Papéis Avulsos de Zoologia

MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO

ISSN 0031-1049

PAPÉIS AVULSOS DE ZOOL., S. PAULO 42(12):299-323 08.XI.2002

SURVEYING NEOTROPICAL SOCIAL WASPS. AN EVALUATION OF METHODS IN THE "FERREIRA PENNA" RESEARCH STATION (ECFPn), IN CAXIUANÃ, PA, BRAZIL (HYM., VESPIDAE, POLISTINAE)

ORLANDO TOBIAS SILVEIRA

ABSTRACT

A survey of social wasps was made in the area of the "Ferreira Penna" Research Station (ECFPn) in Caxiuanã, PA, Brazil. Traditional collecting methods as the use of Malaise traps and the search for individuals and colonies of wasps along trails in the forest and by river margins, were applied in a more systematized fashion. Seventy-nine species belonging to 18 genera were discovered within a discontinuous period of 52 days of collecting. Angiopolybia pallens, Polybia liliacea, *and several* Agelaia *species were the most frequently collected species. Active search for wasps in the forest and by river margins was far more efficient than Malaise traps regarding the discovery of polistine species.*

KEYWORDS: Vespidae, Polistinae, social wasps, survey, Caxiuanã, ECFPn.

RESUMO

O artigo apresenta e discute os métodos empregados e resultados de um levantamento das vespas sociais da Estação Científica Ferreira Penna (ECFPn), em Caxiuanã, PA, Brasil. Métodos tradicionais, como armadilhas

Museu Paraense Emílio Goeldi/MCT, Coordenação de Zoologia, Av. Perimetral, s/n, Caixa Postal 399, 66040-170, Belém, PA, Brasil. E-mail: tobias.silveira@zipmail.com.

Trabalho recebido para publicação em 15.I.2001 e aceito em 21.VI.2002.

de Malaise e a procura ativa por indivíduos e colônias de vespas em trilhas e pelas margens de rios, foram usados segundo um esquema de amostragem mais sistematizado do que é usual em tais levantamentos, com o fim de produzir dados mais facilmente analisáveis e comparáveis. Setenta e nove espécies de 18 gêneros de Polistinae foram registradas num período de 52 dias descontínuos de trabalho de campo. Angiopolybia pallens, Polybia liliacea *e algumas espécies de* Agelaia *foram as mais freqüentes. A procura ativa pelas vespas no interior da floresta e pelas margens de rios foi muito mais eficiente em respeito à descoberta de espécies, do que as armadilhas de Malaise.*

PALAVRAS-CHAVE: Vespidae, Polistinae, vespas sociais, levantamentos, Caxiuanã, ECFPn.

INTRODUCTION

Social wasps stand out as characteristic elements of neotropical insect faunas. The social behavior, markedly expressed on nest architecture and in the aggressive way females defend the colonies, makes of these wasps objects of the interest of people in general, and insect collectors in particular. Neotropical social vespids are representatives of the Polistinae, a group comprising 26 genera and more than 900 species, more numerous and diversified in the tropical and subtropical regions of the planet (Carpenter *et al.*, 1996; Richards, 1971, 1978). In Brazilian Amazonia, 20 genera and more than 200 species have been recorded, representing about 2/3 of the Brazilian fauna. As predators of insects, social wasps play an important role in the alimentary chain in terrestrial environments, and some species of the genera *Agelaia* and *Angiopolybia* are habitual consumers of the carcasses of dead animals (O'Donnell, 1995).

Because social wasps are such interesting and conspicuous insects, they are comparatively well represented in collections, and the taxonomy of the neotropical Polistinae is relatively well worked-out. Most species can be readily identified with published keys (Cooper, 1996a, 1996b, 1997a, 1997b, 1998b; Richards, 1978). In addition, preliminary hypotheses on the phylogenetic relationships among the polistine genera are already available (Carpenter, 1991; Carpenter *et al.*, 1996), and the perspectives of extending that knowledge to groups of species within the genera are also promising (Carpenter *et al.*, 2000, on *Polybia*; Silveira, 2000, thesis on *Mischocyttarus*). Reconstruction of phylogenetic relationships is a prerequisite to analyses of biogeographic patterns, and has also great importance in comparative diversity studies (Faith, 1995; Williams *et al.*, 1993). The recent developments on the systematics of the Polistinae support the expectation that the group would be very useful in analy-

ses involving the characterization and comparison of regional faunas. In Amazonia, where social wasps are very diverse, this potential seems particularly important. However, there is still much inventory work to do in the region so that its vast territory can be reasonably covered. Besides the difficult access to most parts of the region, two other factors have prevented the rapid accumulation of more comprehensive information on local faunas of social wasps: the relatively large effort necessary to reach a satisfactory knowledge of the occurring species, and the difficulties of estimating the relative abundance of species. Comparisons of local faunas by the use of information in collections always confront the obstacles arising from unsystematic collecting methodologies. In general, appropriate information about the effort spent in finding a certain number of species is not available, and data about the relative abundance of the species are hardly recoverable.

Most attempts of estimating the abundance of populations of social wasps have been based on the counting of colonies in transects or in quadrats (Archer, 1985; Kitayama *et al.*, 1989; Kojima, 1993; Ohgushi *et al.*, 1988; Rocha *et al.*, 1989; Roth and Lord, 1987). Quadrats have been used to estimate densities of colonies in western-central Brazil, in "cerrado" or grassland vegetation (Diniz *et al.*, 1998; Raw, 1998). However, in areas of very dense and high vegetation as the Amazonian forests, the task of exploring the environment while looking for wasps nests is expected to be far more difficult, and perhaps it would also be hard to reach a sufficiently large number of samples. Another point is that, for an inventory of social wasps, the total distance explored within the area is certainly a crucial factor in the maximization of the number of species found. The "line census" technique used by Ohgushi *et al.* (1988) in a work on the ecological distribution and density of colonies of Stenogastrinae in Southeast Asia, seems more adequate for surveying social wasps in Amazonia. It may be adapted to work along river margins, and to produce a reasonable number of samples so that variances can be estimated.

This paper presents the results of a survey of the social wasps in the area of the "Ferreira Penna" Research Station (ECFPn) in Caxiuanã, PA, Brazil, based on traditional collecting methods as the use of Malaise traps (Archer, 1990; Carpenter and Wenzel, 1999; Kojima and van Achterberg, 1997) and the search for individuals and colonies of wasps along trails in the forest and by river margins, applied in a more systematized fashion. In addition to a list of species of social wasps, the tentative use of "sampling units" allowed me to provide indirect estimates of the abundance of a majority of the species. It also made possible the construction of species accumulation curves, useful in the evaluation of the efficiency of the collecting methods, and of the level achieved in the inventory of the species (Colwell and Coddington, 1994).

