

## Interrelationships between small mammal ectoparasites and habitats on the Maracá Island, Roraima, Brazil

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### ABSTRACT

An ecological evaluation of habitats on the Maracá Island, Roraima, Brazil, is proposed, based on the comparative study of mammalian ectoparasite fauna. Habitats were clustered into groups with similar fauna, based on the richness, diversity, abundance, prevalence and interchange of ectoparasites and analyzed phenetically using ectoparasites as characters. A phenogram indicated two spatial groups: natural habitats, represented by the forest and the *Curatella/Byrsonima* savanna at Santa Rosa and modified or mixed habitats represented by the seasonally flooded savanna, the Ecological Station and the area around the Ecological Station water tank. Interchange of ectoparasites between hosts showed a higher impact of the forest on the Santa Rosa savanna than vice versa, indicating that currently the savanna is suffering retraction.

**KEYWORDS:** ectoparasites, habitats, small mammals, ecological interrelationships, Maracá Island, Brazil

### INTRODUCTION

During 1987-1988 a floristic, faunistic and geologic survey called "Maracá Rain Forest Project" was carried out in Maracá Island, State of Roraima,

Brazil, sponsored by the Instituto de Pesquisas da Amazônia (INPA), ex-Secretaria Especial do Meio Ambiente (SEMA) and the Royal Geographical Society. Several Brazilian and foreign researchers developed activities in this project. Partial results of these studies, including ectoparasites of small mammals and their interactions with the hosts were previously published [1, 2].

Although rodents and marsupials constitute the main hosts for fleas, mites and lice in Neotropics [3], the feeding preferences of these ectoparasites can be specific or generalist. The generalism of species is an important parameter in the study of epidemiological questions relating to the transmission of certain pathogens. For this reason, ectoparasites have been studied more as vectors than infesting agents. In the last case, specific association may constitute an auxiliary method for the taxonomic identification of the respective hosts providing support for the findings of mammalogists [4]. Sometimes these associations have been used to evidence evolutionary relationships among hosts [5-8].

In the last years, the host parasite interactions have been employed to correlate data of host species (body size, metabolic rates, phylogeny, density) or geographical parameters (latitudinal gradients and climatic variables) with richness, abundance and prevalence of ectoparasites species [9-14]. Recently, the effects of environmental factors on the diversity and abundance of two ectoparasite groups, fleas and mites parasitic on small mammals (rodents and marsupials), were studied in different localities across Brazil [15].

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The aim of this study was to compare the habitats or ecological formations of the Maracá Island with regards to the richness, diversity, abundance and prevalence of their ectoparasite faunas. We also searched for genesis and evolution of those formations based on the interchange of ectoparasites among them.

## MATERIALS AND METHODS

Maracá is a huge riverine island of some 92,000 ha formed by the bifurcation of the Uraricoera River, located approximately 110 km northwest of Boa Vista ( $3^{\circ}15'$  to  $3^{\circ}35'$  N;  $61^{\circ}22'$  to  $61^{\circ}58'$  W). The island is 60 km long and up to 25 km wide and it is situated near the junction of the Amazonian forest and the dry savanna (Fig. 1). The rain forest is the dominant morpho-climatic unit on the Maracá Island, interrupted in places by patches of natural savanna, seasonally flooded wetlands, creeks and low hills. It appears that the savanna originated during the last ice age, and has since been progressively substituted by tropical forest, thus restoring the primitive (plesiochoric) state [16, 17].

In the period between 22/02 and 05/03/88, which corresponds to the dry season on the Maracá Island, 26 small mammals (25 rodents and one marsupial) were collected from the rain forest (RF), the *Curatella/Byrsonima* savanna at Santa Rosa (SR), the seasonally flooded savanna below the Ecological Station (FS), shrubby vegetation near Station water tank area (WT) and from inside the outbuildings of the Ecological Station itself (ES). Sherman and Tomahawk traps were employed, baited and checked daily, with a total effort of 2,920 trap nights. Various bait types were used, including seed mixtures (maize, rice, peanut and sunflower); fruits (jackfruit, coconut and banana); roots (manioc) and peanut butter, rodent viscera and 'Scotts's emulsion' (cod-liver oil).

