HELMINTH COMMUNITY STRUCTURE OF THE CAIMAN, CAIMAN CROCODILUS YACARE (CROCODYLIA, ALLIGATORIDAE) IN THE BRAZILIAN "PANTANAL".

J. B. CATTO[1] & J. F. R. AMATO[2]

(1) Centro de Pesquisa Agropecuaria do Pantanal, EMBRAPA, Rua 21 de Setembro, 1880, 79320-900 Corumbá, MS, Brasil. (2) Departamento de Biologia Animal, Universidade Federal Rural do Rio de Janeiro, BR 165, km 7, Caixa Postal 74512, 23851-970 Seropédica, RJ, Brasil.

SUMMARY. The helminth parasite community of crocodilians has been little studied to the present. The helminth distribution, the interspecific relationships, the host sex influence, the season of the year, and the habitat (location of capture) of the host were studied through 64 necropsies of the caiman, Caiman crocodilus yacare, the only species and subspecies occurring in the Brazilian "Pantanal", in order to compare its parasite community structure with those of other reptiles, amphibians, fishes, and birds. The helminth infracommunities of the caimans in the Brazilian "Pantanal" have interactive community characteristics. These caimans are parasitized by a large number of species, many of them congeneric, with high prevalences and intensities of infection. Although these predisponent factors for intraspecific interaction are present, there were no negative significative associations or negative covariation between the concurrent species pairs present. The variable host sex, did not influence the prevalences and the intensities of infection; the variable season of the year, did influence the intensity of infection of two species: Ortleppascaris alata and Herpetodiplostomum caimancola; and the variable habitat of the host, influenced the prevalence of one species: Polyacanthorhynchus rhopalorhynchus, and the intensities of infection of seven other species. The higher complexity and diversity of the infracommunities of the caimans in the Brazilian "Pantanal", in relation to those of other reptilians, amphibians, and even fishes and birds, is attributed to the selective diet of the hosts, composed of organisms which might work as intermediate hosts for the many helminth species found.

KEY WORDS: Caiman crocodilus yacare, Caimans, Brazilian "Pantanal", Ecological analysis.

INTRODUCTION

Caiman crocodilus yacare Daudin, is found in Argentina, Bolivia, Brazil, and Paraguay, in lotic and lentic waters of the Paraguay and Parana river basins. However, this species is most abundant in the Brazilian "Pantanal", a 140,000 km2, partially flooded lowland situated at the border of those three countries. Although millions of caimans have been killed illegally in the last decade, the current population in the Brazilian "Pantanal" is estimated at hundreds of thousands of animals.

This species has been studied recently with the aim of exploitation in Nature and in captivity, as it has been done with other crocodilian species. Besides the importance that the helminthoses may have on the population dynamics of the host, species identification, life cycle, and pathogeny are vital factors for adoption of prophylactic and therapeutic measures in captive rearing. The exploitation of crocodilians on a commercial basis is a recent activity, but some studies already show the relationship between parasitism, retarded growth, and mortality (BENITEZ et alii, 1980; TELFORD & CAMPBELL, 1981; FOGGIN, 1987; LADDS & SIMS, 1990).

The crocodilian's helminth fauna has been used in host-parasite coevolution studies (BROOKS, 1979; BROOKS & O'GRADY, 1989), but, except for two surveys, in which ecological traits were estimated, the literature is restricted to species' descriptions. HAZEN et alii (1978) performed necropsy on 12 alligators in South Carolina, USA, determining prevalence, abundance, and distribution of helminths in the gastrointestinal tract. GOLDBERG et alii (1991) estimated the prevalence and

the abundance of stomach nematodes in caimans captured in Paraguay.

Ten helminth species have been described as parasites of the caiman in the Brazilian "Pantanal": 3 digenetic trematodes - *Pachypsolus sclerops* Travassos, 1922, *Odhneriotrema microcephala* Travassos, 1922, *Proterodiplostomum longum* (Dubois, 1988); 1 acantocephalan - *Polyacanthorhynchus rhopalorhynchus* (Diesing, 1851); and 6 nematodes - *Dujardinascaris longispicula* (Travassos, 1933), *Brevimulticaecum baylisi* (Travassos, 1933), *B. stekhoveni* (Baylis, 1947), *Micropleura vazi* (Travassos, 1933), *Ortleppascaris alata* (Baylis, 1947), and *Dujardinascaris paulista* Travassos, 1933. Recently, from material collected in the survey analyzed here, CATTO & AMATO (1993a, b) and CATTO & AMATO (1994) registered 12 additional species of digenetic trematodes in *C. c. yacare*, five of which were described as new species.