Materials and Methods

The Ferreira Penna Research Station (ECFPn)

The ECFPn is situated in the northern part of the Brazilian state of Pará (1:32'S 51:20'O/1:50'S 51:41'O), south of Amazon river and just west of Marajó island, in the municipality of Melgaço (Fig. 1). The Research Station covers an area of 33.000 ha within the "Floresta Nacional de Caxiuanã", and is under the administration of the "Museu Paraense Emílio Goeldi". The area is dominated by "terra firme" high forest (80%), but there are also other vegetation types, mainly fringes of "várzea" and "igapó" forest along the margins of black-water rivers. Botanic surveys have found great floristic diversity in the ECFPn (Almeida *et al.*, 1993; Lisboa *et al*., 1997). The climate is the *Am* type (Köppen) with abundant rainfall during several months, though dropping to less than 60 mm in October and November. The annual precipitation ranges from 2.000 to 2.500 mm. The mean annual temperature is 26 °C, with the relative humidity around 85%.

The expeditions

Four expeditions with duration of 15 days were made to the ECFPn: 1st) March-April, 2nd) June-July, 3rd) November 1998, 4th) April-May 1999. Field

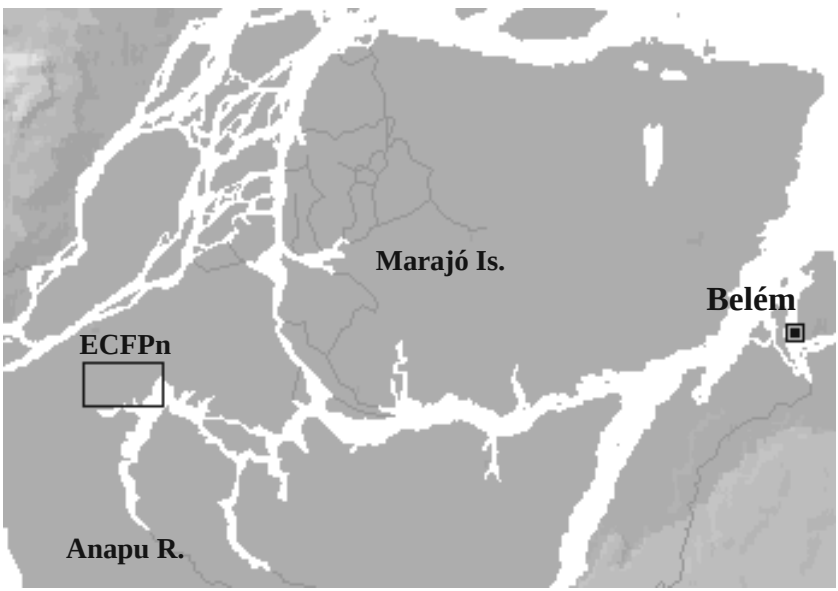

Figure 1. Map showing localization of the ECFPn, in Caxiuanã, west of Belém and Marajó Island, in Pará state.

work was conducted so as to progressively cover an area as largest as possible of the ECFPn. In the first expedition, surveying was restricted to the surroundings of the ECFPn buildings and the Curuá and Curuazinho rivers. In the other three expeditions, work was conducted respectively in the areas of the Puraquequara and Tijucaquara rivers (2nd), Arauá, Sapucuzinho and Caxiuanã rivers (3rd), Laranjal stream and the west margin of "Caxiuanã bay" (4th). A straight line crossing the sampled areas measures approximately 25 km.

Malaise traps

Three kinds of traps were used in Caxiuanã: 1) *Two Meter Malaise Trap* (TMM) based on the Townes model, with one collecting chamber; 2) *Six Meter Malaise Trap* (SMM) with two collecting chambers; 3) *Suspended Malaise Trap* (SUM) with one collecting chamber (Rafael and Gorayeb, 1982). In each survey, 10 TMM traps were installed at a correspondent number of sites in primary forest, spaced by at least 500 m so as to diminish the chances of any two or more traps of capturing individuals from the same colony or from a very localized group of colonies. Five SUM traps were installed at heights of 15-20 m, generally at the same sites used for a correspondent number of the TMM traps. All traps were put to use in periods of 10 days, and the killing agent (potassium cyanide) was changed at the 5th day. The unit sample was the full 10-days period, but results obtained by the 5th day were also examined.

The single SMM trap was always installed at the same point in primary forest, in all phases of the inventory.

Active search for wasps

Searches for colonies and foraging individuals were made in trails in the forest and by boat (moved with paddles) along the margins of rivers and small streams. The intended unity sample was a linear distance of 1,000 m but a certain level of variation was allowed. Most of the trails had already been measured and demarcated previously by other workers at the ECFPn, but by the river margins the distances had to be estimated. Most searches had a duration of about two hours, and were performed by four persons. One of them was a guard from the ECFPn staff not always engaged in the work of finding nests. João Raimundo Araújo (contracted field assistant), native from Caxiuanã and exceptionally skilled for visual examination of the forest, found most of the nests. OTS also participated in all the surveys, and José A. Pena e José O. Dias (assistants from the Museu Goeldi staff) participated each in two of the four expeditions. Two collectors had insect nets, and binoculars were used to explore higher trees, but most of the effort was applied to the vegetation up to 10 m from the ground.

Specimens are deposited in the collection of the Museu Paraense Emílio Goeldi (MPEG).

Limitation of the sampling schemes and the measure of abundance

One objective of the work in Caxiuanã was to establish a simple sampling protocol that could be reproduced in other areas, so that more comparable information would be available than it is usually the case. However, it soon became apparent that such a protocol should be implemented in accord with the usual time and funding limitations of faunistic work in Amazonia, and some prerequisites of statistical analyses had to be relaxed: 1) the randomization of the sampling locations was not attempted: in each expedition, Malaise traps were placed in groups within somewhat restricted areas (considering the total area of the ECFPn). The same generally occurred in respect of searches in trails and by river margins, so that samples could not strictly be assumed to be independent; 2) in the case of searches, sample size was not rigorously the same since a certain level (about 30%) of variation occurred around the originally intended 1,000 m path length. Other sources of heterogeneity between samples were varying speed, and the hour of the day (and weather conditions) at which a search was performed, this being more influent on the capture of foraging wasps.

