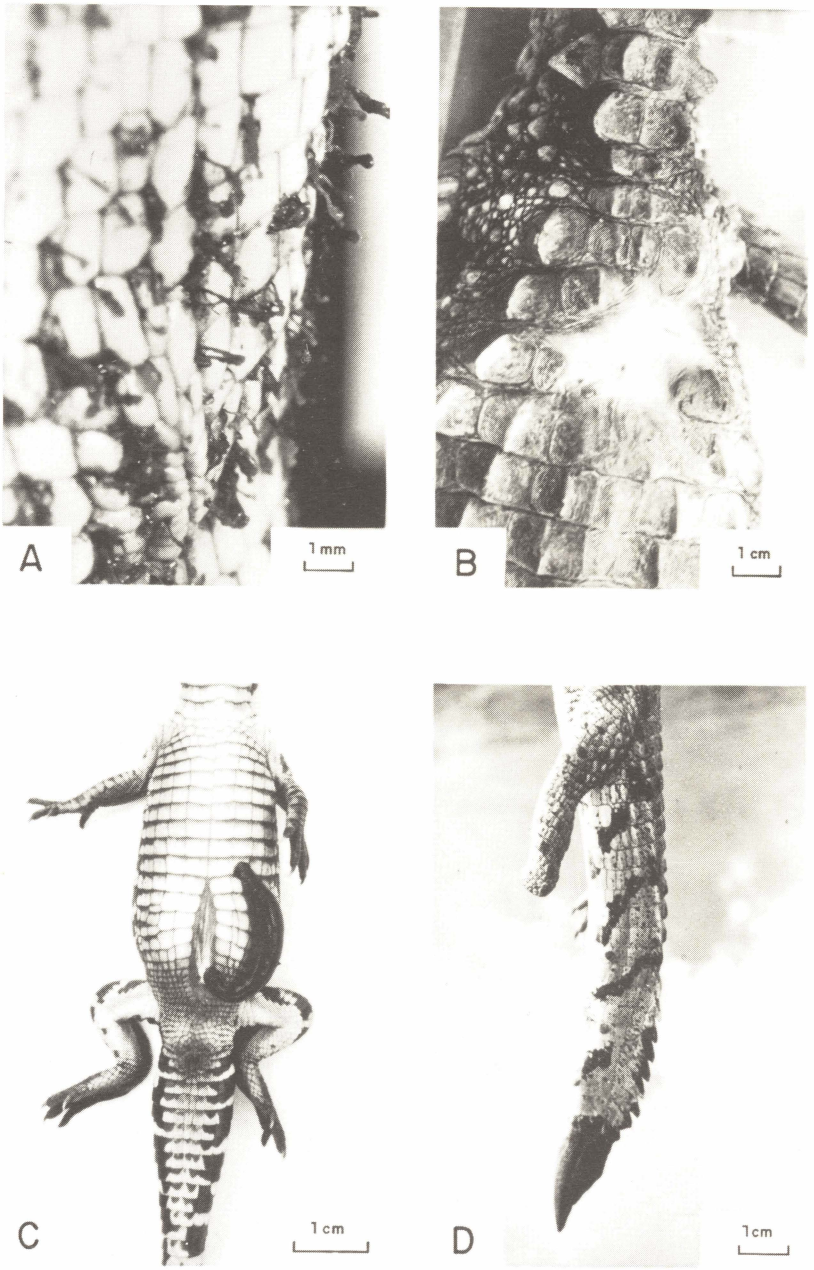

Figure 2:
A: *Limnias ceratophylli* on the ventral surface of a *Melanosuchus niger.*
B: A major scar on the trunk of *Paleosuchus trigonatus.*
C: A leech attached to the umbilicus of a hatchling *Caiman crocodilus.*
D: A *Caiman crocodilus* missing a foot and with a partially-regenerated tail tip.

In the Parque Nacional da Amazônia the relative leech loads were reversed between the two genera. In *C. crocodilus* there was only one case of infection out of nine animals examined but all twelve *P. trigonatus* were infected (Fisher's exact test, $P < 0.0001$).

