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Distribution and abundance of four caiman species (Crocodylia: Alligatoridae) in Jaú National Park, Amazonas, Brazil*

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* This study is dedicated to the memory of our friend,
the Brazilian herpetologist and political activist Glória Moreira [1963-1997].

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Abstract: Jaú National Park is a large rain forest reserve that contains small populations of four caiman species. We sampled crocodilian populations during 30 surveys over a period of four years in five study areas. We found the mean abundance of caiman species to be very low (1.0 ± 0.5 caiman/km of shoreline), independent of habitat type (river, stream or lake) and season. While abundance was almost equal, the species' composition varied in different waterbody and study areas. We analysed the structure similarity of this assemblage. Lake and river habitats were the most similar habitats, and inhabited by at least two species, mainly *Caiman crocodilus* and *Melanosuchus niger.* However, those species can also inhabit streams. Streams were the most dissimilar habitats studied and also had two other species: *Paleosuchus trigonatus* and *P. palpebrosus*. The structure of these assemblage does not suggest a pattern of species associated and separated by habitat. Trends in species relationships had a negative correlation with species of similar size, *C. crocodilus* and *P. trigonatus*, and an apparent complete exclusion of *M. niger* and *P. trigonatus*. Microhabitat analysis suggests a slender habitat partitioning: *P. trigonatus* was absent from river and lake Igapó (flooded forest), but frequent in stream Igapó. This species was the most terrestrial and found in microhabitats similar to *C. crocodilus* (shallow waters, slow current). *Melanosuchus niger* inhabits deep, fast moving waters in different study areas. Despite inhabiting the same waterbodies in many surveys, *M. niger* and *C. crocodilus* did not share the same microhabitats. *Paleosuchus palpebrosus* was observed only in running waters and never in stagnant lake habitats. Cluster analysis revealed three survey groups: two constitute a mosaic in floodplains, (a) a cluster with both *M. niger* and *C. crocodilus*, and another (b) with only *C. crocodilus*. A third cluster (c) included more species, and the presence of *Paleosuchus* species. There was no significant difference among wariness of caimans between disturbed and undisturbed localities. However, there was a clear trend to increase wariness during the course of consecutive surveys at four localities, suggesting that we, more than local inhabitants, had disturbed caimans. The factors that are limiting caiman populations can be independent of human exploitation. Currently in Amazonia, increased the pressure of hunting, habitat loss and habitat alteration, and there is no evidence of widespread recovery of caiman populations. In large reserves as Jaú without many disturbance, most caiman populations can be low density, suggesting that in blackwater environments their recovery from exploitation should be very slow.

Key words: Reptilia, Crocodylia, Amazonia, abundance, richness, wariness, Jaú National Park, Brazil.

Jaú National Park (JNP) is the world's largest rain forest reserve, located in Central Amazonia, in a nearly pristine condition. A declining human population of a thousand people inhabit the area and take its subsistence from the forest. Most of them live in ten small villages, and some are scattered throughout the area. Their staple foods are fish, turtles and manioc; their subsistence is supplied by products that they extract to sell. Main products are liana faggots, brazil nuts, copaíba oil, cassava flour, live turtles, aquarium fishes and timber

(Guazelli *et al.* 1998). Water bodies are predominantly poor nutrient blackwater environments that may affect plant richness and floristic composition of the igapó (flooded forest) (Ferreira 1997). The rains are abundant and the dry season short. As is common in other central Amazonia areas, the forest is flooded during rainy season and the isolated pools dry up when rains are scarce (Richards 1996).

The crocodilian assemblage is composed of four Alligatoridae species (blunt head and armoured crocodilians). Species interactions of amazonian crocodilians are poorly known and studies examining patterns of that community have controversial conclusions (Medem 1971, Magnusson 1985). Two gregarious species inhabit quiet waters of great rivers and lakes: *Melanosuchus niger* (Spix, 1825) and *Caiman crocodilus* (Linnaeus, 1758). Studies discovered that *Melanosuchus* is absent from many areas of historic distribution, and this had been related to commercial hunting (Medem 1971, 1981, 1983, Brazaitis *et al.* 1990, 1996a, b).

Two other species are the solitary, small, and heavily armoured caimans of the genus *Paleosuchus* Gray, 1862: *Paleosuchus trigonatus* (Schneider, 1801) observed in running waters and forest streams, and the dwarf *P. palpebrosus* (Cuvier, 1807) widely distributed throughout savannas and forests streams. They are sympatric species in some localities, but exclusive in other areas (Medem 1971, 1981, 1983). The thick bony plated skin of *Paleosuchus* is considered a successful adaptation to terrestrial life (Medem 1981); since it is not suitable for tanning, commercial hunting for this skin is low.

We found a rather small caiman population in JNP in a survey through different areas, habitats, and seasons. Crocodilian po-pulations of 1-10 individuals/km were more frequently reported, while very dense populations (more than 10 individuals/km) were less frequently observed in different parts of the world (see Glastra 1983, Montague 1983, Gorzula and Paolillo 1986, Seijas 1986, Bayliss 1987, Gorzula and Seijas 1989, Espinosa 1995, Brazaitis *et al.* 1996b, Mohd Sah and Stuebing 1996, Da Silveira *et al.* 1997). We examined the patterns of abundance and ecological relationships among sympatric caimans in JNP, combining descriptive data with community analysis techniques described by Ludwig and Reynolds (1988).

We investigated specifically: (1) the caiman species abundances, diversity, and the similarities between surveys, (2) the caiman species assemblage structure, (3) the human impact on caiman populations, (4) and the size-age structures, which are important demographic parameters for conservation.