In both traps and searches, an indirect measure of the relative abundance of the species was estimated by their frequency in samples (number of samples in which the species was present/total number of samples). Other quantities observed were the numbers of colonies and species per sample, and the number of individuals captured in traps.

Species accumulation curves

The process of addition of species relative to the increasing collecting effort was evaluated with the program ESTIMATES 501 (Cowell, 1997), which produces estimates of the "maximum number of species" for a given collecting curve. One very useful aspect of the program is that it makes possible to estimate how many additional samples would be necessary to achieve a certain number of species.

Results and Discussion

Composition of the fauna

The survey in Caxiuanã revealed a rich fauna of social wasps. Seventy-nine species belonging to 18 genera were discovered within a discontinuous

period of 52 days of collecting (Table 1). The twenty-four species of *Mischocyttarus* and 18 species of *Polybia* comprise together a little more than 50% of the list. Five of the species are certainly undescribed, and several are newly recorded for Pará state.

Mischocyttarus – nine subgenera or major groups are represented in the species list, with a supremacy of *Kappa* and the *artifex* group of *Haplometrobius*. The absence of *Scytokeraia* species is not surprising since that subgenus is not expected to occur in Brazilian Amazonia, but the absences of *Phi* (the *alfkenii* group) and *Omega* are more noticeable. Three undescribed species were encountered as single individuals captured in Malaise traps. The species referred as "sp. *heliconius* group" was treated erroneously by Richards (1978) as *M. undulatus* (Ducke), and is yet to be properly named (see Carpenter, 1999). The species referred as "sp. *prominulus* group" could not be identified with certainty, being related to *M. alboniger* Richards. *Mischocyttarus duckei* (du Buysson), *M. melanops* Cooper, *M. adolphi* Zikán, *M. saturatus* Zikán, *M. sylvestris* Richards, and *M. tectus* Cooper are all newly recorded for oriental Amazonia.

Apoica sp. nr. *thoracica* – the color pattern differs from that of *A. thoracica* du Buysson.

Agelaia sp. nr. *cajennensis* – a nest of this species was enclosed by leaves of a 3-meter sapling in the forest. The colony was accidentally encountered when the plant stem was cut, most individuals escaping after that.

Protopolybia sp. nr. *scutellaris* – a species similar to *P. scutellaris* Bequaert, but the nest presents an envelope.

Polybia – the second genus in number of species, subgenera *Myrapetra* and *Trichinothorax* dominating the list. Only the small and rather rare subgenera *Furnariana* and *Platypolybia* (and *Synoecoides*; see Carpenter *et al.*, 2000) were not encountered in Caxiuanã. *Polybia* (*Alpha*) sp. was found as a single individual in a Malaise trap, and could not be determined with certainty as either *signata* Ducke or *bifasciata* Saussure.

Performance of the methods and relative abundance of species

1) TMM traps

1.1. Total species and frequency in samples

Twenty-three species of 6 genera were captured in the TMM traps (Table 2). Considering the total collecting effort (40 sites/traps X 10 days), and that these 23 species represent only 29% of the species found in the ECFPn with all methods, it is apparent that using such traps is not too profitable a method for surveying social wasps, at least in environments like the forest in Caxiuanã. However, from the viewpoint of a rapid preliminary survey, using TMM traps may be a satisfactory procedure for collecting the more common species in a given place. The mean species accumulation curve for this method

Table 1. Records of the 79 species of social wasps found in the ECFPn, Caxiuanã, PA, Brazil, within a discontinuous period of 52 days of field work. "#" identifies the respective modes of discovering; "C" means that colonies were found. In the column relative to habitat/site of collecting, "build." refers to buildings of the ECFPn, and "sec.veg." to secondary vegetation.

Species	trap	search	informed	other	habitat/site
1 – ***Polistes*** *occipitalis* Ducke		#(C)			bay
2 – *P. pacificus* F.		#(C)	#(C)	#(C)	sec.veg.
3 – *P. versicolor* (Olivier)		#(C)	#(C)	#(C)	sec.veg.
4 – *P. goeldii* Ducke		#		#	stream
5 – ***Mischocyttarus*** *labiatus* (F.)		#			forest
6 – *M. tomentosus* Zikán		#(C)		#	sec.veg.
7 – *M. carbonarius* (Saussure)		#(C)			forest
8 – *M. duckei* (du Buysson)	#				forest
9 – *M. lecointei* (Ducke)		#(C)			forest
10 – *M. melanops* Cooper		#(C)			stream
11 – *M. foveatus* Richards		#(C)		#(C)	forest, river, stream, bay
12 – *M. imitator* (Ducke)		#(C)	#(C)	#(C)	river, build.
13 – *M. adolphi* Zikán				#, #(C)	forest
14 – *M. injucundus* (Saussure)		#(C)			sec.veg.
15 – *M. juruanus* Richards		#(C)		#(C)	river, bay
16 – *M. metathoracicus* (Saussure)			#(C)		forest
17 – *M. saturatus* Zikán		#(C)		#(C)	forest, stream
18 – *M. collarellus* Richards		#(C)		#	stream, bay
19 – *M. tectus* Cooper		#			forest
20 – *Mischocyttarus* sp. *artifex* group		#			forest
21 – *Mischocyttarus* sp. 2 *artifex* group		#			forest
22 – *M. sylvestris* Richards	#	#(C)			forest
23 – *M. oecothrix* Richards		#(C)			forest, stream
24 – *M. synoecus* Richards		#(C)			forest
25 – *M. surinamensis* (Saussure)				#	bay
26 – *Mischocyttarus* sp. *prominulus* group		#(C)			forest
27 – *Mischocyttarus* sp. *heliconius* group	#				forest
28 – *Mischocyttarus* sp. *iheringi* group	#				forest
29 – ***Apoica*** *pallida* (Olivier)		#(C)		#	river, bay
30 – *Apoica* sp. nr. *thoracica*		#(C)			forest
31 – *A. pallens* (F.)				#(C)	forest
32 – *A. arborea* Saussure				#	build.
33 – ***Agelaia*** *testacea* (F.)	#	#			forest
34 – *A. angulata* (F.)	#	#			forest
35 – *A. angulicollis* (Spinola)	#	#			forest
36 – *A. fulvofasciata* (Degeer)	#	#		#	forest, river, bay
37 – *A. cajennensis* (F.)	#	#		#(C)	forest, bay, build.
38 – *Agelaia* sp. nr. *cajennensis*				#(C)	forest
39 – *A. myrmecophila* (Ducke)	#	#			forest
40 – *A. pallipes* (Olivier)	#	#		#	forest