The hosts were trapped in plastic bags and killed with sulphuric ether, at the capture site. The ectoparasites were collected by brushing and after preservation in 70% ethanol they were mounted on slides for taxonomic identification. Some specimens of acari and chewing lice were not specifically identified for they are immatures. Voucher specimens of ectoparasites were deposited

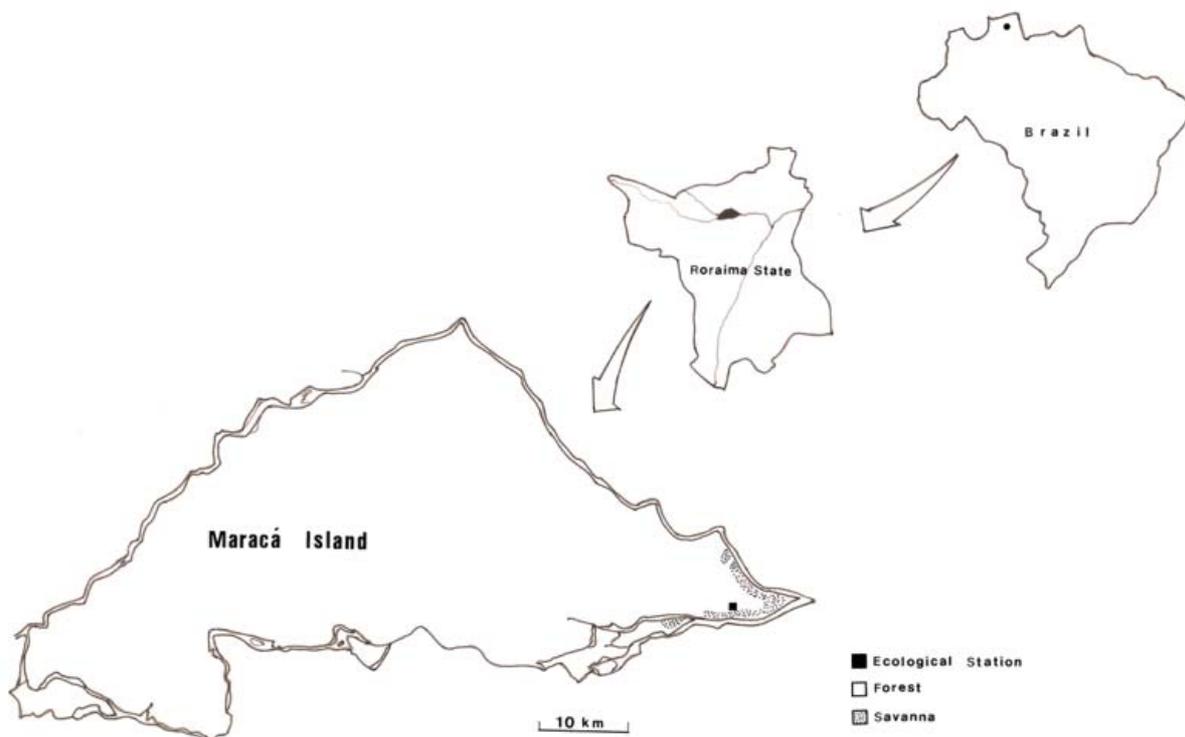


Fig. 1. Map of the Maracá Island in the State of Roraima, Brazil.

in the Sector of Ectoparasites of the Department of Parasitology of Federal University of Minas Gerais (UFMG). Skins and skulls of the hosts are in the Department of Zoology of UFMG, Brazil.

Further sets of ectoparasites were used. They were collected from 28 hosts taken during a small mammal population survey in the same habitats. These included specimens killed by snap-traps, whose ectoparasites were therefore not removed at the time of death nor shortly afterwards. These sets were collected by Aléxia da Cunha during two distinct study periods: November 1987/January 1988 and January/February 1989.

For each habitat we calculated ectoparasite species richness ( $S$  = number of species), Shannon specific diversity index ( $H = -\sum P_i [\log n P_i]$ ), mean abundance and prevalence [18]. Comparisons between the habitats were made using the samples of ectoparasites collected on the hosts and employing the simple matching coefficient, in which the ectoparasites were used as characters for the evaluation of phenetic similarity between the respective habitats. The characters were coded in two states (0 = absent, 1 = present), following the model used in numerical taxonomy [19]. The matching coefficients were obtained for each habitat by establishing the proportion between the value of the character states of shared characters and the total number of characters studied, for each pair of habitats. A phenogram was constructed by the unweighted pair-group method analysis (UPGMA) after determining the association coefficients by the simple matching method.