MATERIALS AND METHODS

Study area: The study was conducted during 1993 and 1996 at Jaú National Park, situated 200 km Northwest from Manaus, Amazonas State, Brazil (1º00’-3º00’S, 61º30’-64º00’W). In 1980, the Jaú River and its riparian areas up to the banks of the Unini and Carabinani rivers were established as a National Park (Act nº 85.200) to preserve their biological and cultural values. Because few rivers in Amazonia have this level of protection, the JNP provides an opportunity to study crocodilian assemblages and their habitat associations along a relatively undisturbed river. JNP has 22 720 km^2. The climate is wet tropical (Köppen Af), with rainy and dry seasons, the mean annual temperature ranges between 24-26 °C, and the annual rainfall ranges between 1 750 and 2 500 mm. Rainfall occurs throughout the year, but the dry season is in July-November and the wet season is in December-June. The annual variation of river level is near 7 m, and the majority of the Igapó forest is flooded from 221 to 264 days each year (Anonymus 1998). The waters from the area have low conductivity, acid pH, low dissolved O_2, and few suspended matter, with mean water temperature of 26.2 °C (Díaz-Castro 1999).

Sampling and data collection: The transects surveyed were selected within the JNP study areas targeted by eight fieldteams involved in the basic surveys to design the management plan of the reserve. We performed nocturnal spotlight surveys, on open water, riverbanks and shoreline areas, using aluminium boats (6 m) equiped with 15-25 HP outboard engines as the only platform.

We covered 231 km of the Jaú river and tributaries in three areas and times: (i) Cutiaú (October 1993, March 1994, January 1996), (ii) Central (July 1993, January and February 1994), (iii) West (January 1996). We covered also 111 km of (iv) Rio Negro and the Jaú mouth (July and October 1993, April and September 1995), and 28 km of (v) the Unini River and tributaries, in north JNP (September 1996).

To evaluate human impact we compared abundances between less and more disturbed areas. Less disturbed or rarely accessible to non-dwellers, include all Jaú river areas (i, ii, and iii), and more disturbed areas (with regular traffic of regional ships and most active trade of manufactured and extractive products) include the Jaú mouth, Rio Negro (iv) and Unini river (v).

We extensively searched the waters of JNP to find the caimans. Surveys were conducted at night, begining 1 hr after sunset. Caimans were located by eye-reflection using hi-powered spot-lights (powered by a 12 volts car battery). We moved slowly toward the animals to identify species, estimate sizes, and then captured a sample of animals to correct for size estimates. A common sampling error is imprecise size estimates (Magnusson 1983). Based on size measurements of animals, we produced a regression equation relating measured total lenght (M) to estimated total length (E).

The length of the survey routes were determined in two ways: (a) by standing the limits from geographical references established during fieldwork, or (b) by ploting precise geographical coordinates obtained with the Global Positioning System Receiver Garmin® 45. The distances traveled were measured on a drawn map of JNP (produced by Fundação Vitória Amazônica-FVA, based on Landsat-TM images), with flexible ruler (in mm), and converted to scale. Caiman abundance was expressed as the number of animals of each species (excluding hatchling pods) seen per kilometer.

We identified the species in the field by direct observation of morphologic characteristics of at least three living animals: head shape, jaw pattern, and body color. The animal sizes (total lengths) were estimated at distances < 10 m.

Assemblage analysis: The impact of human presence was evaluated by comparison of the differences in the proportion of unidentified caimans (eye proportion = wariness) between less and more disturbed areas and during survey series conducted in four localities. Often, the animals fled before our approach and were classified as eyes. These constituted the main proportion of eyes reported, but some eyes represented animals spoted inside inaccessible Igapó covering. We do not summed eyes to abundance of any other species, as in other studies (*e.g.* Seijas 1988, Da Silveira *et al.* 1997). The dominant species can be different for different surveys, so we chose to analyse eyes apart; too many eyes-only observations may result in a common bias in crocodilian surveys (Bayliss 1987), but can indicate the disturbance level of localities and wariness (Pacheco 1996, Ron *et al.* 1998). We followed the suggestion of Ron *et al.* (1998) that stated that an increase in the proportion of eyes reflects an increase in wariness and a behavioral response to human disturbance.

To examine habitat partitioning we identified habitat patches and microhabitats that we could easily categorize. Each survey was designed to represent only one of four habitat categories: lake, river, river-lake, and stream. These categories are self-explaining, except river-lake, that refers solely to long islands, with great lakes inside and separated by wide channels (Figs. 1, 2). For every individual caiman encountered, we assigned one of nine microhabitat classifications (considering vegetation type, water depth and flow) designated as: (1) Grass: constitutes the floating grass carpet; (2) Rapids: include shallow waters with swift running current; (3) Pool: deep waters

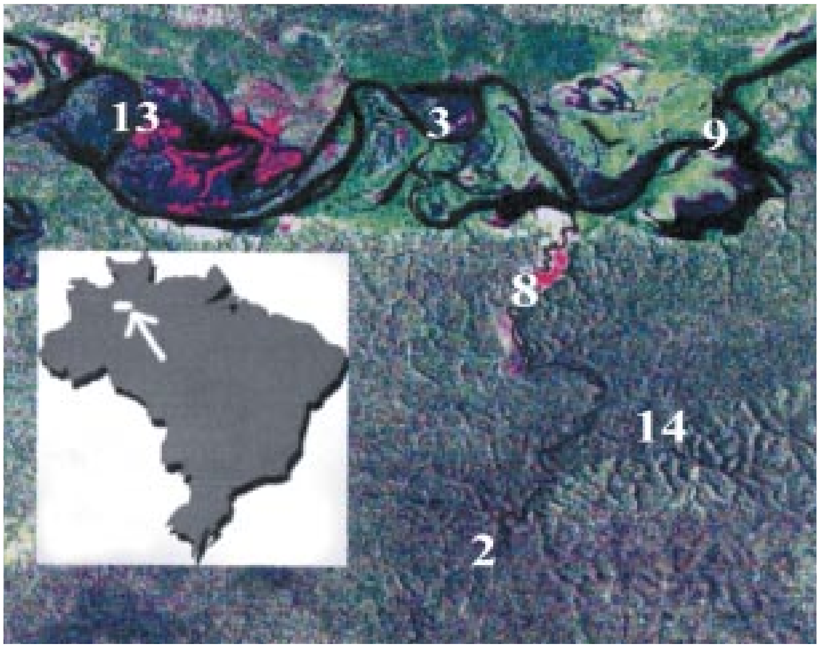

Fig. 1. Surveys and habitats in the Central study area of Jaú National Park. River habitats (3, 9, 13), Stream habitats (2, 8, 14). Survey number legend as Table 2. Clipping of Landsat TM image 1 : 250 000. Detail: location of JNP in Brazil.