Continued

Species	trap	search	informed	other	habitat/site
41 – *A. centralis* (Cameron)	#	#		#	forest
42 – ***Angiopolybia*** *pallens* (Lepeletier)	#	#(C)		#	*all
43 – *A. paraensis* (Spinola)	#	#		#	forest
44 – ***Pseudopolybia*** *difficilis* (Ducke)	#	#(C)			forest
45 – ***Parachartergus*** *richardsi* Willink		#,#(C)			forest, stream
46 – *P. fraternus* (Gribodo)		#(C)			forest, river, stream, bay
47 – ***Leipomeles*** *dorsata* (F.)		#(C)			forest
48 – ***Charterginus*** *fulvus* Fox				#(C)	sec.veg.
49 – ***Protopolybia*** *chartergoides* (Gribodo)				#(C)	sec.veg.
50 – *P. emortualis* (Saussure)		#(C)			river
51 – *Protopolybia* sp. nr. *scutellaris*				#(C)	sec.veg.
52 – ***Brachygastra*** *bilineolata* Spinola			#(C)	#(C)	sec.veg., stream
53 – *B. lecheguana* (Latreille)			#(C)		river
54 – ***Chartergus*** *metanotalis* Richards		#(C)	#(C)		river, stream
55 – *C. globiventris* Saussure			#(C)		sec.veg.
56 – ***Polybia*** *dimorpha* Richards	#				forest
57 – *P. platycephala* Richards		#(C)			forest, stream, bay
58 – *P. bistriata* (F.)		#(C)			stream, sec. veg.
59 – *P. bicyttarella* Richards	#				forest
60 – *P. scrobalis* Richards	#	#(C)		#(C)	forest, stream, sec.veg.
61 – *P. parvulina* Richards		#(C)			stream
62 – *P. quadricincta* Saussure	#	#(C)	#(C)	#	forest
63 – *Polybia* (*Alpha*) sp.	#				forest
64 – *P. gorytoides* Fox		#(C)		#(C)	forest
65 – *P. rufitarsis* Ducke		#(C)	#(C)		forest, bay
66 – *P. affinis* du Buysson		#(C)		#	forest
67 – *P. micans* Ducke		#(C)		#, #(C)	forest, bay
68 – *P. jurinei* Saussure		#, #(C)			forest, river
69 – *P. rejecta* (F.)		#(C)	#(C)	#(C)	forest, river, stream, bay
70 – *P. liliacea* (F.)	#	#		#	forest
71 – *P. striata* (F.)	#				forest
72 – *P. dimidiata* (Olivier)		#,#(C)	#(C)	#	forest, bay
73 – *P. singularis* Ducke	#				forest
74 – ***Synoeca*** *virginea* (F.)	#	#,#(C)		#	forest, river, stream, bay
75 – *S. surinama* (L.)			#(C)		river
76 – ***Epipona*** *tatua* (Cuvier)				#	river
77 – ***Asteloeca*** *traili* (Cameron)		#(C)			river
78 – ***Metapolybia*** *cingulata* (F.)			#(C)	#(C)	forest, build.
79 – ***Clypearia*** *sulcata* (Saussure)	#				forest

Table 2. Frequencies of social wasps in Two-meter Malaise traps (TMM) relative to a total of 40 samples (40 sites X 10 days) obtained in primary forest in the ECFPn, in Caxiuanã, PA, Brazil. Information is also given on the total numbers of individuals, and the areas of the ECFPn where the species were found. s: surroundings of the ECFPn buildings; c: Curuazinho-heliporto; p: Puraquequara; t: Tijucaquara; n: acampamento; a: Arauá; s: Sapucuzinho; x: Caxiuanã river; l: Laranjal; f: Calafate.

Species	Frequency (%)	(n) individuals	s	c	p	t	n	a	s	x	l	f
1 – *Angiopolybia pallens*	0.42	48	#	#	#	#	#	#	#	#		
2 – *Polybia liliacea*	0.40	58	#	#	#		#				#	#
3 – *Polybia singularis*	0.22	17			#	#		#	#	#		
4 – *Agelaia fulvofasciata*	0.20	16		#	#	#					#	#
5 – *Agelaia centralis*	0.18	8			#			#	#		#	#
6 – *Agelaia cajennensis*	0.08	3			#				#	#		
7 – *Agelaia testacea*	0.08	3			#						#	#
8 – *Polybia dimorpha*	0.08	5	#		#							
9 – *Polybia scrobalis*	0.05	2	#	#								
10 – *Synoeca virginea*	0.05	2	#					#				
11 – *Angiopolybia paraensis*	0.05	2	#									
12 – *Agelaia pallipes*	0.05	2	#		#							
13 – *Agelaia myrmecophila*	0.05	2								#		
14 – *Polybia gorytoides*	0.05	2						#			#	
15 – *Agelaia angulicollis*	0.02	5		#								
16 – *Pseudopolybia difficilis*	0.02	3										#
17 – *Agelaia angulata*	0.02	1	#									
18 – *Polybia quadricincta*	0.02	1			#							
19 – *Polybia* (*Alpha*) sp	0.02	1									#	
20 – *Polybia dimidiata*	0.02	1							#			
21 – *Polybia striata*	0.02	1									#	
22 – *Mischocyttarus sylvestris*	0.02	1				#						
23 – *Mischocyttarus* sp. gr. *iheringi*	0.02	1							#			

(Fig. 2) shows that it would be possible to find about half the total number of trapped species with only 10 samples (10 traps X 10 days), or 1/4 of the collecting effort. Furthermore, five species were collected exclusively in TMM traps, one *Mischocyttarus* species being undescribed.

The numbers on Table 2 show that only five species were trapped with some regularity. *Angiopolybia pallens* and *Polybia liliacea* were the two most frequent species, present in about 40% of the samples, and in a majority of the sampled areas. *Polybia singularis*, *Agelaia fulvofasciata*, and *A. centralis* formed an intermediary group, with frequencies around 20%. The remaining 18 species were mostly of the genera *Polybia* and *Agelaia*, and were far less commonly found in traps.

1.2. Numbers of individuals and species per sample

Figure 3 (A and B) shows box-whiskers plots for the numbers of individuals and species captured in TMM traps in each of the four surveys (n=10).