Although both hosts and ectoparasites have been collected some time ago, the data was re-examined in the light of the new approaches. Ecological formations at the Maracá Island were statistically compared, using the chi-square test ( $\chi^2$ ) for the interchange of ectoparasites and median test ( $t$ ) for median abundance, calculated between each pair of formations, at 2 df. The  $\chi^2$ -test with the Yates correction also was applied to compare the prevalences among the respective formations.

## RESULTS AND DISCUSSION

A total of 54 small mammals belonging to seven species of rodents and two of marsupials were captured, as well as 1,774 ectoparasites (13 genera

and 22 species) grouped in different Orders. Mammals and Siphonaptera nomenclature follows the respective proposals of authors [20, 21]. The following hosts and ectoparasites species were collected: rodent species - *Necromys* sp., *Holochilus brasiliensis* (Desmarest), *Nectomys squamipes* (Brants), *Oligoryzomys fulvescens* (Saussure), *Proechimys guyannensis* (Geoffroy), *Proechimys* sp. and *Cavia porcellus* (L.); marsupial species - *Marmosa murina* (L.) and *Monodelphis brevicaudata* (Erxleben); acari species - *Amblyomma* sp., *Ornithonyssus* sp., *Echinonyssus* sp. n., *Androlaelaps fahrenheitsi* (Berlese), *Gigantolaelaps goyanensis* Fonseca, *Laelaps dearmasi* Furman and Tipton, *Laelaps flexa* Furman, *Laelaps paulistanensis* Fonseca, *Mysolaelaps parvispinosus* Fonseca, *Tur amazonicus* Fonseca, *Tur apicalis* Furman and Tipton, *Tur aragaoi* (Fonseca) and *Tur aymara* Fonseca; lice species - *Hoplopleura splendida* Johnson, *Cummingsia* sp., *Gliricola* sp., *Gliricola* sp. n., *Gliricola porcelli* (Schrank) and *Gliricola venezuelanus* Emerson and Price; flea species - *Gephyropsylla klagesi klagesi* (Rothschild), *Gephyropsylla klagesi samuelis* (Jordan and Rothschild) and *Rhopalopsyllus australis* ssp.

The number of individuals of mammal species captured from different habitats or environments were as follows: *Necromys* sp.: ES ( $n = 16$ ), WT ( $n = 6$ ); *H. brasiliensis*: SR ( $n = 2$ ), FS ( $n = 4$ ); *N. squamipes*: RF ( $n = 1$ ); *O. fulvescens*: SR ( $n = 2$ ), FS ( $n = 1$ ); *P. guyannensis*: SR ( $n = 7$ ), RF ( $n = 6$ ); *Proechimys* sp.: RF ( $n = 2$ ), WT ( $n = 2$ ); *C. porcellus*: FS ( $n = 2$ ); *M. murina*: SR ( $n = 1$ ); *M. brevicaudata*: RF ( $n = 2$ ). Although the small mammal fauna of the Maracá Island is quite poor in number of species and individuals compared to other parts of the country, two species (one mite and one biting louse) are new to science and awaiting description.

Table 1 presents the data on the occurrence of ectoparasites on these species in each of the capture habitats, given as the number and the respective proportion of ectoparasite individuals recorded. The ectoparasite species richness ( $S$ ) and specific diversity index ( $H$ ) obtained for each habitat were investigated and based on the data of Table 1 were: SR ( $S = 13$ ,  $H = 1.60$ ); RF ( $S = 14$ ,  $H = 2.02$ ); FS ( $S = 7$ ,  $H = 1.13$ ); ES ( $S = 3$ ,  $H = 0.40$ ) and WT area ( $S = 3$ ,  $H = 0.82$ ).

**Table 1.** Ectoparasite fauna in different habitats on the Maracá Island, Roraima, Brazil. A, Santa Rosa savanna; B, forest; C, seasonally flooded savanna; D, Ecological Station; E, water tank area; N, number of ectoparasites; P, proportion of ectoparasites in the samples (x 100); ( ) number of mammal species in each habitat.