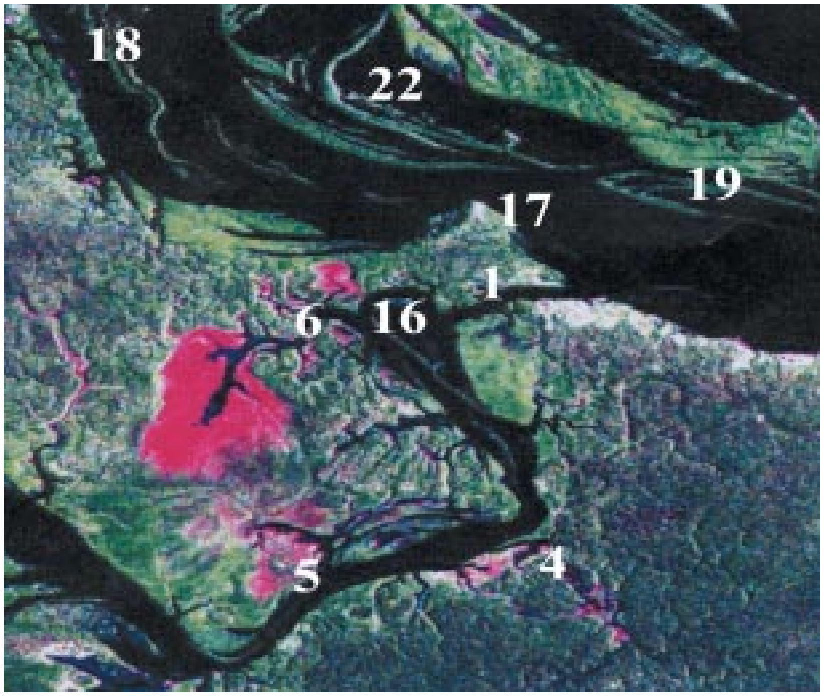

Fig. 2. Surveys and habitats in the Rio Negro study area of Jaú National Park. River-Lake habitats (18, 19, 22), River habitats (1, 5, 16, 17), Stream habitat (4), Lake habitat (6). Survey number legend as Table 2. Clipping of Landsat TM image 1 : 250 000.

with no current; (4) Deep: the deep waters with swift moving currents; (5) Stream Igapó: flooded forest with little current, short flooding period, and high plant diversity; (6) Land: all land locations including animals on sandbank, mud beaches, rocks, and clay banks; (7) Margins: shallow waters with little or no current; (8) Lake Igapó: flooded forest with no current, longest flooding period, and lowest plants richness; (9) River Igapó: flooded forest with little current, but intermediate flooding period and plant richness.

For search of species associations, we constructed a presence-absence matrix with surveys as columns and caiman species as rows, and then calculated Jaccard Distance (JD) as follows:

$$1-2W/(A+B-W)$$

where W is the sum of shared abundances and A and B are the sums of abundances in individual sample units.

We used another matrix of quantitative measures of species abundance (surveys as columns and species as rows) to identify species correlations (covariation of abundances between species) (Ludwig and Reynolds 1988). We used Spearman correlation coefficients to determine species affinities. All indexes, calculations and statistical tests, were performed using Systat 5.03 (Anonymous 1990-1993).

We used Cluster analysis to examine crocodilian assemblage structure (an uncommon procedure, since crocodilian studies usually were focused on one species), because this classification technique places similar samples or surveys into groups or clusters. These clusters may delimit or represent different crocodilian assemblages based on their overall resemblance. A possible random utilization of resources can be indicated by no structure. But if there are any ecological separations and associations between species, well-defined clusters of surveys can emerge using hierarchical, agglomerative and polythetic classifications with species abundance data, which can be summarized in a dendrogram (Ludwig and Reynolds 1988). The data of abundances matrix were added to a constant (0.01), log-transformed and relativized by standard deviates of species abundances. The distance measure used was relative euclidian and the group linkage method was median. Cluster analyses were performed using Pc-ord 2.01 software (McCune and Mefford 1995). Voucher specimens were deposited in the herpetology collection of the Instituto Nacional de Pesquisa da Amazônia in Manaus, Brazil.

RESULTS

Distribution and abundance: During the sampling, we identified 290 individuals. Species observed were common caiman (*C. crocodilus*), black caiman (*M. niger*), Schneider's caiman (*P. trigonatus*), and dwarf caiman (*P. palpebrosus*). Common caiman was the most frequently observed (69 %), followed by black caiman (14 %), Schneider's caiman (12 %), and dwarf caiman (4 %) across all surveys combined (Table 1).

TABLE 1

Number of crocodilians sighted within species and size classes in Jaú National Park during 1993-1996 nocturnal spotlight surveys

			Numbers in size classes*						
Species	N	H	2 - 6	6 - 10	10 - 14	14 - 18	18 - 22	> 22	NR
Caiman crocodilus	201	44	25	53	38	28	7	1	5
Melanosuchus niger	40	8		4	5	3	6	11	3
Paleosuchus trigonatus	36			14	11	8			3
Paleosuchus palpebrosus	13		2	3	8				

* Size classes in m x 10^{-1}. N: total crocodilians sighted. H: hatchlings. NR: size not estimated.