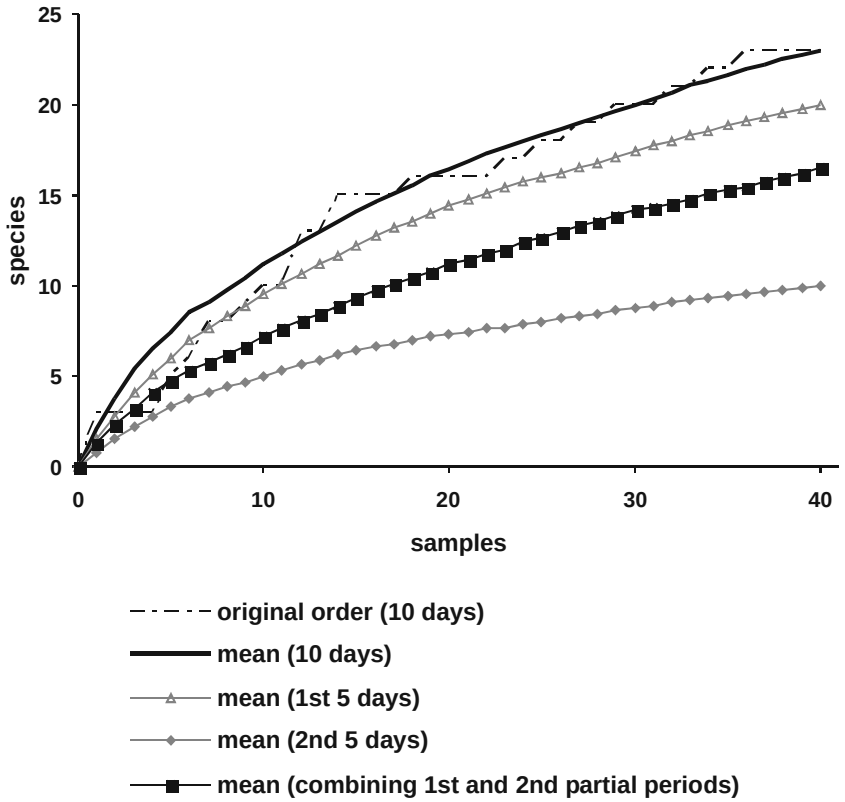

Figure 2. Species accumulation curves for social wasps captured in 40 collecting sites with Two-meter Malaise traps (TMM) in the ECFPn, in Caxiuanã, PA, Brazil. Curves without markers represent addition of 10-days samples, and curves with markers refer to partial 5-days samples. Smooth curves are mean curves from 100 instances of randomization of sample accumulation order. The mean curve for all 80 partial 5-days samples was truncated at "sample 40".

For both variables, the means were similarly very low across all phases of the inventory, but considerable variation was observed within phases around the respective means. Such a combination implies that there were no significant quantitative differences among the four surveys. The mean number of captured individuals per trap varied between 4-6, the mean number of species per trap was always around 2, and the total number of species in all traps also varied quite narrowly between 8-11. This is in accord with the relative uniformity of climatic conditions in Caxiuanã around the year, seasonal effects being probably negligible in that locality. Because a set of 10 TMM traps was installed in a different area of the ECFPn in each expedition, the same idea of uniformity regarding quantitative aspects also applies to comparisons between

different forest sites. Nonetheless, the lists of trapped species were considerably different between surveys/areas. Values of percent complementarity between areas of the ECFPn were larger than 60% in all comparisons. However, in face of the low efficiency of passive flight interception traps, and the

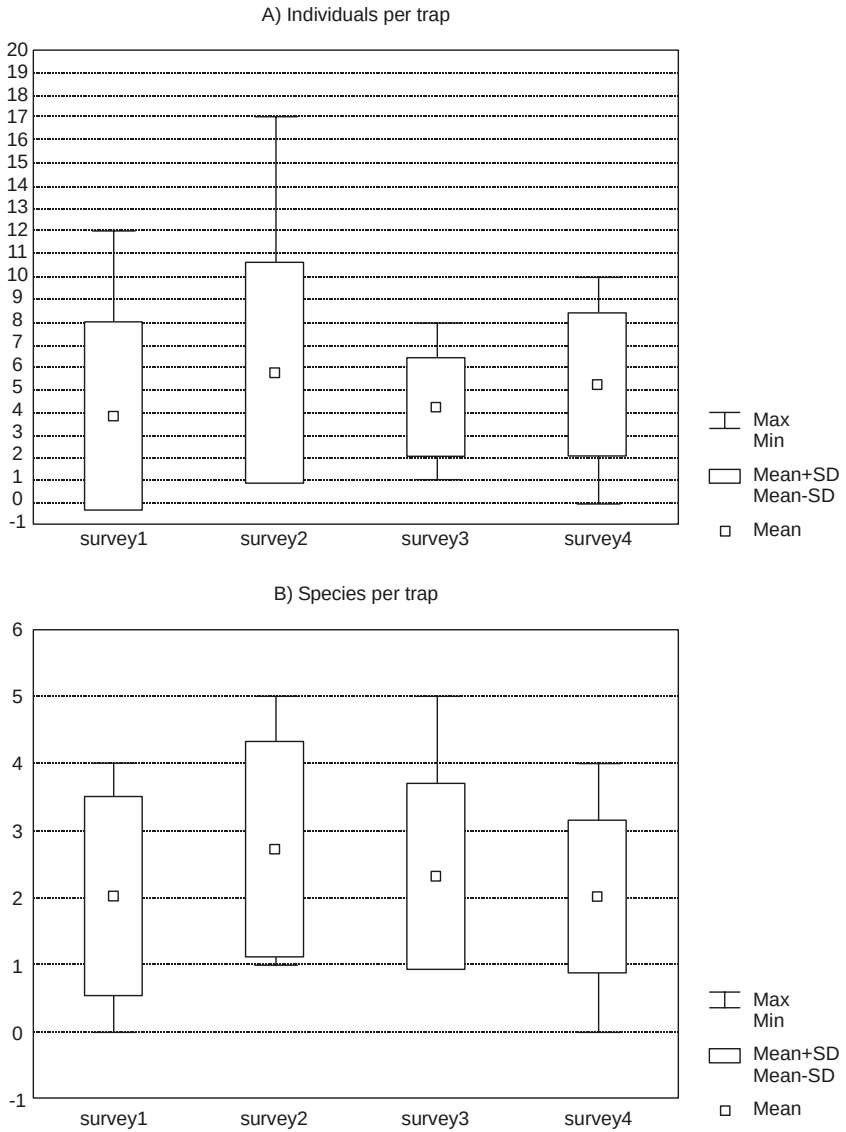

Figure 3. Box-whiskers plots for the numbers of individuals and species of social wasps captured in TMM traps in each of the four surveys in the ECFPn, in Caxiuanã, PA, Brazil (n= 10).

apparent low levels of abundance of most species (unpredictability of finding a present species), it does not seem prudent to consider complementarity values as reflecting real compositional differences or species distribution patterns.