Ectoparasite species	Habitats									
	A (12)		B (11)		C (7)		D (16)		E (8)	
	N	P	N	P	N	P	N	P	N	P
Acari:										
<i>Amblyomma</i> sp.	-	-	7	1.69	-	-	-	-	-	-
<i>Echinonyssus</i> sp. n.	-	-	5	1.21	-	-	-	-	-	-
<i>Ornithonyssus</i> sp.	9	1.08	2	0.49	-	-	-	-	-	-
<i>A. fahrenheiti</i>	6	0.72	9	2.18	-	-	-	-	-	-
<i>G. goyanaensis</i>	8	0.97	4	0.97	13	26.53	-	-	-	-
<i>L. dearmasi</i>	-	-	-	-	-	-	76	88.37	204	51.00
<i>L. flexa</i>	66	7.98	-	-	24	48.99	-	-	-	-
<i>L. paulistanensis</i>	3	0.36	-	-	1	2.04	9	10.46	-	-
<i>M. parvispinosus</i>	-	-	-	-	1	2.04	1	1.17	-	-
<i>T. amazonicus</i>	4	0.48	1	0.24	-	-	-	-	-	-
<i>T. apicalis</i>	59	7.13	27	6.56	-	-	-	-	14	3.50
<i>T. aragaoi</i>	-	-	7	1.69	-	-	-	-	-	-
<i>T. aymara</i>	131	15.86	80	19.43	1	2.04	-	-	-	-
Total	286	34.58	142	34.46	40	81.64	86	100	218	54.50
Phthiraptera:										
<i>H. splendida</i>	2	0.24	6	1.45	-	-	-	-	-	-
<i>Cummingsia</i> sp.	-	-	1	0.24	-	-	-	-	-	-
<i>Gliricola</i> sp.	-	-	-	-	1	2.04	-	-	-	-
<i>Gliricola</i> sp. n.	519	62.76	154	37.39	-	-	-	-	182	45.50
<i>G. porcelli</i>	-	-	-	-	8	16.32	-	-	-	-
<i>G. venezuelanus</i>	-	-	53	12.87	-	-	-	-	-	-
Total	521	63.00	214	51.95	9	18.36	-	-	182	45.50
Siphonaptera:										
<i>G. k. klagesi</i>	17	2.06	56	13.59	-	-	-	-	-	-
<i>G. k. samuelis</i>	2	0.24	-	-	-	-	-	-	-	-
<i>R. australis</i> ssp.	1	0.12	-	-	-	-	-	-	-	-
Total	20	2.42	56	13.59	-	-	-	-	-	-
Total	827	100	412	100	49	100	86	100	400	100

Although the sampling of parasites is dependent upon the sampling of their hosts [22], the number of ectoparasites taken from the savanna at Santa Rosa (SR) was twice that recorded in the forest (RF) (Table 1), in spite of the similar host samples collected in these two formations. Both SR and RF presented the same host richness and similar

ectoparasite richness; however, with the exception of *P. guyannensis*, the two formations included different host species. Concerning ectoparasites, while acari were found in all formations, lice and fleas occurred, respectively, in four and two of them (Table 1). Nine species were encountered exclusively in some habitats, being five in RF,

two in SR and other two in FS. Other 13 species shared at least two formations. Only three mite species occurred in three different formations.

Table 2 shows the mean abundance and the prevalence of each species of ectoparasite in the five formations studied. The mean abundance

observed in SR was almost twice that recorded in RF and almost nine times that from the FS. Contrary to the fleas, the mean abundance of acari and lice in SR was approximately twice that from the RF. Both in SR and RF, lice presented greater mean abundance than acari; however, similar

**Table 2.** Mean abundance and prevalence of mammalian ectoparasites according to habitats on the Maracá Island, Roraima, Brazil. A, Santa Rosa savanna; B, forest; C, seasonally flooded savanna; D, Ecological Station; E, water tank area; ( ) number of mammal species in each habitat; MA, mean abundance; P, prevalence.