As biologists who study free living organisms have been doing for a long time, parasitologists are now evaluating and discussing the structure mechanisms in helminth communities. Since this is the first study in which prevalence and abundance of helminth species in crocodilian hosts have been estimated, it is possible to make comparisons between the helminth communities of crocodilians and that of other vertebrates, and to discuss the variables which influence the organization of their helminth communities.

The objectives of this study are: 1. to determine the parasite community structure of *C. c. yacare*; 2. to determine the influence of the host's sex, habitat (location of capture) - lakes or "vazantes", and the season of the year on the composition of the parasite community structure of *C. c. yacare*; and 3. to compare the parasite community structure of *C. c. yacare* with that of other reptiles, amphibians, fishes, and birds.

MATERIALS AND METHODS

The study area and the host sample size

The caimans were captured in lakes and "vazantes" (seasonal shallow, drainage watercourses) in the Nhecolândia (18° 59'S, 56° 39'W) and the Paiaguás (18° 06'S, 56° 36'W), subregions of the Brazilian "Pantanal". From 1986 to 1989, 64 subadult and adult caimans (60 to 117 cm snout to vent length) were captured live, sexed, measured, weighted, and killed by intracerebral injection of ethyl alcohol.

The helminth data base

At necropsy, the organs were separated, opened, washed, rasped, and the contents sieved through a 149μ mesh. The recovery of all helminth specimens was attempted, except when the presence of more than 200 proterodiplostomes, acanthostomes or telorchiids in the intestine was suspected, in which case two subsamples of 10% were examined after the whole contents had been examined for other helminth groups. The digenetic trematodes and acanthocephalans were processed according to AMATO (1985). The nematodes were fixed in AFA (ethyl alcohol 70% - 93 parts, formalin 37% - 5 parts and glacial acetic acid - 2 parts) at 65°C, stored in 70% ethyl alcohol, cleared in Amann's lactophenol, and mounted in Canada balsam.

Definitions

The terms prevalence, mean intensity, abundance, and infrapopulations were used according to MARGOLIS *et alii* (1982), and infracommunity, was used according to HOLMES & PRICE (1986).

The terms interspecific association and interspecific covariation, in this study, were used according to LUDWIG & REYNOLDS (1988). Interspecific association refers to how often species are found in the same host, *i.e.*, the affinity or lack of it for occurrence of two species (pairwise association) or simultaneous association in a large number of species (overall association). Interspecific covariation is the degree of covariation in infrapopulations of two concurrent species, *i.e.*, how much the abundance of a particular species is influenced by the abundance of another coexistent species.

The structure of the metazoan parasite community was investigated by determining the importance value (I) according to THUL *et alii* (1985) who classified the parasites species as dominant, codominant, and subordinate, respectively.

Statistical analysis

The distribution of the observed number of helminth species in each individual host was tested by Poisson, normal, and negative binomial distributions, using the chi-square goodness of fit test (Statgraphics Statistical Graphics System, STS Inc., 1986).

Seventy-nine percent of the total number of helminth specimens collected in the host samples belonged to the 14 most prevalent species (>28%). This number was chosen arbitrarily, as 28% of 64 hosts is 18, which was considered a reasonable number of hosts to apply statistical analysis. Therefore, the other nine species collected were not considered for the following analysis.

The distributions of specimens of the 14 most prevalent species in the hosts were analyzed individually for negative binomial distribution using the chi-square goodness of fit test. Clumped distribution was investigated using the chi-square to test significant departure of the variance/mean ratio from unity, and was measured by the negative binomial parameter (Negbinomial BaS program, LUDWIG & REYNOLDS, 1988). The negative parameter k approaches zero as overdispersion increases and, conversely, k approaches α as the variance approaches the mean. Since most helminth species in this analysis revealed a non-normal distribution, non-parametric statistics were used in subsequent analyses.

The influence of the sex, the season of the year, and the habitat (location of capture) variables on the prevalence and on the intensities of infection of the helminth species were tested by the chi-square and Mann-Whitney tests, respectively (Statgraphics Statistical Graphics System, STS Inc., 1986).

Interspecific associations (Jaccard's coeficient and chi-square test) were computed for pairwise combinations of species, as well as the variance ratio for overall species association (Spassoc BaS program, LUDWIG & REYNOLDS, 1988). Interspecific association was investigated between pairs of concurrent species under the null hypothesis that the species are independently distributed by a chi-square statistic computed from a 2 x 2 contingency table, without the Yates correction. The variance ratio (VR) (SCHLUTER, 1984), was used to test, simultaneously, whether species are associated. Under a null hypothesis of no association among species the expected value of VR is 1.0. If VR > 1 or < 1, the statistic "W", where "W" approximates a chi-square distribution, was used to test the significant departure from the expected value of no association. Interspecific covariation between infrapopulations of concurrent species was investigated using the Spearman rank correlation coeficient (Negbinomial BaS program, LUDWIG & REYNOLDS, 1988). The Brillouin's diversity index, H, using common logarithms was calculated as a measure of helminth species diversity in infracommunities. The values obtained in the present study, calculated using the common logarithm, must be multiplied by 2.3026 to be comparable to the values obtained by KENNEDY et alii (1986) calculated using the natural logarithm (GOATER et alii, 1987).