1.3. Results from five-days trapping periods

Significantly different numbers were generally verified, in a same sampling site, between each of the complementary partial trapping periods of five days. That is, the contribution of one partial period was in general different from that of its complementary (Fig. 4). In Figure 2, one sees that the mean accumulation curve for "first partial periods" nearly approaches the mean curve for the 10-days samples, while that for "second partial periods" accumulates species at considerably lower rates. Such differences between complementary partial samples possibly resulted from changes in climatic conditions, rainy days causing the reduction of foraging activity of wasps colonies, and lowering the number of captures. The mean accumulation curve for the entire set of 80 partial 5-days samples (that is, combining the best and the worst results) is probably a better indication of the results expected for trapping wasps during five days in areas like Caxiuanã. The curve shows that 16 species would be expected at the level of sample 40, which seems a reasonable result representing about 70% of the total number of species collected by trapping along periods of ten days.

2) SMM trap

One trap of this kind was always installed in the same point in primary forest. In spite of the far larger interception surface and of the additional collecting chamber, the SMM trap had efficiency roughly equivalent to that of TMM traps working in periods of 10 days. By the end of the discontinuous 40 days period, the SMM trap produced totals of 16 individuals and 8 species of the genera *Agelaia*, *Angiopolybia*, *Mischocyttarus*, and *Polybia*. The two *Mischocyttarus* species were only collected with this trap. The numbers suggest that using a larger trap, and trapping for more than ten days at one given site may not produce much better results. It seems preferable to distribute the cost in time and materials using smaller traps at a larger number of sites.

3) SUM traps

The 20 installations of this kind of trap at heights of 15-20 m from the ground produced the worst results. Eighteen individuals of 7 species and 4 genera were captured, with a mean of 0.9 individuals per sample (Table 3). Only *Agelaia fulvofasciata* attained a certain level of frequency, comparable to that observed in TMM traps. However, one of the suspended traps captured the single specimen of the genus and species *Clypearia sulcata*.

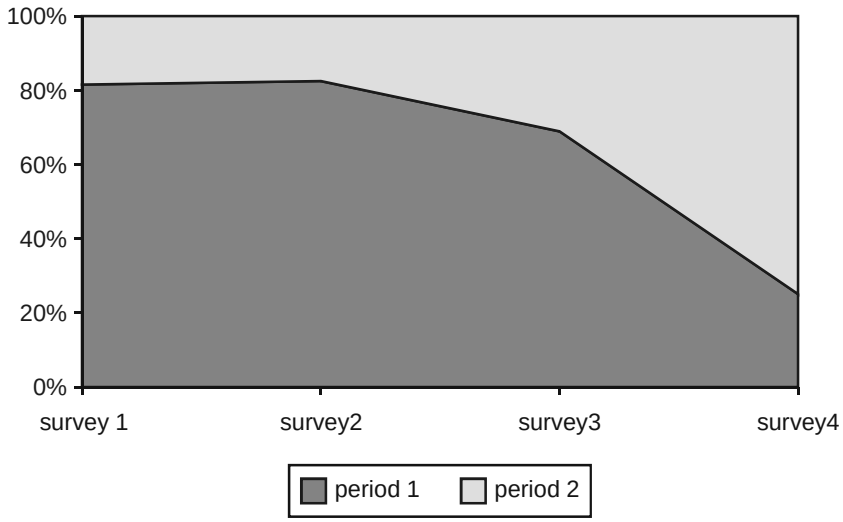

Figure 4. Mean percentage difference in the contributions of the two complementary 5-days trapping periods over the total number of individuals of social wasps captured along 10-days in Two-meter Malaise traps (TMM), in each of the four surveys in the ECFPn, in Caxiuanã, PA, Brazil.

Table 3. Frequencies of social wasps in Suspended Malaise traps (SUM; 15-20 m) relative to a total of 20 samples (20 sites X 10 days), obtained in primary forest in the ECFPn, in Caxiuanã, PA, Brazil. Information is also given on the totals of individuals.

Species	Frequency	(n) individuals
1 – *Agelaia fulvofasciata*	0.25	6
2 – *Agelaia myrmecophila*	0.05	1
3 – *Angiopolybia pallens*	0.05	1
4 – *Polybia liliacea*	0.10	6
5 – *Polybia platycephala*	0.10	2
6 – *Polybia bicyttarella*	0.05	1
7 – *Clypearia sulcata*	0.05	1
	Total individuals	18
	Mean individuals/trap	0.9

4) Searches for wasps in forest and by river margins

4.1. Total species and frequency in samples

Searches in the forest and searches by the margins of water bodies produced very different results. Twenty-two samples obtained in primary forest (rarely crossing secondary vegetation) produced a total of 42 species, while 23 samples taken by boat along the margins of rivers and small streams produced only 27 species (Tables 4 and 5). These numbers certainly reflect different rich-

Table 4. Absolute and relative frequencies of social wasps in the ECFPn, in Caxiuanã, PA, Brazil, based on the number of samples (searches along linear 1,000 m distances) in which a species was recorded, for each class of environment: trail in primary forest; mixed trail including secondary vegetation (for/sec); narrow stream; margin of wider river; margin of Caxiuanã bay (more than 1 km wide).