The abundances of species varied across surveys (Table 2). We surveyed 371 km of shoreline, 287 km during the wet season (20 surveys) versus 84 km in the dry season (10 surveys). The total number of caimans (*i.e.*, all species combined) observed in the dry season surveys (1.1 ± 0.5 caimans/km) was greater than in the wet season (0.9 ± 0.5 caimans/km), but these differences were not significant between seasons ($t_{0.05(2),28} = 0.829$, $p > 0.5$). The higher abundance (2.3 caimans/km, two species, stream habitat) was observed in wet season. The second highest abundance (2.2 caimans/km, one species, lake habitat) was observed in dry season.

Therefore the mean caiman abundance was 1.0 ± 0.5 caimans/km. Low abundance surveys predominated: in 17 surveys we counted less than 1.0 caiman/km, while in eight surveys we observed moderate abundances (1.0-2.0 caiman/km). The highest abundances were observed in less disturbed areas, while the lowest abundances were observed in more disturbed areas. The ranges of abundances were similar between rivers (0.3-2.1 caimans/km), lakes (0.6-2.2 caimans/km) and streams (0.5-2.3 caimans/km), but was minor in river-lake surveys (0.2-1.2 caimans/km).

No caiman species were distributed continuously across the entire study area. The common caiman ocurred in 25 surveys (mean abundance 0.4 ± 0.3 caimans/km), the black caiman was observed in 12 surveys (0.2 ± 0.1 caimans/km), Schneider's *P. trigonatus* was observed only in five surveys (but with mean abundance of 0.6 ± 0.3 caimans/km), and *P. palpebrosus* was observed in seven surveys (mean of 0.1 ± 0.1 caimans/km).

Comparing the species composition between surveys we found two groups: *C. crocodilus* - *M. niger*, and *P. trigonatus* - *P. palpebrosus* (Fig. 3). Despite the coefficient of community does not take into account the relative abundance of species assemblage, we measured the differences in community structure and expressed the relative weakness of the two possible associations, the pair *C. crocodilus* - *M. niger* (0.480) and the pair *P. trigonatus* - *P. palpebrosus* (0.333), and revealed that there is no association (or complete exclusion) between *M. niger* and *P. trigonatus*.

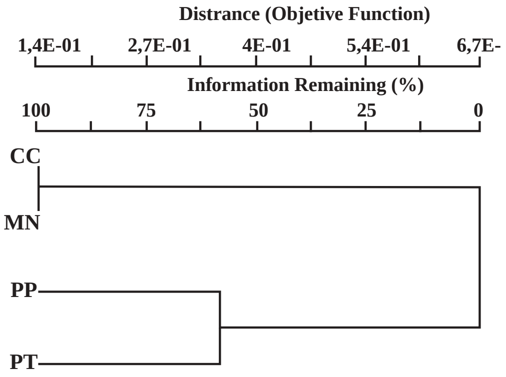

Fig. 3. Crocodilian species associations in Jaú National Park, from a presence/absence matrix based on data of Table 2. Measure distance was Jaccard coefficients and group linkage method was Centroid. CC: *Caiman crocodilus,* MN: *Melanosuchus niger,* PP: *Paleosuchus palpebrosus,* PT: *P. trigonatus*.

Similarity among surveys may be expressed by measuring the correlation between species abundances. There was a small negative correlation between *C. crocodilus* and *P. trigonatus* that was significant (-0.459, ANOVA$_{1,27}$ F = 5.501, p = 0.027) and a positive, but not significant (0.401, p = 0.08) correlation between *P. palpebrosus* and *P. trigonatus*. There was a small covariation of *C. crocodilus* and *M. niger* abundances that was highly non-significant (0.004, p = 0.900). The structure of caiman assemblage does not ressemble a pattern of separated sets of species associated to specific habitats. The only actual trend we observed in species relationships was that populations of similar size species (*C. crocodilus* and *P. trigonatus*) were mutually excludents and may have a niche overlap.

Size-age structures: In order to correct estimated total length of observed, and not captured animals, a linear regression line of predicitive size was used for all species ($M = 0.004 + 0.966\ E$, $F_{1,18} = 60.046$, $p < 0.001$, $R^2 = 0.757$) (Fig. 4). Frequency distributions of estimated size for black caiman and dwarf caiman were skewed toward the

TABLE 2

Surveys of caimans in Jaú National Park.