Throughout this paper, statements of statistical significance refer to P ≤ 0.05.

RESULTS

The helminth fauna

Caiman c. yacare from the Brazilian "Pantanal", has a complex helminth community. Prevalence and mean
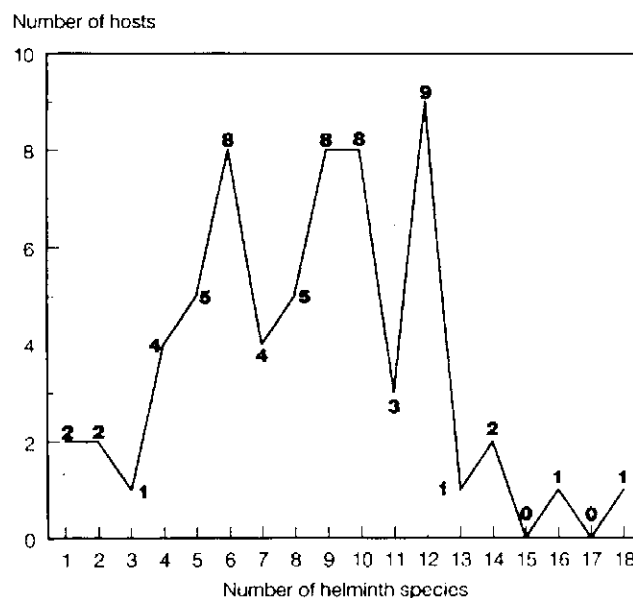

Number of hosts

Fig. 1. Distribution of the helminth species of the caiman, *Caiman crocodilus yacare*, in the Brazilian "Pantanal".

intensities (SE) of 23 helminth species from male and female caimans captured in freshwater lakes and "vazantes" in spring-summer (October to March) and fall-winter (April to September) and in the entire host sample are listed in Table 1. All hosts had at least one parasite species. Hosts had on average 8.3 (range 1-18) species and 1.262 (range 1-7.850) specimens. The digenetic trematodes were the dominant group with 15 species, comprising 79.5% of the total number of specimens collected. Within this group, eight species of proterodiplostomes represented 95.4% and 76% of the total number of digenetic trematodes and helminth specimens collected, respectively. The ascaridoid nematodes, with five species, were the second most diverse and abundant group and contributed with 17% of the total helminth specimens collected. The genus *Brevimulticaecum*, with two species, represented 73% of the nematodes and 13.5% of the total number of helminth specimens. Two digenetic trematode species and three nematode species are new to the host and/or geographical distribution record (Table 1).

Eleven species (48%) were classified as: **dominant** - 6 proterodiplostomes, 3 ascaridoid nematodes, 1 acanthocephalan, and 1 micropleurid nematode; 6 (26%) were classified as **codominant** - 2 proterodiplostomes, 2 acanthostomes, 1 ascaridoid nematode, and 1 telorchiid digenetic trematode; and **subordinate** the remaining six species (26%) (Table 1).

Table 1 - Distribution of the helminth parasites from the caiman, *Caiman crocodilus yacare*, in the Brazilian "Pantanal". Prevalence (P%), mean intensity of infection (I, ±SE), according to sex, season of the year, habitat (location of capture), and total host sample size