Species	Frequency (absolute, relative)									
	forest, n=19		for/sec, n=3		stream, n=7		river, n=12		bay, n=4	
1 – *Angiopolybia pallens*	9	0.47	1	0.33	4	0.57	2	0.17	1	0.25
2 – *Agelaia angulata*	6	0.32	–		–		–		–	
3 – *Agelaia centralis*	5	0.26	–		–		–		–	
4 – *Angiopolybia paraensis*	5	0.26	–		–		–		–	
5 – *Agelaia fulvofasciata*	4	0.21	1	0.33	–		1	0.08	1	0.25
6 – *Polybia quadricincta*	4	0.21	1	0.33	–		–		–	
7 – Agelaia pallipes	3	0.16	–		–		–		–	
8 – *Mischocyttarus lecointei*	3	0.16	–		–		–		–	
9 – *Polybia rejecta*	2	0.10	–		4	0.57	3	0.25	2	0.50
10 – *Synoeca virginea*	2	0.10	–		1	0.14	2	0.17	2	0.50
11 – *Mischocyttarus saturatus*	2	0.10	1	0.33	2	0.29	–		–	
12 – *Mischocyttarus oecothrix*	2	0.10	1	0.33	2	0.29	–		–	
13 – *Polybia gorytoides*	2	0.10	2	0.67	–		–		–	
14 – *Mischocyttarus synoecus*	2	0.10	–		–		–		–	
15 – *Mischocyttarus carbonarius*	2	0.10	–		–		–		–	
16 – *Agelaia testacea*	2	0.10	–		–		–		–	
17 – *Pseudopolybia difficilis*	2	0.10	–		–		–		–	
18 – *Mischocyttarus foveatus*	1	0.05	–		7	1.00	6	0.50	2	0.50
19 – *Parachartergus fraternus*	1	0.05	–		1	0.14	1	0.08	2	0.50
20 – *Polybia dimidiata*	1	0.05	2	0.67	–		–		1	0.25
21 – *Polybia scrobalis*	1	0.05	1	0.33	1	0.14	–		–	
22 – *Parachartergus richardsi*	1	0.05	–		1	0.14	–		–	
23 – *Polybia micans*	1	0.05	–		–		–		2	0.50
24 – *Polybia affinis*	1	0.05	1	0.33	–		–		–	
25 – *Polybia jurinei*	1	0.05	–		–		1	0.08	–	
26 – *Polybia liliacea*	1	0.05	–		–		–		–	
27 – *Leipomeles dorsata*	1	0.05	–		–		–		–	
28 – *Agelaia angulicollis*	1	0.05	–		–		–		–	
29 – *Agelaia cajennensis*	1	0.05	–		–		–		–	
30 – *Apoica* sp. nr. *thoracica*	1	0.05	–		–		–		–	
31 – *Mischocyttarus* sp. group *artifex*	1	0.05	–		–		–		–	
32 – *Mischocyttarus* sp.2 group *artifex*	1	0.05	–		–		–		–	
33 – *Mischocyttarus* sp. group *prominulus*	1	0.05	–		–		–		–	
34 – *Mischocyttarus tectus*	1	0.05	–		–		–		–	
35 – *Polybia bistriata*	–		2	0.67	3	0.43	–		–	
36 – *Polistes versicolor*	–		2	0.67	–		–		–	
37 – *Polistes pacificus*	–		2	0.67	–		–		–	
38 – *Mischocyttarus tomentosus*	–		1	0.33	–		–		–	
39 – *Mischocyttarus labiatus*	–		1	0.33	–		–		–	
40 – *Mischocyttarus injucundus*	–		1	0.33	–		–		–	
41 – *Mischocyttarus sylvestris*	–		1	0.33	–		–		–	
42 – *Agelaia myrmecophila*	–		1	0.33	–		–		–	

Continued

Species	Frequency (absolute, relative)				
	forest, n=19	for/sec, n=3	stream, n=7	river, n=12	bay, n=4
43 – *Apoica pallida*	–	–	3 0.43	6 0.50	1 0.25
44 – *Mischocyttarus juruanus*	–	–	–	8 0.67	4 1.00
45 – *Mischocyttarus collarellus*	–	–	1 0.14	–	2 0.50
46 – *Chartergus metanotalis*	–	–	1 0.14	2 0.17	–
47 – *Polybia platycephala*	–	–	1 0.14	–	1 0.25
48 – *Mischocyttarus melanops*	–	–	4 0.57	–	–
49 – *Protopolybia emortualis*	–	–	–	2 0.17	–
50 – *Polybia rufitarsis*	–	–	–	–	2 0.50
51 – *Polybia parvulina*	–	–	1 0.14	–	–
52 – *Asteloeca traili*	–	–	–	1 0.08	–
53 – *Mischocyttarus imitator*	–	–	–	1 0.08	–
54 – *Polistes goeldi*	–	–	1 0.14	–	–
55 – *Polistes occipitalis*	–	–	–	–	1 0.25

Table 5. Statistics referring to "number of colonies" and "number of species" of social wasps recorded in 45 searches (linear 1,000 m unity samples) in the ECFPn, in Caxiuanã, PA, Brazil, by class of environment: trail in primary forest; mixed trail including secondary vegetation (for/sec); narrow stream; margin of wider river; margin of Caxiuanã bay (more than 1 km wide). "Trails" and "Margins" summarize data collected "on land" and "by boat". COL/s: mean number of colonies per sample; COL/100: mean number of colonies per 100 m per sample; R/p: mean number of species per sample; R: total number of species encountered; CV: coefficient of variation.

Environment	(n)	COL/s	CV %	COL/100	R/p	CV %	R
forest	19	1.3	80.3	0.14	4.0	56.3	34
for/sec	3	6.3	32.9	0.79	7.3	15.8	16
stream	7	7.3	48.0	0.82	5.4	36.6	16
river	12	3.2	57.4	0.33	3.0	42.6	13
bay	4	19.5	72.1	1.95	6.0	13.6	14
Trails	22	2.0	–	0.22	4.4	–	42
Margins	23	7.3	–	0.76	4.3	–	27

ness conditions of the two general classes of environment, but methodological aspects possibly had some effect on the results. In each trail sampled, a large proportion of the species (about 66%) was generally found by collecting foraging individuals. On the other hand, by the river margins, restrictions to pursuit of flying wasps imposed by working inside a small boat were certainly important. On average, only 24% of the species in each sample were found by catching foraging individuals.

Frequencies of the species in samples are presented on Table 4. The two main classes, "trails in forest interior" and "river margins", are split so as to distinguish a few sampled trails that crossed larger tracts of secondary vegeta-

tion, and also to differentiate water bodies according to their amplitude: narrow streams in forest, wider rivers, and the very wide "Caxiuanã bay". *Angiopolybia pallens* was present in about half the samples in forest and in narrow streams, and was also found in the other environments. Other species encountered in most kinds of environment were *Agelaia fulvofasciata*, *Polybia rejecta*, *Synoeca virginea*, and *Parachartergus fraternus*, but with generally lower frequencies than *Angiopolybia pallens*. Several of the *Mischocyttarus* species were more easily found along the streams or by the margins of the wider water bodies. *Mischocyttarus foveatus* was almost always encountered in such environments, and *M. juruanus* was indeed exclusively found on the margins of the wider rivers, in conditions of high luminosity. A large number of nests of this species was found along the west margin of "Caxiuanã bay", specially on leaves of *Montrichardia linifera* (Araceae). *Apoica pallida* was also fairly common and exclusively collected along river margins.