Epizoics

Giant rotifers (*Limnias ceratophylli*) were found on the trunk, limbs, tail and jaws of a *M. niger* from Lago Amanã (Fig. 2a). Another *M. niger*, from the Rio Amazonas near Manaus which was given to the author, also had *L. ceratophylli* distributed over the ventral surface. That *L. ceratophylli* was found on 2 of 7 *M. niger* from the Rio Amazonas and its associated white water lakes and paranás, but not on any of the 60 individuals of other species taken nearby indicates that it may not be able to colonize other species. The two animals with rotifers did not appear to be suffering any ill effects.

Discussion

The distribution of *C. crocodilus* may be influenced by that of *M. niger* (MAGNUSSON 1982) and in areas of Colombia where *C. crocodilus* has been hunted out, *P. trigonatus* can be found in lake and paraná habitats that it does not normally occupy (Federico MEDEM pers. comm.). Also, during some seasons species may appear to be intermingled because habitat features are not obvious. Neither VANZOLINI & GOMES (1979) nor I were able to identify obvious differences in habitat selection between *C. crocodilus* and species of *Paleosuchus* when water levels were high in the Rio Japurá/Lago Amanã areas, but the species showed distinct preferences for different bank types when the water was low. The two species of *Paleosuchus* are often found together, but where one is common the other is generally rare (MEDEM 1981). Obviously, habitat preferences cannot be determined simply by noting which species are present or absent: studies will need to address specific questions and habitat preferences will have to be expressed as probability statements rather than presence or absence. A major limitation of all studies of habitat preferences reported to date, including this one, is that the researchers were primarily interested in other questions and data on habitat preferences were collected opportunistically. Below I present my interpretation of the habitat preferences of Amazonian crocodilians, not as established facts, but as hypotheses that need to be rigorously tested.

Caiman crocodilus occurs throughout the larger rivers and lakes of northern South America, but does not appear to be able to colonize the small forest streams that are typical of much of Amazonia. There are no detailed studies of the temperature relations of *C. crocodilus* but all *C. crocodilus* reported here were caught in areas with water temperatures 28° - 31°C. The water temperature in small forest streams in central Amazonia varies between 24° and 26°C (MAGNUSSON & LIMA unpubl.). STATON & DIXON (1975) reported a mean cloacal temperature of 30.0°C (25.3° - 33.0°C) for *C. crocodilus* in the Venezuelan Llanos. DIEFENBACH (1975) reported mean preferred temperatures between 29.9°C and 34.8°C (28.5° - 36.2°) depending on the size, for *C. crocodilus* in laboratory experiments. MEDEM (1981) showed that *P. palpebrosus* was more common in canals (water temperature 21° - 22°C) than in lakes where *Caiman crocodilus apaporiensis* was common (25° - 28°C). The habitat of *C. crocodilus* therefore can be typified as warm, shallow, open, muddy or grassy areas. Such areas usually have an abundance of insects which are the main food of small *C. crocodilus* (MAGNUSSON & DA SILVA unpubl.). To determine which of temperature, water depth, food availability, and interactions with other species are the most important determinants of the distribution of *C. crocodilus* will require manipulative experiments.

The distribution of *M. niger* has been changed drastically by hunting. It was once one of the most common crocodilians in Amazonia, but now is rare and patchily distributed (MAGNUSSON 1982; REBÊLO & MAGNUSSON 1983). The distribution of *M. niger* seen in the surveys reported here indicates that it prefers the deeper parts of large rivers and lakes and does not use small forest streams. OTTE (1978) found that *M. niger* occupied oxbow lakes (cochas) and *C. crocodilus* occupied the main river in the Manu National Park, Peru. The area had been free from hunting for several decades so it may have approximated an undisturbed situation. The major factors differentiating the habitats of *C. crocodilus* and *M. niger* seem to be water depth and degree of shading. Shallow water and grass mats may help *C. crocodilus* avoid larger *M. niger.*

Paleosuchus trigonatus is the only crocodilian known to use the extensive networks of small forest streams in Amazonia. This is partly due to specialized nesting behavior (MAGNUSSON et al. in press) but the species may also have physiological adaptations for a habitat which is relatively cool and in which there is little opportunity to bask. *Paleosuchus trigonatus* generally occurs in large water bodies only near the mouths of small forest streams. Such individuals may be transients, or they may be colonizing habitats from which other species have been extirpated by humans.