Ectoparasite species	Habitats									
	A (12)		B (11)		C (7)		D (16)		E (8)	
	MA	P (%)	MA	P (%)	MA	P (%)	MA	P (%)	MA	P (%)
Acari:										
<i>Amblyomma</i> sp.	-	-	0.64	36.36	-	-	-	-	-	-
<i>Echinonyssus</i> sp. n.	-	-	0.45	9.09	-	-	-	-	-	-
<i>Ornithonyssus</i> sp.	0.75	16.67	0.18	9.09	-	-	-	-	-	-
<i>A. fahrenheiti</i>	0.50	25.00	0.82	27.27	-	-	-	-	-	-
<i>G. goyanensis</i>	0.67	8.33	0.36	9.09	1.86	42.85	-	-	-	-
<i>L. dearmasi</i>	-	-	-	-	-	-	4.75	12.50	25.55	75.00
<i>L. flexa</i>	5.50	16.67	-	-	3.43	42.85	-	-	-	-
<i>L. paulistanensis</i>	0.25	8.33	-	-	0.14	14.28	3.69	6.25	-	-
<i>M. parvispinosus</i>	-	-	-	-	0.14	14.28	0.06	6.25	-	-
<i>T. amazonicus</i>	0.33	16.67	0.09	9.09	-	-	-	-	-	-
<i>T. apicalis</i>	4.91	50.00	2.54	45.45	-	-	-	-	1.75	25.00
<i>T. aragaoui</i>	-	-	0.64	18.18	-	-	-	-	-	-
<i>T. aymara</i>	10.92	41.67	7.27	54.54	0.14	14.28	-	-	-	-
Total	23.83	83.33	12.91	100	5.71	71.42	5.37	18.75	27.25	100
Phthiraptera:										
<i>H. splendida</i>	0.17	8.33	0.54	18.18	-	-	-	-	-	-
<i>Cummingsia</i> sp.	-	-	0.09	9.09	-	-	-	-	-	-
<i>Gliricola</i> sp.	-	-	-	-	0.14	14.28	-	-	-	-
<i>Gliricola</i> sp. n.	43.25	58.33	14.00	27.27	-	-	-	-	22.75	25.00
<i>G. porcelli</i>	-	-	-	-	1.14	14.28	-	-	-	-
<i>G. venezuelanus</i>	-	-	4.81	9.09	-	-	-	-	-	-
Total	43.41	66.67	19.45	63.63	1.28	28.57	-	-	22.75	25.00
Siphonaptera:										
<i>G. k. klagesi</i>	1.42	41.67	5.09	18.18	-	-	-	-	-	-
<i>G. k. samuelis</i>	0.17	8.33	-	-	-	-	-	-	-	-
<i>R. australis</i> ssp.	0.08	8.33	-	-	-	-	-	-	-	-
Total	1.67	50.00	5.09	18.18	-	-	-	-	-	-
Total	68.92	91.67	37.45	27.27	7.00	71.42	5.37	18.75	50.00	100

values were observed in WT for the two groups of ectoparasites. Although all environments presented differences with regard to the mean abundance and prevalence, they were not significant ( $p > 0.05$ ). Interestingly for Siphonaptera the abundance was higher in the forest, while the prevalence was higher in the Santa Rosa savanna. However the data concerning the prevalence of fleas must be interpreted with caution, having in view the method of capture of some hosts, in which the specimens were killed by snap-traps, and the ectoparasites not removed at the time of death nor shortly afterwards. It is important to stress that fleas leave those hosts that have been confined in traps for the longest, and abandon the carcass completely after death [3, 23].

The occurrence of large numbers of predatory animals in one or other habitat, bringing about reduction in the small mammal population, could be another factor limiting the ectoparasite infestations recorded in the studied habitats. Abundance is a parameter that could be employed as an indicator of the state of health of the respective host. Thus, high mean abundance might be related to the inability of the host to oppose the action of the parasite by means of its immune system and/or its behavior (for example, by grooming) [9]. However, the diminution of hosts in a given area regulates, in the general sense, the increase in the ectoparasite population in the surviving hosts, as occurs in epizootic plague. Also it is important to point out that other factors, such as mating, greater permanence and the exploration of burrows, influence the infestation of respective hosts.

Lice, fleas and mites differ substantially in their biology and behaviour. In lice, all the stages develop on their respective hosts. Only adult fleas are ectoparasitic whilst the immature stages develop in the soil, inside or close to the nests of the respective hosts and, consequently, are susceptible to predation by other ectoparasites or environmental modifications. Fleas are obligate haematophages, whereas the feeding modes of mites are vastly variable and range from obligatory haematophagy to predation on small arthropods found in hosts' burrows [15]. On other hand, mesostigmatid mites present a varied diet, considering that some of them may obtain blood of a host via predation on

other blood-feeding organisms rather than via direct blood sucking, also dispersing by phoresy. Thus, in the face of this perspective, Brazilian fleas and mites were considered as body and nest dwellers, respectively [15]. Prevalence and mean abundance of these ectoparasites could thus assist nature conservation studies since they could be indicators of habitat changes when compared temporally in a single locality or habitat. The characteristics of the habitats are also important factors for determining the respective infestation parameters [24].