	Surveys	Dates	H (hours)	Habitat Type	Study Area	km	Season	Caimans/km						Hatchlings	
								CC	MN	PP	PT	Eyes	Total	Pods	count
1	Jaú mouth	Jul,17,93	04:00	River	RN	11.7	W	0.43	0.08	0.00	0.00	0.17	0.68		
2	Miratucu	Jul,19,93	03:23	Stream	CE	21.6	W	0.00	0.00	0.00	0.78	0.21	0.99		
3	C.Grande-Miratucu	Jul,29,93	02:15	River	CE	11.0	W	0.45	0.00	0.00	0.00	0.54	0.99		
4	Preto	Oct,19,93	02:20	Stream	RN	4.9	D	0.82	0.00	0.20	0.20	0.41	1.63		
5	Preto mouth-Manichuau	Oct,20,93	01:11	River	RN	8.3	D	0.36	0.00	0.00	0.00	0.36	0.72		
6	Supiá Lake	Oct,20,93	00:32	Lake	RN	4.9	D	2.04	0.00	0.00	0.00	0.20	2.24		
7	Cutiuaú Lake	Oct,29,93	04:02	Lake	CT	11.5	D	0.96	0.26	0.00	0.00	0.09	1.31		
8	Miratucu (lower)	Jan,17,94	02:12	Stream	CE	9.0	W	0.00	0.00	0.00	0.89	0.22	1.11		
9	Miratucu mouth-Catoá	Jan,17,94	03:32	River	CE	7.7	W	0.78	0.13	0.13	0.00	1.04	2.08	1	8
10	Macaco	Jan,23,94	01:12	Stream	CE	9.3	W	0.54	0.32	0.00	0.00	0.32	1.19		
11	Umanapana	Jan,24,94	02:10	Stream	CE	6.4	W	0.00	0.00	0.31	0.62	1.41	2.34		
12	Macaco mouth-Maranhoto	Jan,30,94	03:01	River	CE	21.6	W	0.37	0.00	0.00	0.00	0.28	0.65		
13	Miratucu mouth-Pajé	Feb,15,94	02:53	River	CE	20.1	W	0.20	0.00	0.05	0.00	0.05	0.30		
14	Miratucu (Gerley)	Feb,18,94	03:00	Stream	CE	14.0	W	0.00	0.00	0.14	0.36	0.50	1.00		
15	Moura-Nazaré	Mar,05,94	03:05	Lake	CT	12.4	W	0.89	0.00	0.00	0.00	0.32	1.21	2	16
16	Uruá-Jaú mouth	Sep,02,94	01:00	River	RN	4.0	D	0.25	0.75	0.00	0.00	0.25	1.25		
17	Negro	Apr,06,95	03:12	River	RN	14.3	W	0.35	0.00	0.00	0.00	0.14	0.49		
18	Negro (Enseada)	Apr,07,95	02:36	River/Lake	RN	18.5	W	0.05	0.16	0.00	0.00	0.00	0.21		
19	Negro (Panema)	Apr,08,95	05:34	River/Lake	RN	24.5	W	0.53	0.00	0.00	0.00	0.28	0.81	2	8
20	Negro (Onças)	Apr,09,95	04:22	River/Lake	RN	32.3	W	0.22	0.03	0.00	0.00	0.28	0.53		
21	Jaú mouth	Apr,10,95	03:00	River	RN	14.3	W	0.21	0.07	0.00	0.00	0.56	0.84	1	3
22	Negro (Grande)	Sep,01,95	04:01	River/Lake	RN	21.6	D	0.37	0.00	0.00	0.00	0.37	0.74		
23	S.Maria-Praia Alta	Jan,19,96	02:37	River	WE	12.3	W	0.16	0.00	0.08	0.00	0.16	0.40		
24	S.Maria-Feijão	Jan,23,96	02:33	River	WE	5.9	W	0.17	0.34	0.17	0.00	0.51	1.19		
25	Pinto	Jan,21,96	01:50	River	WE	13.6	W	0.22	0.22	0.00	0.00	0.29	0.73	2*	9
26	Cutiuaú Lake	Jan,25,96	01:18	Lake	CT	6.5	W	0.15	0.00	0.00	0.00	0.46	0.61		
27	Unini (Sumaúma)	Sep,05,96	01:43	Lake	U	1.2	D	0.00	0.00	0.00	0.00	0.81	0.81		
28	Papagaio	Sep,11,96	01:06	River	U	12.0	D	0.08	0.16	0.00	0.00	0.25	0.50	1	4
29	Unini (Tapiira)	Sep,14,96	01:54	River/Lake	U	7.7	D	0.65	0.00	0.00	0.00	0.52	1.17		
30	Mauaru	Sep,17,96	02:10	Stream	U	7.7	D	0.13	0.13	0.00	0.00	0.26	0.52		

H: duration of observation period, CC: *Caiman crocodilus*, MN: *Melanosuchus niger*, PP: *Paleosuchus palpebrosus*, PT: *Paleosuchus trigonatus*. Study areas: RN: Rio Negro, CE: Central, CT: Cutiaú, WE: West, U: Unini. Seasons: W: wet season, D: dry season. * including one pod of *M. niger* hatchlings.

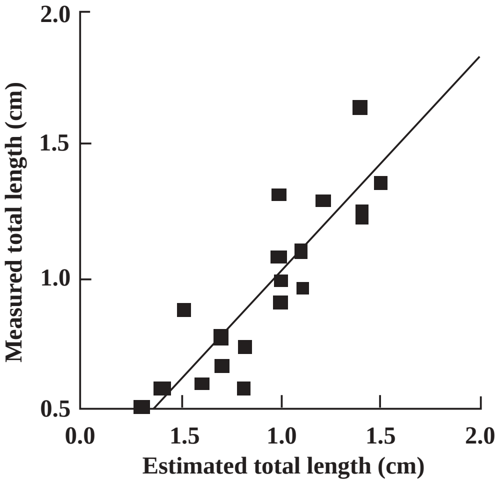

Fig. 4. Relationship between estimated and measured size of a sample of caimans captured at Jaú National Park. Regression line: Measured = 0.004 + (0.966) Estimated. $F_{1,18}$ = 60.046, R^2 = 0.757.

larger size classes, which were expected for long-lived species with continual growth. Large *M. niger* include some 4 m long individuals, while large *P. palpebrosus* has animals of 1.0-1.4 m in length. The length frequencies for *C. crocodilus* showed a predominance of juveniles and subadults, and for *P. trigonatus* a predominance of middle size classes of subadults.

Few juveniles were observed. Among common caiman, eight pods of hatchlings were observed, 22 % of individuals of these species were juveniles, most observed in the early wet season (six pods in Rio Jaú and one pod in Rio Negro), and one in early dry season (Rio Unini). Common caiman pods were observed in nearly every habitat type, but mostly in river habitats. Juveniles composed 20 % of the overall observations of black caiman, that corresponds to one pod of hatchlings observed in upper Jaú in the early wet season. No juvenile Schnider's or dwarf caimans were observed.