Helminth species	Status*	Site**	Male P(%)	Male I	Female P(%)	Female I	Fall-winter P(%)	Fall-winter I	Spring-summer P(%)	Spring-summer I	Lakes P(%)	Lakes I	"Vazantes" P(%)	"Vazantes" I	Total P(%)	Total I
Digenea																
Paradiplostomum abreviatum	ED	a	62	859±296	68	273±108	55	184±29	70	955±89	66	86±28	62	1132±343	64	673±208
Herpetodiplostomum caimancola	GC	a	60	18±6	36	22±7	44	9±3	59	25±7	48	7±3	56	27±7	53	19±5
Cystodiplostomum hollyi	GD	a	62	123±40	52	47±17	66	75±25	54	129±53	48	32±9	67	139±44	59	105±30
Prolecithodiplostomum constrictum	FC	a	28	16±7	21	27±22	25	24±14	27	15±8	29	4±1	14	31±13	26	18±7
Proterodiplostomum medusae	GD	a	73	123±70	57	101±29	74	155±71	64	194±79	70	48±16	67	273±89	68	176±53
Proterodiplostomum tumidilum	ED	a	31	518±260	31	600±412	37	598±341	27	490±277	18	83±60	40	696±275	31	543±214
Proterodiplostomum globulare	ED	a	55	144±106	26	51±23	40	271±241	51	46±18	40	18±7	51	192±139	46	128±89
Proterodiplostomum breve	ED	a	33	354±193	15	335±51	11	140±115	40	33±190	22	132±80	32	460±233	28	351±160
Proctocaecum dorsale	FC	a	24	105±58	10	22±13	11	84±78	29	89±56	0	0	35	92±50	20	92±50
Caimanicola marajoara	GC	a	15	29±10	21	24±20	22	13±5	13	44±17	3	17	27	28±10	17	27±9
Pseudotelorchis yacarei	EC	a	31	92±57	26	12±5	29	13±6	29	113±72	22	10±6	35	99±61	29	71±4
Pseudotelorchis caimanis	ES	d	0	0	5	6	0	0	2	6	3	6	0	0	1	6
Stephanoprora jacaretinga	ES	agh	2	1	10	83±53	7	22±11	2	1	0	0	8	15±9	4	15±9
Cyatocotyle brasiliensis	ES	agh	2	1	15	6±2	11	6±2	2	1	0	0	10	5±0	6	15±2
Pachypsolus sclerops	GS	a	0	0	5	1	3	1	0	0	0	0	2	1	1	'
Acanthocephala																
Polyacanthorhynchus rhopalorhynchus	GD	a	51	31±7	73	35±11	74	41±9	72	26±8	55	11±5	86	42±8	73	32±6
Nematoda																
Brevimulticaecum stekhoveni	GD	b	67	161±40	57	67±42	62	185±62	64	101±32	59	123±65	67	144±33	64	136±32
Brevimulticaecum baylisi	GD	b	75	144±53	68	38±10	62	118±31	81	114±58	70	49±16	75	159±63	73	115±38
Dujardinascaris longispicula	ED	b	33	129±41	31	83±53	37	144±59	29	90±32	29	76±38	35	140±47	32	116±32
Dujardinascaris chabaudi	ES	bgh	4	12	0	0	7	12	0	0	0	0	5	12	2	12
Ortleppascaris alata	GC	abg	26	23±9	36	6±2	37	19±6	27	15±11	25	15±7	35	18±9	31	17±6
Micropleura vazi	ED	c	82	24±5	68	21±4	70	25±8	83	21±4	92	22±4	67	32±7	78	23±4
Capillaria sp.	?S	abgh	15	5±1	21	6±1	11	6±3	21	5±1	11	15±3	21	6±1	17	5±1
Mean species richness			8.5±0.5		7.7±0.6		7.5±0.6		7.8±0.6		7.1±0.6		10.5±1.3		8.3±0.4	
Mean intensity of infection			1517±342		1217±592		1511±336		943±264		343±74		1963±394		1262±246	
Brillouin's index			0.57±0.03		0.55±0.03		0.54±0.03		0.60±0.04		0.60±0.04		0.58±0.03		0.57±0.02	
Host sample size			45		19		37		27		27		37		64	

* E specialist, G generalist, D dominant, C co-dominant, S subordinate.

** a-intestine, b-stomach, c abdominal cavity, d oviduct, g new geographic record, h-new host record.

The helminth distribution pattern

The colonization or dispersion of helminth species in the host population did not differ from normal ($x^2 = 2.69$, DF = 6, P = 0.84) and Poisson ($x^2 = 4.75$, DF = 6, P = 0.57) distributions, but did differ from the negative binomial distribution ($x^2 = 57.62$, DF = 8, P< 0.05) (Fig. 1). In contrast, the variance of the distribution of the 14 most abundant helminth species was significantly greater than the mean, which characterizes a clumped distribution. The value of k, the parameter of the negative binomial distribution, in each of the 14 most abundant species was low, and was independent of host sex, season of the year, and habitat (locality of capture). This is corroborated by eight species in which the distribution of specimens in the entire host sample did fit a negative binomial distribution (Table 2).

The effects of the sex of the hosts, season of the year, and habitat of the hosts (location of capture) on prevalence and abundance

The sex of the host did not influence the infrapopulations and the prevalences, significantly. None of the species

Table 2 - Values for the negative binomial parameter (k) of frequency distributions for the 14 most prevalent species parasites of the caiman, *Caiman crocodylus yacare*, in the Brazilian "Pantanal", according to sex, season of the year, habitat (location of capture), and total host sample size.