The data collected during the surveys reported here indicate that *P. palpebrosus* occupies parts of lakes, canals and streams that have steep sides and not covered by extensive grass mats. However, there is no indication that it can live in the permanent, small forest streams of terra firme forest. The habitats used by *P. palpebrosus* in Colombian Amazonia are similar (MEDEM 1981). In Lago Calado and Lago Amanã, where the *M. niger* populations have been reduced to remmants, *P. palpebrosus* and *C. crocodilus* appear to divide the habitat in the same way that *M. niger* and *C. crocodilus* divide the habitat in the Parque Nacional da Amazônia. The interaction between *P. palpebrosus* and *M. niger* in undisturbed habitat is potentially one of the most intersting problems in crocodilian biology but I know of no areas in which such a study could now be undertaken.

The habitats used most commonly by *C. crocodilus* (shallow, open, grassy areas) are common in areas disturbed by humans so the distribution of *C. crocodilus* has increased slightly in recent times and will probably increase much more in the future. In the Manaus area, only *P. trigonatus* occurs in small forest streams flowing through undisturbed forest. However, where the banks of streams have been cleared and erosion and pollution have caused eutrophication and growth of grass, *C. crocodilus* has entered and *P. trigonatus* has disappeared. *Caiman crocodilus* even breeds along the drainage channels in the center of Manaus, a city of 900,000 inhabitants.

In this study there were no significant differences in habitat selection between size classes or sexes within any of the species but such differences have been reported for *Alligator mississippiensis* (McNEASE & JOANEN 1978), *Crocodylus porosus* (WEBB & MESSEL 1978), and *Crocodylus niloticus* (PARKER & WATSON 1970). The present distribution of *M. niger* may be much more restricted than that before intensive hunting. The sizes of *C. crocodilus* in the Parque Nacional da Amazônia (which received partial protection from poachers for about 5 years before the survey) were significantly larger than in the other areas (which are hunted regularly). The effects of hunting are not always easy to assess so the results presented here should be treated with caution; they may not reflect the pristine state. Studies of habitat segregation by Amazonian crocodilians in areas that have never been hunted (if they exist) could be of enormous value in evaluating present distributions.

Missing members were the most common major injuries to crocodilians in this study. This probably reflects the fact that major injuries to the trunk or head are likely to be fatal. It is not possible to tell from the data whether the constant injury rate among size classes results from most attacks being directed towards small animals, from a higher death rate among animals with major deformities, or both. WEBB & MESSEL (1977) reported higher injury rates for *Crocodylus porosus* in some habitats in northern Australia but there were no significant differences between habitats in this study.

The giant rotifers found on some *M. niger* did not seem to inconvenience their host but such infestations may reduce the value of the hide. The only other epizoic reported for South American crocodilians is a protozoan (Borthicallidae) that was found on *C. crocodilus* and *M. niger* in Peru (RUESTA 1981).

Stomach-parasite infections can be linked directly to habitat selection. However, the effect of parasites on natural populations is largely unknown. It might be expected that a heavy nematode infection would reduce food assimilation and leeches are known to induce temporary eosinophilia in *Alligator mississippiensis* (GLASSMAN et al. 1979). Whether those effects are significant in the life history of the animals remains open to conjecture. The data presented here illustrate that habitat selection does have long-term, cumulative effects (nematodes through prey taken) and short term, temporary effects (leeches through direct exposure) on the populations. Other aspects such as food, opportunity to thermoregulate, and predators are undoubtedly of equal or greater importance but these aspects must await controlled experiments and the collection of more data before they can be approached profitably.

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