Species-habitat relations: Comparing the species composition between surveys using coefficients of community (Jaccard) for habitat categories, we found differences. Ranking the mean coefficients for habitat, the most similar were (1) lakes, (2) lakes and river-lakes, and (3) river-lakes (inhabited by the *C. crocodilus* - *M. niger* pair). Moderately similar were (4) rivers and river-lakes, (5) rivers and lakes, and (6) rivers (inhabited by *C. crocodilus* - *M. niger* pair, with occasional *P. palpebrosus*). Dissimilarities were higher among (7) streams, (8) rivers and streams, (9) streams and river-lakes, and (10) streams and lakes.

Surveys in streams were not quite homogeneous, they were different within stream surveys and different in each stream, among upper and lower courses of the stream. In some stream surveys, we found *P. trigonatus* populations, but in others we did not.

The examination of microhabitats used by caimans (Fig. 5) suggests a thin habitat partitioning. *Paleosuchus trigonatus* were absent from river and lake Igapó, but were frequent in stream Igapó. This species was the most terrestrial and frequently observed on land. The only microhabitat category that they used as frequent as *C. crocodilus* were margins. However, *P. trigonatus* was frequently observed in water as deep as *M. niger.*

The most frequently used microhabitat by *C. crocodilus* and *M. niger* were river and lake Igapó, but this two species differ in use of other microhabitats: *C. crocodilus* predominate in shallow waters (margins) and land locations, while *M. niger* predominated in deep moving waters, but were absent from stream Igapó. Carpets of floating grass are rare in JNP and only *C. crocodilus* was observed in such habitat.

Paleosuchus palpebrosus was observed only in running water microhabitats: river Igapó, margins, stream Igapó and rapids, and never in stagnant waters of lake habitats. Only *Paleosuchus* was observed in fast running rapids.

The general pattern of microhabitat use was strongly oriented to river Igapó, lake Igapó and margins (30 %, 20 %, and 18 % of observations, respectively).

Assemblage structure: The patterns of clustering of surveys were summarized in the dendrogram in Fig. 6. Using an arbitrary cutoff distance of 4.3, we distinguish three clus-

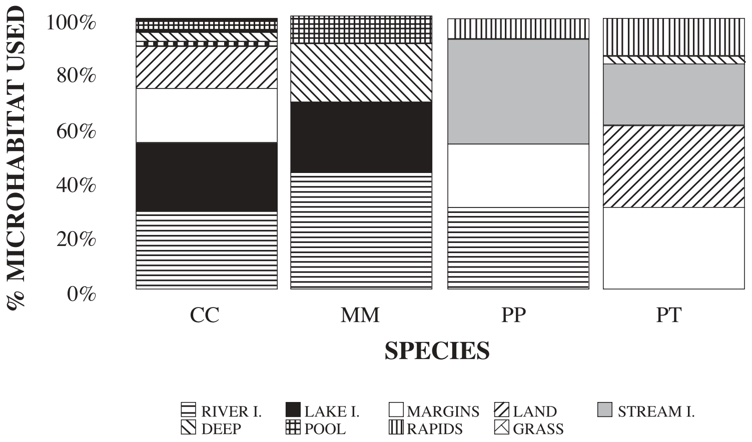

Fig. 5. Microhabitat used by caimans in Jaú National Park. CC = *Caiman crocodilus,* MN = *Melanosuchus niger*, PP = *Paleosuchus palpebrosus*, PT = *Paleosuchus trigonatus*, I. = Igapó.

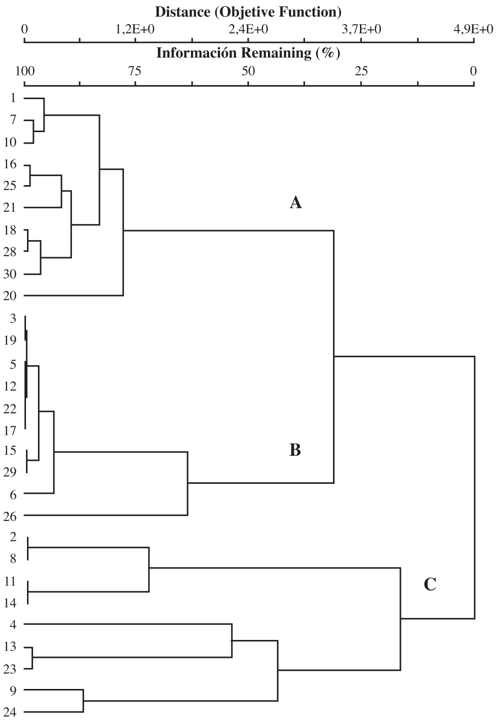

Fig. 6. Cluster analysis of surveys of caimans of Jaú National Park, based on the abundance data of Table 2. Data added to a constant (0.01), log-transformed and relativized by standard deviates of species abundances. Distance measure was relative euclidian and group linkage method was Median. Percent chaining: 7.53. Clusters: A: surveys with *Melanosuchus niger* and *Caiman crocodilus* set, B: surveys with only *Caiman crocodilus,* C: surveys with at least one *Paleosuchus* species. Survey number legend as Table 2.

ters, which can be described only by species composition: Cluster A represents surveys where we find *C. crocodilus* and *M. niger*. Cluster B represents surveys where we find only *C. crocodilus* populations. Both patterns were common and observed in all habitats types and study areas, making a mosaic. Cluster C represents some of the most rich in species surveys, but what was distinctive was the presence of at least one *Paleosuchus* in all these surveys, in river and stream habitat types, in Central and West study areas. Populations of *P. trigonatus* were find only in streams, and *P. palpebrosus* in river and streams.