Helminth species	Male	Female	Spring-summer	Fall-winter	Lakes	"Vazantes"	Total
Digenea							
Paradiplostomum abreviatum	0.13*	0.15*	0.13*	0.14*	0.21*	0.08*	0.14*[a]
Herpetodiplostomum caimancola	0.25*	0.10*	0.19*	0.22*	0.17*	0.20*	0.19*
Cystodiplostomum hollyi	0.16*	0.14*	0.21*	0.12*	0.13*	0.15*	0.15*[a]
Prolecithodiplostomum medusae	0.24*	0.13*	0.28*	0.17*	0.28*	0.16*	0.21*[a]
Proterodiplostomum tumidilum	0.68	0.17*	0.07*	0.03*	0.03*	0.05*	0.04*
Proterodiplostomum globulare	0.16*	0.07*	0.14*	0.14*	0.12*	0.13*	0.13*[a]
Proterodiplostomum breve	0.05*	0.01*	0.11*	0.08*	0.05*	0.02*	0.03*[a]
Pseudotelorchis yacarei	0.07*	0.08*	0.09*	0.06*	0.08*	0.07*	0.07*[a]
Acanthocephala							
Polyacanthorhynchus rhopalorhynchus	0.33*	0.31*	0.29*	0.36*	0.29*	0.53*	0.32*
Nematoda							
Brevimulticaecum stekhoveni	0.16*	0.18*	0.14*	0.18*	0.20*	0.13*	0.16*[a]
Brevimulticaecum baylisi	0.25*	0.21	0.15*	0.34*	0.26*	0.22*	0.25*[a]
Dujardinascaris longispicula	0.05*	0.08*	0.05*	0.05*	0.05*	0.05*	0.05*
Ortleppascaris alata	0.08*	0.17*	0.11*	0.15*	0.10*	0.13*	0.09*[a]

* Variance significantly greater than mean P < 0.05.

[a] Frequency distributions fit the negative binomial distribution P ≤0.05

showed significant differences in prevalence, but two had abundances influenced significantly by the season of the year. *Ortleppascaris alata* was more abundant in fall-winter (P = 0.02), while *Herpetodiplostomum caimancola* was more abundant in spring-summer (P = 0.03) (Table 3).

The habitat of host influenced helminth distribution. Seven species had significantly larger infrapopulations (Table 3) and one, *Polyacanthorhynchus rhopalorhynchus*, occurred more frequently in "vazantes" than in lakes ($x^2 = 7.65$, P = 0.015). Furthermore, other species not included in these analyses (*Proctocaecum dorsale*, *Cyatocotyle brasiliensis*, *Stephanoprora jacaretinga*, and *Caimancola marajoara*), although having relatively high prevalences (4.6-20.3%), occurred exclusively or almost exclusively in hosts found in "vazantes" (Table 1).

The interspecific associations and covariation

Twelve of the 91 possible pairwise associations among the 14 most prevalent species were negative, but not significant. Twenty-seven of the 79 positive associations were significant, mainly among proterodiplostomes and ascaridoid nematodes. Although the 21 possible associations among seven species of proterodiplostomes and six possible associations among four species of ascaridoid nematodes represented 29.5% of the 91 possible associations, the 16 significant associations among these groups did represent 68% of the significant associations

Table 3 - Helminth parasites of the caiman, *Caiman crocodylus yacare*, with intensities of infection influenced by the season of the year and the habitat (location of capture).

Helminth species	Season of the year		Habitat	
	Z	P	Z	P
Proterodiplostomum medusae	0.45	0.4602	2.58	0.0112
Paradiplostomum abreviatum	1.66	0.0959	2.98	0.0028
Cystodiplostomum hollyi	1.22	0.2192	2.27	0.0227
Herpetodiplostomum caimancola	2.11	0.0342	2.43	0.0177
Brevimulticaecum stekhoveni	-0.91	0.3611	2.04	0.0408
Brevimulticaecum baylisi	-1.33	0.1513	2.03	0.0461
Ortleppascaris alata	-2.31	0.0206	-0.75	0.4500
Polyacanthorhynchus rhopalorhynchus	-1.92	0.0537	2.78	0.0052

Z=normal aproximation to "U".
P=Probability level.

observed (Table 4). Simultaneously, the overall association among the 14 most prevalent species was positive and significant (VR = 3.15, W = 201.62, P ≤ 0.01).

Table 4 lists the values of the Spearman's correlation coefficient (rs) for the 27 pairs of species with significant interspecific associations. Six pairs of species had negative, but not significant, covariance. Seven of the nine pairwise significant, positive, covariations were among proterodiplostomes and two among ascaridoid nematodes.

DISCUSSION

The mean species richness per host, prevalence, and mean intensities of infection indicate that the caiman's helminth communities in the Brazilian "Pantanal" are more complex than those of the American alligators in South Carolina, USA. HAZEN et alii (1978) collected a total of six species of helminths in alligators, which hosted fewer species (mean = 2.6) and specimens (mean = 561). In the same host, *C. c. yacare*, GOLDBERG et alii (1991) collected in Paraguay an equivalent number of species of gastric nematodes, but both the prevalences (<14%) and the size of the infrapopulations (<12) were much lower than those reported in the present study. There are many variables which influence the helminth dispersion, and alligators are a different host species in another hemisphere. Lower prevalences and smaller infrapopulations observed in the same host captured from the margins of the river in the Brazilian "Pantanal" borders are, probably, due to the influence of the habitat (location of capture), which is discussed below.