Character states coded as "0" or "1" for 22 ectoparasites of the five habitats are presented in Table 3. The association coefficients between

**Table 3.** Distribution of character states (as 0 or 1) for each character (= ectoparasites) in five habitats on the Maracá Island, Roraima, Brazil. A, Santa Rosa savanna; B, forest; C, seasonally flooded savanna; D, Ecological Station; E, water tank area.

Ectoparasite species	Habitats				
	A	B	C	D	E
<i>Amblyomma</i> sp.	0	1	0	0	0
<i>Echinonyssus</i> sp. n.	0	1	0	0	0
<i>Ornithonyssus</i> sp.	1	1	0	0	0
<i>A. fahrenheiti</i>	1	1	0	0	0
<i>G. goyanaensis</i>	1	1	1	0	0
<i>L. dearmasi</i>	0	0	0	1	1
<i>L. flexa</i>	1	0	1	0	0
<i>L. paulistanensis</i>	1	0	1	1	0
<i>M. parvispinosus</i>	0	0	1	1	0
<i>T. amazonicus</i>	1	1	0	0	0
<i>T. apicalis</i>	1	1	0	0	1
<i>T. aragaoi</i>	0	1	0	0	0
<i>T. aymara</i>	1	1	1	0	0
<i>H. splendida</i>	1	1	0	0	0
<i>Cummingsia</i> sp.	0	1	0	0	0
<i>Gliricola</i> sp.	0	0	1	0	0
<i>Gliricola</i> sp. n.	1	1	0	0	1
<i>G. porcelli</i>	0	0	1	0	0
<i>G. venezuelanus</i>	0	1	0	0	0
<i>G. k. klagesi</i>	1	1	0	0	0
<i>G. k. samuelis</i>	1	0	0	0	0
<i>R. australis</i> ssp.	1	0	0	0	0

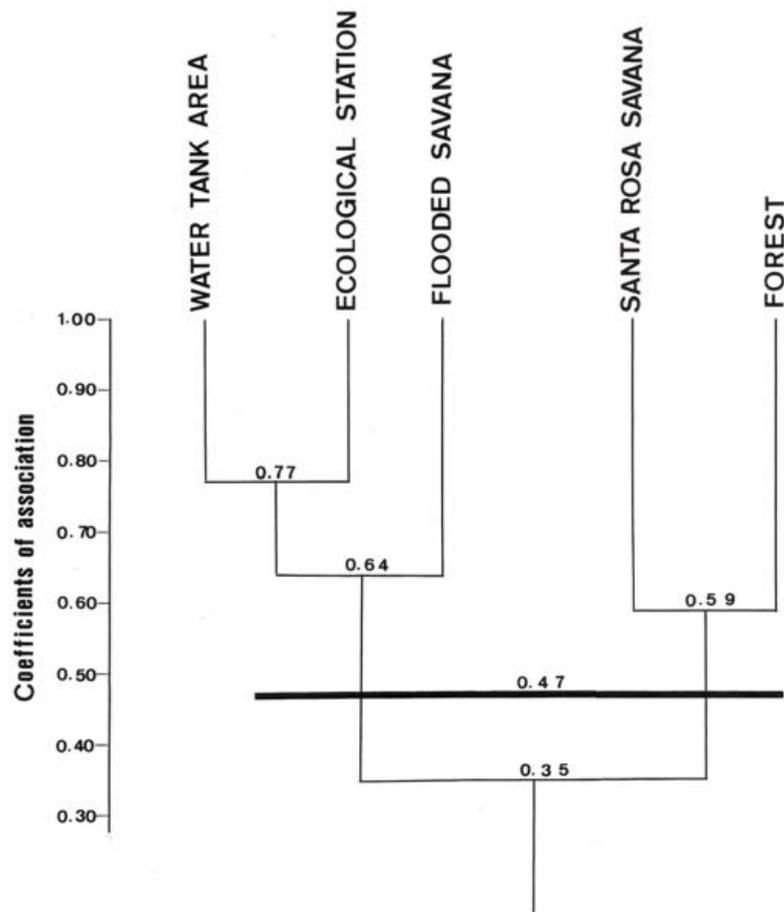
each pair of habitat are shown in Table 4. The phenogram obtained by UPGMA is illustrated in Fig. 2. The natural habitats (Santa Rosa savanna and forest) are ecologically separated from the

**Table 4.** Data matrix for the association coefficient between each pair of habitats on the Maracá Island, Roraima, Brazil. A, Santa Rosa savanna; B, forest; C, seasonally flooded savanna; D, Ecological Station; E, water tank area.