Human impact: Long term human disturbance of this ecosystem was not much evident. We observed a mild slight trend to increase wariness, that could be attributed to human general activities in JNP. The proportion of eyes observed in much disturbed localities (40 %) was greater than in little disturbed ones (38 %), but this diference was not significant ($t_{0.05(2),28} = 0.269$, $p > 0.5$). We observed, however, an increase of wariness that could be attributed to our surveys. When we compared the proportion of eyes in consecutive surveys, there was a trend to increase the proportion of wariness with time in all habitats and study areas, considered by us disturbed or not. Three sequences of three surveys (surveys # 1, 16, and 21 in Jaú mouth, surveys # 2, 8, and 14 in Miratucu stream, and surveys # 7, 15, and 26 in Cutiaú lake) and one sequence of five surveys (# 17, 18, 19, 20, and 22 in Rio Negro), all showed clearly similar increasing wariness trends.

DISCUSSION

This study focused on distribution and abundance of the caiman community of Jaú National Park as they related to habitat caracteristics. The presence and relatively stable abundance of common species at each study site show that these species had wide distributions along the area. However, the abundance of each species varied in association with different habitats and as a response to species interactions. The small relative abundances could reflect bias due to wet season dispersal, since in JNP environmental disturbance are minimal, and there is no marginal habitats. Differences between dry and wet seasons surveys could indicate the existence of many individuals unapparent in the wet season.

Caiman surveys in South American savannas observed large differences of abundance between seasons, and the dry seasons abundances could be two to ten times larger than the wet season abundances (*e.g.* Gorzula 1978, Glastra 1983). But the similar numbers between dry and wet seasons in JNP, suggests that there should not be a great number of caimans hidden inside the flooded forest. Juveniles of *C. yacare* have been reported to occur somewhat appart from adults and in shallower waters (*e.g.* Rebêlo *et al.* 1997). However, we assumed that because the same survey method and similar effort were used among surveys, observational bias remained consistent and the observed differences in abundances for each species likely reflects the caiman assemblage structure in JNP.

The very low densities of fewer than 1 caiman/km that we detected were reported in 70 % of the localities surveyed elsewhere in Amazonian waters by Brazaitis *et al.* (1996a). To compare this study with published surveys carried out in Amazonian waters, Glastra (1983), Espinosa (1995), Brazaitis *et al.* (1996a), Da Silveira *et al.* (1997) and Da Silveira and Thorbjarnarson (1999) reported values between 1-19, 0-2, 0-10, 0-58 and 1-115 caimans/km, respectively. The abundance obtained in this study (0-2 caimans/km) was low in comparison with the majority of values from other caiman surveys in Amazonian waters. But, abundances reported by Da Silveira and Thorbjarnarson (1999) of very abundant populations of *C. crocodilus* and *M. niger* in Mamirauá reserve sector's where hunting pressure is lowest, is a rare event in Amazonia.

The distribution of common caimans reflects their general habitat use as was seen in other studies (Medem 1971, 1981, 1983, Magnusson 1985, Brazaitis *et al.* 1990, 1996a, b). Surveys where we observed only one species always had *C. crocodilus* in floodplain, or *P. trigonatus* in streams of the Central study area. *Melanosuchus niger* and *P. trigonatus* were not observed together in any survey, maybe because of mutual exclusion, although the literature recorded sympatric occurrence of the two species (Medem 1967).

In previous studies *M. niger* populations were so reduced, that it was impossible to determine which is the relationship between that species and *C. crocodilus* (Brazaitis *et al.* 1996a, Da Silveira *et al.* 1997). The authors explained the small numbers as evidence of very reduced populations due to commercial hunting: few *M. niger* survivors were observed "mixed" with several *C. crocodilus*, which could be contributing (as predators or competitors) to hinder the recovery of the populations of *M. niger* submitted to hunting (Magnusson and Rebêlo 1982, Rebêlo and Magnusson 1983). However, without strong evidences of species interference, differences in distribution of sympatric populations were attributed to habitat preferences (Magnusson 1985). Therefore, reduced populations of *M. niger* were considered unable to affect the distribution of *C. crocodilus* (Da Silveira *et al.* 1997), while the reversal is unknown.

The different adult size of the two species and the differential use of microhabitats, could reduce or attenuate the negative effects of sharing the same habitats and eating similar preys. In the blackwater Archipelago of Anavilhanas, *C. crocodilus* abundance does not coincide with food availability and nesting areas of *M. niger*, which predominate in the deeper water channels, with more sediments and floating grass (Da Silveira *et al.* 1997).

The non occurrence of the four species in all surveys suggests effective habitat partitioning. *Melanosuchus niger* and *C. crocodilus* inhabit floodplain habitats, while *P. trigonatus* inhabits forest streams and turbulent waters (Medem 1981, 1983), and their peculiar diet was attributed to habitats selection (Magnusson *et al.* 1987). Notwithstanding, our results of streams with *C. crocodilus* and *M. niger* challenge strictly the habitat separation hypothesis, despite the absence of *P. trigonatus* in river and lake habitats. The importance of interspecific competition in the organization of crocodilian communities is easy to imagine since they are members of the same guild, but is difficult to establish since the mere presence of differences of resource utilization between species is not evidence of competition (Schoener 1974), and if other factors (as predation, food, weather, or something else) keep densities at a low level, the role of competition will be negligible (Begon *et al.* 1996).

Physiological and behavioral mechanisms can also reduce or attenuate the niche overlap between species. Nests of *P. trigonatus* need an extra source of heat (Magnusson *et al.* 1985) while the *C. crocodilus* females build common mound nests (Gorzula and Seijas 1989). Adults of *C. crocodilus* prey upon fishes and large invertebrates, while adults of *P. trigonatus* prey mostly on terrestrial vertebrates (Magnusson *et al.* 1987). *Paleosuchus trigonatus* have a highly terrestrial life (Magnusson and Lima 1991) while *C. crocodilus* spend most of the day in the water (Marcellini 1979).