The fact that from the 8 proterodiplostome, 2 acanthostome, and 4 among the 5 ascaridoid nematode species being dominant or codominant species, corroborates the work of

Table 4 - Interspecific affinity among the 14 most prevalent helminth species from the caiman, *Caiman crocodylus yacare*, in the Brazilian "Pantanal".

Helminth species pairs	Interspecific association (Jacard's coeficient)	Interspecific covariation (rs)
Polyacanthorhynchus rhopalorhynchus / Paradiplostomum abreviatum	0.52*	0.59*
P. rhopalorhynchus / Herpetodiplostomum caimancola	0.53*	0.60*
P. rhopalorhynchus / Proterodiplostomum medusae	0.63*	0.42*
Cystodiplostomum hollyi / P. medusae	0.42*	0.47*
C. hollyi / H. caimancola	0.50*	-0.01
C. hollyi / P. medusae	0.64*	0.48*
C. hollyi / Proterodiplostomum breve	0.37*	0.16
Proterodiplostomum globulare / Proterodiplostomum tumidilum	0.39*	0.77*
P. globulare / P. breve	0.35*	0.33
P. tumidilum / P. breve	0.44*	0.51
H. caimancola / P. medusae	0.59*	0.13
H. caimancola / P. breve	0.45*	0.05
P. medusae / P. breve	0.32*	0.33*
Brevimulticaecum stekhoveni / Brevimulticaecum baylisi	0.63*	0.68*
Ortleppascaris alata / Dujardinascaris longispicula	0.36*	-0.14
D. longispicula / B. baylisi	0.36*	0.48*
P. rhopalorhynchus / O. alata	0.37*	-0.25
C. hollyi / B. baylisi	0.60*	0.22
H. caimancola / O. alata	0.37*	0.36
H. caimancola / D. longispicula	0.45*	-0.08
P. breve / D. longispicula	0.37*	-0.13
P. breve / B. baylisi	0.53*	0.19
H. caimancola / B. baylisi	0.62*	0.02
P. rhopalorhynchus / B. stekhoveni	0.57*	0.37
P. medusae / Pseudotelorchis yacare	0.43*	0.37
B. stekhoveni / P. yacare	0.36*	0.07
P. tumidilum / P. rhopalorhynchus	0.37+	0.15

* Observed positive concurrent species pairs significantly greater than that expected under the null hypothesis that the species are independently distributed, by a chi-square analysis of 2x2 contingency table (P≤0.05).

* Covariation in abundance of species pairs significantly and positively correlated (Spearman's rank correlation, P≤0.05).

BROOKS & O'GRADY (1989), who postulated that the proterodiplostomes-echinostomes and ascaridoid nematodes-acanthostomes/crocodilian systems as being the groups with the oldest coevolutionary history. There is much discussion about the development of parasite communities, as a result of co-speciation (BROOKS, 1980) or host capture (GOATER et alii (1987).

In the same manner as the controversy about the classification of parasite communities as isolationists or interactive evolved to a continuum between these extremes, the parasite communities also represent a continuum between coevolution and stochastic events. The crocodilians/helminths system (BROOKS, 1979; BROOKS & O'GRADY, 1989) appears to be a good example of coevolution influence in the structure of the helminth parasite community.

The colonization of hosts as measured by prevalence and intensity of infection was not influenced by the host sex and scarcely by the season of the year. We have no biological explanations for the larger infrapopulations of *O. alata* in fall-winter and of *H. caimancola* in spring-summer. Since the helminth fauna of the caimans is acquired only by ingestion of intermediate hosts which are part of their diet, the helminth distribution can be influenced only by qualitative and/or quantitative dietary changes which occur with age, sex, and behavior of the host or environmental factors such as season of the year and the habitat. Environmental factors affect the population dynamics of intermediate hosts in the development of larval forms and colonization of intermediate hosts. The climate in the Brazilian "Pantanal" is tropical, therefore inhibition or interruption of feeding common to crocodilians of temperate climate occurs only for some days in winter. Moreover, UETANABARO (1989) did not observe significant influence of age, sex, and season of the year on the diet of subadult and adult caimans in the same region of the present study, fact that may explain the low influence of these variables on the helminth prevalence and abundance.