	A	B	C	D	E
A	-				
B	0.59	-			
C	0.45	0.23	-		
D	0.36	0.23	0.73	-	
E	0.45	0.36	0.55	0.77	-

others by the 0.35 phenon line. The 0.47 phenon line represents the mean phenon line and characterizes two groups: WT/ES/FS against SR/RF. However, the most closely related habitats are WT and ES, such as in the case of a phenogram when using hosts, rather than ectoparasites, as characters. The seasonally flooded savanna represents a peculiar habitat more related to the natural than to the modified habitats. Consequently, the number of ectoparasites being more than twice that of their respective hosts, they might be more adequate to be used as indicators of ecological similarity or vicinity.

For each species of ectoparasite, the frequency of individuals among ectoparasite species and collected in each habitat are indicated (Table 5). Only those species recorded in more than one



**Fig. 2.** Phenogram depicting ecological relationships between habitats of the Maracá Island, Roraima, Brazil, using ectoparasites as characters and obtained by unweighted pair-group method analysis.

**Table 5.** Frequency of the ectoparasites in habitats investigated on the Maracá Island, Roraima, Brazil. A, Santa Rosa savanna; B, forest; C, seasonally flooded savanna; D, Ecological Station; E, water tank area; N, number of caught ectoparasites; %, percentage among ectoparasite species.

Ectoparasite species	Habitats										Total	
	A		B		C		D		E			
	N	%	N	%	N	%	N	%	N	%	N	%
<i>Ornithonyssus</i> sp.	9	82	2	18	-	-	-	-	-	-	11	100
<i>A. fahrenheitzi</i>	6	40	9	60	-	-	-	-	-	-	15	100
<i>G. goyanensis</i>	8	32	4	16	13	52	-	-	-	-	25	100
<i>L. dearmasi</i>	-	-	-	-	-	-	76	27	204	73	280	100
<i>L. flexa</i>	66	73	-	-	24	27	-	-	-	-	90	100
<i>L. paulistanensis</i>	3	23	-	-	1	8	9	69	-	-	13	100
<i>M. parvispinosus</i>	-	-	-	-	1	50	1	50	-	-	2	100
<i>T. amazonicus</i>	4	80	1	20	-	-	-	-	-	-	5	100
<i>T. apicalis</i>	59	59	27	27	-	-	-	-	14	14	100	100
<i>T. aymara</i>	131	62	80	38	1	1	-	-	-	-	212	100
<i>H. splendida</i>	2	25	6	75	-	-	-	-	-	-	8	100
<i>Gliricola</i> sp. n.	519	61	154	18	-	-	-	-	182	21	855	100
<i>G. k. klagesi</i>	17	23	56	77	-	-	-	-	-	-	73	100

habitat are included. The fluxes are also indicated with the species showing different directions of ecological interchange from the greater to the lesser frequencies (Fig. 3). The habitats are listed in order of their apparent succession on Maracá Island. Unlike in the forest, in the Santa Rosa savanna the primary species predominate. Thus *Ornithonyssus* sp., *L. flexa*, *T. aymara* and *Gliricola* sp. n. appear to be passing from the savanna to the forest. Some of them reached modified or more distant habitats (seasonally flooded savanna and the water tank area). Others, such as *A. fahrenheitzi*, *H. splendida* and *G. klagesi klagesi* are typical for the forest, and arriving into the savanna. *Laelaps dearmasi*, *L. paulistanensis* and *M. parvispinosus* are species of modified habitats, into which cricetines of the genus *Necromys* have been introduced.