We observed *P. trigonatus* in 71 % of the stream surveys. Medem (1967, 1971) remarked that what separate the species is any skill to deal with water speed: in his analysis *Paleosuchus* are caimans of (1) running waters of tropical forest streams with rocky or sandy bottom, (2) neighbourhood of rapids, waterfalls, jumps and whirls, (3) narrow channels of large rivers through where masses of water slide swiftly (as in narrow pass), and (4) savanna streams and gallery forests.

For Medem (1967, 1971), *P. trigonatus* would represent the primitive form, while *P. palpebrosus* would be the most specialized. *Paleosuchus palpebrosus* would have developed adaptations to colonize the larger bodies of water, where there is some water flow (as a secon-dary effect, the “carapace” guaranteed an extra protection against drying up in unfavorable habitats and against predation from larger species).

If the flow is the critical factor, the resistance to impact on rocks and the swimming capacity would be factors capable to increase or to reduce the fitness of a species. Magnusson (1989) commented that “It is obvious that the habitats of each [*Paleosuchus*] differ, and that the habitats of both are different from those of other sympatric crocodilians but just which differences are critical remains conjecture.” According to Magnusson (1989), *P. trigonatus* is the specialized form differing from the other crocodilians in its thermal biology (living in moderate temperature and relatively stable forest habitat, with limited opportunities for basking), and may be the largest biomass of great predators in the Terra Firme forest near Manaus, drained by small streams (Magnusson and Lima 1991).

In JNP, *P. trigonatus* is not the only species of forest streams, and different from the Manaus area, most of the individuals we observed were subadults, a stage of life with high dispersion rates (great mobility). In the Manaus semi-urban area, most of the population was constituted by adult animals, whose high survival rate and extended lifetime would have great influence on the population dynamics (Magnusson and Lima 1991).

Conservation: We used a regression line to correct size estimates, a usually neglected tool. The action plan for crocodilian conservation of the Crocodile Specialist Group (Thorbjarnarson 1992), call for more population survey work, that was “urgently needed for a large percentage of the [crocodilian] species”. Surveys were considered needed not only for planning recovery programs, but also as the first step of sustainable yield utilization projects. However, rarely the relationship between actual and estimated sizes of individuals has been presented, and accurate estimates of total numbers are of limited use without some idea of the accuracy of the size estimates (Magnusson 1983).

These data provide the first comprehensive overview of the caiman community in JNP. For common and black caimans in this areas, populations are currently widespread in floodplain, but appear to be not abundant. Schnider’s caiman is specific of some streams. The rare but widespread observation of dwarf caiman suggest that the species is a habitat generalist, but its abundance may be affected by the other species. Their use of the river, however illustrates the importance of riverine systems to all caiman species found within JNP.

The differences in numbers of different species show the influence of different habitat caracteristics and patterns on caiman assemblages. The river and lake Igapó were important to common and black caimans, the deep waters attracted more black caimans, and the stream Igapó and rapids were preferred by *Paleosuchus*.

Very low numbers of caimans were present in JNP , but the observation of pods of hatchlings suggests that there is successful reproduction of the two most abundant species. Without immediate threats of habitat destruction, with large areas of pristine habitats, the situation has been favorable for the recovery of the populations affected by commercial hunting in the past. The international trade in caiman skins periodically increase the demand for all crocodilian-skin products, touted by the fashion industry (Brazaitis *et al.* 1998). The regional market for caiman meat is increasing (Da Silveira and Thorbjarnarson 1999) and current evidences of localized recovery are supporting a proposal to downlist *M. niger* in Brazil (Ronis da Silveira pers. comm.). As large caiman populations are rarely found, we do not support the increase of utilization of *M. niger* and the efforts to widespread use of the species.

The discovery of small populations of *M. niger* in scattered distributions throughout Amazonia, are considered an effect of overexploitation (Plotkin *et al.* 1983, Brazaitis *et al.* 1996a, b, 1998), and does not fit the historical records that reported larger populations (Bates 1876, Carvalho 1951, Aguirre 1956). Small, disjunct, isolated populations that are reported do not mean that the species has recovered everywhere and can not support the efforts to reassessment of the status of the species and allow it in the trade.

We do not know what was the level of disturbance that the caimans of JNP experienced in the past. If measures of wariness reflect such disturbance (and we agree that it may reflect very recent episodes), our study shows that researchers disturbed the caimans more than local inhabitants. Based on reports of local inhabitants, we can say that where today is the JNP, commercial hunting of *C. crocodilus* and *M. niger* stopped in 1973. This could be consequence of legal prohibition or depletion of population stocks.

Current inhabitants cause little impact on caiman populations, but this is not because there is hunting restriction, since it is also forbidden the commercial fishing of turtles. They catch turtles once there is market for them. Now, local inhabitants rarely eat caiman meat, or kill large and potentially dangerous animals. However, when the fashion comes back, we must be aware about the management and conservation of the low density populations in poor blackwater areas.

The aquatic ecosystems of the Amazonia blackwater rivers and streams constitute nutrient poor areas, considered uncapable to maintain populations as large as the ones reported for “white waters” (loam silted rivers).

Blackwater rivers are considered acid, low nutrient, high nitrogen ecosystems with headwaters inside forests with sandy podzols soils (Sioli and Klinge 1962). Blackwater rivers and the lands they drain have low subsistence potential for human populations and they are notorious "starvation rivers" (Meggers 1996). As top predators even the caiman populations should be limited by habitat productivity. Small populations have a general problem in conservation biology, since they can be at risk simply because of their size, which requires studies on the effects of low numbers on population persistence (Caughley and Gunn 1996). Thus the factors that are limiting these populations, however, can be independent of human exploitation.

Currently, in Amazonia increased the pressure of hunting, habitat loss and habitat alteration, and there is no evidence of widespread recovery of caiman populations. Our data show that in large reserves without many disturbances, most caiman populations can have low density, suggesting that in blackwater environments their recovery from exploitation should be very slow.

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