The variable habitat (location of capture) (lakes *versus* "vazantes") influenced mainly the distribution of the helminth specimens. Seven of the most prevalent species had larger infrapopulations in "vazantes" (Table 3) and four other species, with relatively high prevalence, occurred exclusively in this environment. The unique occurrence of *C. marajoara* in lakes is attributed to the recent movement of the host to this habitat. There are no qualitative and/or quantitative studies about the diet of caimans in "vazantes", but the seasonal character of these watercourses results in periods of concentration of definitive and intermediate hosts, increasing the transmission of parasites. The occurrence of some species of digenetic trematodes, exclusively, in "vazantes" is probably due to the exclusive occurrence of intermediate hosts of these species in this environment. The life cycles of the helminth parasites of the caiman are unknown, but BROOKS & O'GRADY (1989) showed that the acanthostomes, which colonized crocodilians, came from fish in estuarine environments or lotic waters where the majority of crocodilian species live. The most probable explanation is that the small teleosts, intermediate hosts of the acanthostomes, do not occur in the lentic waters of lakes.

Although the species' dispersion in each host did indicated a random distribution similar to that observed by GOATER *et alii* (1987), in three out of four species of salamanders, the dispersion of the specimens of each helminth species was clumped (Table 2), as commonly occurs with the majority of the helminth species (ANDERSON, 1982). The observation that the variance was significantly greater than the mean in all of the analyzed species, resulting in a *k* parameter close to zero, independently of host sex, season of the year, and habitat in the entire host population, shows that, although the infrapopulations of some of the species were influenced by the variable habitat, the pattern of dispersion or clumped degree did not change. This agrees with WALLACE & PENCE (1986), who, by studying the helminth dispersion in blue-winged teals, concluded that the degree of overdispersion does not change, but the relative number of specimens in the infracommunities does. Therefore, besides the heterogeneity in the population of the host (age, sex, and condition), individual host factors (genetics and immunity), and larval helminth clumped distribution in the intermediate hosts are important to the stability of the pattern of dispersion in the host population (WALLACE & PENCE, 1986). In our study, 17% of the caimans hosted 76% of the total of helminths collected, *i.e.*, generally one individual host had large infrapopulations of many helminth species or, conversely, one individual host was parasitized by only a few specimens of many helminth species. Thus, individual host susceptibility or clumped larval distribution in the intermediate hosts may not be substantial, but is sufficient for the stability of the pattern of the helminth aggregated distribution. *Caiman c. yacare* in the Brazilian "Pantanal" is parasitized by a large number of congeneric species which, probably, make use of the same intermediate hosts.

The large species number and the many congeneric species, with high prevalence and large intensities of infection, may indicate that the infracommunities of the caimans are not depauperate and that vacant niches may not be common, both of which are traits of interactive infracommunities (STOCK & HOLMES, 1988).

KENNEDY *et alii* (1986), after accepting the great complexity of bird infracommunities in relation to those of fish, listed some host variables which favor the production of diverse, complex parasite communities: complexity of the alimentary canal, endothermy, high vagility, broad diet, selective feeding on prey which serve as intermediate hosts for many helminth species, and exposure to direct helminth life cycle, which enter by penetration. Crocodilians have a simple alimentary canal, similar to that of fish, have low vagility, are ectothermic, have a small exposure to helminths with direct life cycle, and are dietary generalists. All of these factors, except one (the broad diet), predispose

the crocodilians to a depauperate and not complex helminth fauna, as we found in this study. In spite of crocodilians being dietary generalists, studies carried out in the same area (UETANABARO, 1989) showed that caimans in freshwater lakes in the Brazilian "Pantanal" feed, mainly, on molluscs, crustaceans, insect larvae, and fish, in the decreasing order. Although the life cycles of digenetic trematodes and ascaridoid nematodes, the main groups of caiman parasites, are unknown, molluscs are probably the first and second intermediate hosts of the majority of the digenetic trematode species. SPRENT (1979) reported frogs as intermediate hosts of *Dujardinascaris*. Thus, the caiman's habit, in the Brazilian "Pantanal", of feeding on prey which serve as intermediate hosts for many helminth species is, apparently, sufficient to override all the other factors identified by KENNEDY *et alii* (1986) for the production of depauperate infracommunities. Our data also contradicts GOATER *et alii* (1987), who, after comparing the helminth communities of four species of ectothermic, generalist, insectivorous salamanders with endothermic insectivorous bats (LOTZ & FONT, 1985), suggested that "the distinction in isolationist *versus* interactive parasite communities may be primarily a function of whether the host is ectothermic or endothermic". GOATER *et alii* (1987) also proposed that natural helminth communities comprised of phylogenetically unrelated species, as in salamanders, will be primarily isolationist in character, while helminth communities comprised of congeners and phylogenetically related species, as in the lesser scaups, in which the species transmitted by two species of amphipods were dominant (BUSH & HOLMES, 1986), will be interactive.