The presence of a certain parasite on a certain host may be a consequence of parallel evolution between the two (co-speciation), or of ecological adaptation (co-accommodation) [25]. In the same way we could regard the occurrence of a certain fauna in a certain habitat as the result of ancient colonizations or adaptative processes in progress. The existence of two distinct neighbouring biomes

on Maracá, and the expansion or retraction of one of them over the other during distinct epochs, therefore offers an opportunity for analysis in space and time. Thus, one of Manter's rules [25] states that "a host species harbors the largest number of parasite species in the area where it has resided longest, so if the same or two closely-related species of host exhibit a disjunct distribution and possess similar parasite faunas, the areas in which the hosts occur must have been contiguous at a past time". Although the savanna-forest system on Maracá has never been separated, in spite of the geographic position of the savanna-forest boundary to have changed along the time, the savanna at Santa Rosa could be considered a more primitive habitat, since currently it is being substituted by the forest, according to evidences supported by different studies [16, 17, 26]. Both the two habitats presents the same ectoparasite species richness ( $S = 13$ ) and the forest exhibits a higher diversity index than the Santa Rosa savanna (2.02 against 1.60). Besides, five of the 22 species (22.7%) were collected only in the forest. From the direction of ectoparasite interchange between the studied habitats (Fig. 2) it may be noted that the impact of the forest on the savanna



**REFERENCES**

1. Linardi, P. M., Botelho, J. R., Rafael, J. A., Valle, C. M. C., Cunha, A. and Machado, P. A. R. 1991, *Acta Amaz.*, 21, 131.
2. Linardi, P. M., Botelho, J. R. and Rafael, J. A. 1991, *Acta Amaz.*, 21, 141.
3. Marshall, A. G. 1981, *The Ecology of Ectoparasitic Insects*, Academic Press, London.
4. Linardi, P. M. 1977, *Bol. Mus. Hist. Nat. UFMG Zool.*, 23, 1.
5. Stammer, H. J. 1957, *Zool. Anz.*, 159, 255.
6. Hennig, W. 1966, *Phylogenetic Systematics*, Urbana, Illinois.
7. Brooks, D. R. 1981, *Syst. Zool.*, 30, 229.
8. Brooks, D. R. 1987, *Int. J. Parasitol.*, 17, 291.
9. Stanko, M., Miklisová, D., de Bellocq, J. G. and Morand, S. 2002, *Oecologia*, 131, 289.
10. Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. and Degen, A. 2004, *J. An. Ecol.*, 73, 1121.
11. Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S. and Poulin, R. 2005, *Global Ecol. Biogeogr.*, 14, 167.
12. Bossard, R. L. 2006, *J. Parasitol.*, 92, 260.
13. Krasnov, B. R., Shenbrot, G. I., Khokhlova, I., Mouillot, D. and Poulin, R. 2008, *J. Biogr.*, 35, 592.
14. Lareschi, M. and Krasnov, B. R. 2010, *Med. Vet. Entomol.*, 24, 284.
15. Linardi, P. M. and Krasnov, B. R. 2012, *Med. Vet. Entomol.*, doi: 10.1111/j.1365-2915.2012.01025.x.
16. Haffer, J. 1969, *Science*, 165, 131.
17. Prance, G. T. 1982, *Ann. Missouri Bot. Gard.*, 69, 594.
18. Begon, M., Harper, J. L. and Townsend, C. R. 1988, *Ecologia, Individuos, Poblaciones y Comunidades*, Omega, Barcelona.
19. Sneath, P. H. A. and Sokal, R. R. 1973, *Numerical Taxonomy*, WH Freeman and Company, San Francisco.
20. Wilson, D. E. and Reeder, D. M. 2005, *Mammal Species of the World: a Taxonomic and Geographic Reference*, Johns Hopkins University Press, Baltimore.
21. Linardi, P. M. and Guimarães L. R. 2000, *Sifonápteros do Brasil*, Museu de Zoologia USP/FAPESP, São Paulo.
22. Feliu, C., Renaud, F., Catzeflis, F., Hugot, J-P., Durand, P. and Morand, S. 1997, *Parasitology*, 115, 453.
23. Pollitzer, R. 1954, *Plague*, World Health Organization, Monograph Series 22, Geneva.
24. Krasnov, B. R., Shenbrot, G. I., Medvedev, S. G., Vatschenok, V. and Khokhlova, I. S. 1997, *Parasitology*, 114, 159.
25. Brooks, D. R. 1979, *Syst. Zool.*, 28, 299.
26. Hemmig, J., Ratter, J. and dos Santos, A. A. 1988, *Maracá: Roraima/Brasil*, Lloyds Bank/ICI Brasil S. A., São Paulo.
27. Brooks, D. R. 1985, *Ann. Missouri Bot. Gard.*, 72, 660.