The crocodilian host-parasite system has been pointed out as an example of coevolution between hosts and their helminths (BROOKS, 1979; BROOKS & O'GRADY, 1989) and caimans in the Brazilian "Pantanal" harbor many congeneric species. The significantly positive, overall association between the most prevalent species and the 27 positive, significant pairwise associations, mainly between phylogenetically related species (proterodiplostomes and ascaridoid nematodes), corroborate the assertion by GOATER *et alii* (1987) and our hypothesis that the caimans in the Brazilian "Pantanal" feed, selectively, on intermediate hosts used by many phylogenetically related helminth species. Similarly, the nine positive, significant, interspecific covariations (Table 4) occurred between phylogenetically related species.

Due to the absence of significant, negative, interspecific associations and covariation, interspecific competition, if it exists, is not sufficiently strong to the point that the presence of a species hampers or inhibits the colonization of the same individual host by another species. Thus, although

the occurrence of congeneric species in the high intensity infections is frequent, a predisponent factor for an interactive community, the helminth community of *C. c. yacare* is not. We are collecting further data to analyze the distribution of each species along the intestine to investigate competition for microhabitat.

In a review of 393 surveys of helminth communities of 155 species of amphibians and reptiles, AHO (1990) found a maximum of 10 helminth species in one host species (mean 3.0 ± 0.12). Individually, each host was parasitized, at most, by five species (mean 0.8 ± 0.1) and 572 specimens (mean 59.6 + 19) of helminths. Comparing the helminth communities of herps with those of other vertebrates (fish, birds, and mammals), AHO (1990) concluded that the differences were dramatic, classifying amphibians and reptiles as the hosts with the most depauperate helminth fauna of all vertebrates. The helminth populations observed in this study (in terms of species richness, prevalence, mean number of helminth species, and abundance) are greater than in any other host-parasite system and greater than those observed in fish HOLMES (1990) and similar to those found in birds and mammals (KENNEDY *et alii*, 1986), in spite of the complex alimentary tract, high vagility, and greater exposure to direct helminth life cycles in birds. The values of the diversity indices found in *C. c. yacare* are high when compared to those obtained by GOATER *et alii* (1987) in salamanders, and higher yet, than those obtained by KENNEDY *et alii* (1986) in fresh-water fishes and birds. BUSH & AHO (1990) called attention to the necessity of parasitologic studies with an ecological approach in the tropics, since temperate-zone studies predominate in the literature. The tropical and humid climate with undefined seasons allows the caimans from the Brazilian "Pantanal" to have less qualitative and quantitative dietary restriction throughout the year and, in spite of diminished feeding in winter, they do not utilize the dormant period, common to ecthotermic animals of temperate climates. These factors, associated with the selective feeding on prey which serve as intermediate hosts for various helminth species, are responsible for the more complex helminth community of caimans in relation to fish, amphibians, and other reptiles.

SUMÁRIO

A comunidade parasitária de helmintos dos crocodilianos tem sido pouco estudada até a presente data. A distribuição dos helmintos no hospedeiro, as relações interespecíficas, a influência do sexo, estação do ano e o habitat (local de captura) dos hospedeiros foram estudados ao longo de 64 necropsias de jacarés, *Caiman crocodilus yacare*, a única espécie e subespécie que ocorre no Pantanal brasileiro, com o objetivo de comparar a estrutura de sua comunidade parasitária de helmintos com aquelas de outros répteis, anfíbios, peixes e aves. As infracomunidades de helmintos dos jacarés do Pantanal brasileiro possuem características de comunidades interativas. Estes jacarés são parasitados por grande número de espécies, muitas das quais congenéricas, com altas prevalências e intensidades de infecção. Embora existam fatores predisponentes para interação intraespecífica, não existiram associações negativas significativas ou covariação negativa entre os pares de espécies co-ocorrentes presentes. A variável sexo do hospedeiro, não influenciou as prevalências e as intensidades de infecção; a variável estação do ano, influenciou a intensidade de infecção de duas espécies: *Ortleppascaris alata* e *Herpetodiplostomum caimancola*; e a variável habitat do hospedeiro (local de captura), influenciou a prevalência de uma espécie - *Polyacanthorhynchus rhopalorhynchus*, e as intensidades de infecção de sete outras espécies. A maior complexidade e diversidade de infecção das infracomunidades dos jacarés no Pantanal brasileiro, em relação àquelas de outros répteis, anfíbios, e mesmo de peixes e aves, é atribuída à dieta seletiva dos hospedeiros, a qual é integrada por organismos que funcionam como hospedeiros intermediários para muitas espécies de helmintos encontradas.

PALAVRAS-CHAVE: *Caiman crocodilus yacare*, jacarés, Pantanal, análise ecológica.

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