The higher frequency of *Angiopolybia pallens* in active searches is in accordance with the results obtained in TMM traps, and indicates that this is probably the most common social wasp in Caxiuanã. However, it is apparent that the search methods are biased to some degree. *Polybia liliacea* was nearly as frequent as *Angiopolybia pallens* in TMM traps, but was recorded only once in active searches by way of the capture of a single foraging individual. While all of the nests of *A. pallens* were at less than 5 m from the ground, none of *P. liliacea* was found in Caxiuanã, and Richards (1978) mentions a nest of this species at a height of 11 m, in the Brazilian state of Mato Grosso (J. M. Carpenter also saw numerous nests in Mato Grosso, none below 10 m; personal communication). If some wasp species show in fact a consistent preference for nesting on higher branches and trees, then chances seem to be very low of finding such nests in the forest canopy, even with the use of binoculars. However, because *P. liliacea* was frequently captured in traps at the forest floor, a larger number of foraging individuals would be expected to be found in searches in the trails.

Figures on the percentage incidence and richness of genera in samples (Fig. 5, A and B) show *Mischocyttarus* and *Polybia* as the most important genera in all kinds of environment. This is in general agreement with the measures of "prevalence" presented by Jeanne (1991) for the New World Polistinae, electing *Polybia* and *Mischocyttarus* respectively as the 1st and 2nd ranked genera. However, the results from Caxiuanã also indicate that *Agelaia* and *Angiopolybia* may attain comparable levels of importance in forest interior habitats, if incidence is given a somewhat higher weight (Fig. 5A).

4.2. Number of colonies and species per sample

Table 5 shows some figures relative to numbers of colonies and species by class of environment where searches were made in the ECFPn. Trails in the

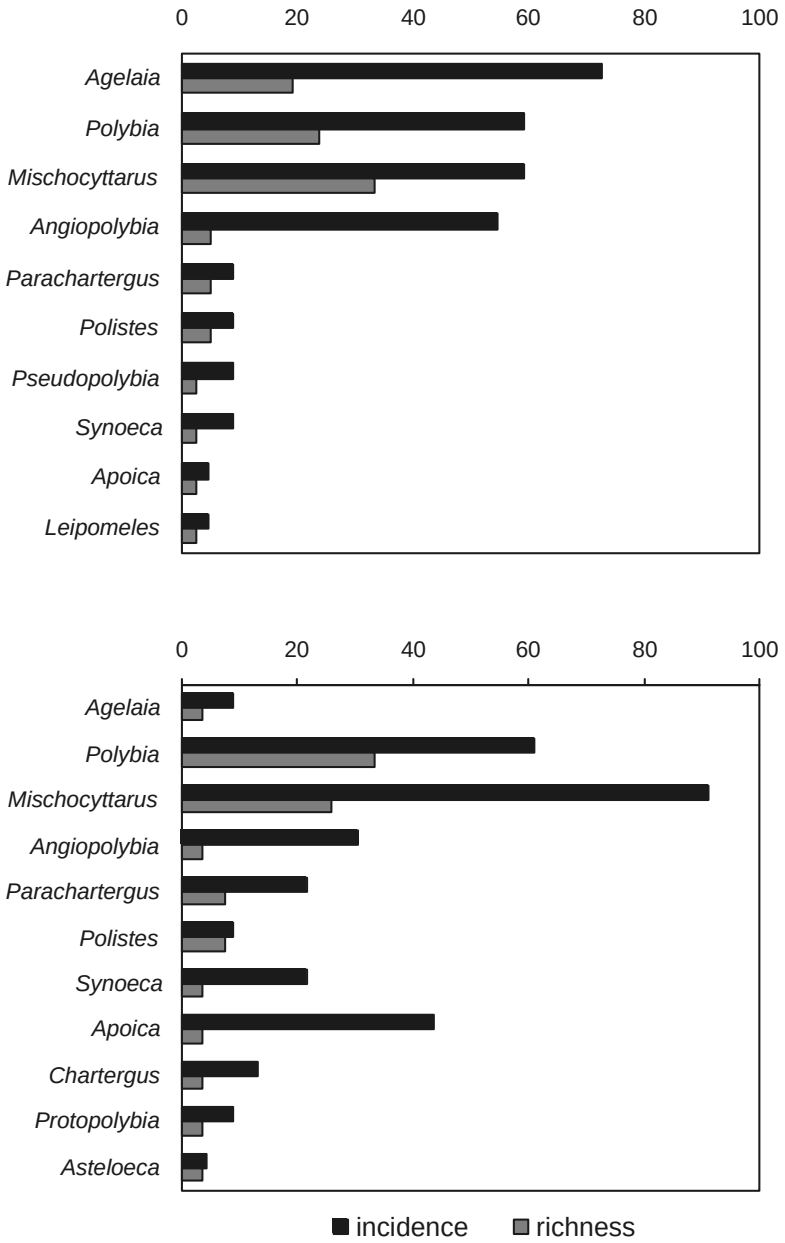

Figure 5. Percentage incidence and richness of polistine genera relative to total samples and species in searches made in the ECFPn, Caxiuanã, PA, Brazil.; A) 22 samples in trails; B) 23 samples by river margins.

forest were far less productive in terms of discovering colonies of social wasps, on a per sample base, except for those samples that included parts of secondary vegetation. The mean number of colonies per sample was very low (1.3), and the mean number of colonies per 100 m per sample (0.14) is smaller than the 0.3 colonies per 100 m reported by Ohgushi *et al.* (1988) for polistine wasps along both sides of a 3 km road crossing submontane rain forest in Southeast Asia. However, for the Caxiuanã forest samples, variance around the mean was very large, so that wasps nests may be reasonably common in some forest places. Furthermore, the larger numbers of colonies per sample found at river margins often reflected the higher frequency of a few species of *Mischocyttarus*, *Apoica*, and *Polybia*. Of the 78 nests of ten species found along the west margin of the "Caxiuanã bay", 57 nests (about 73%) were of the single species *Mischocyttarus juruanus*.

4.3. Accumulation curves for searches in trails and by river margins

Addition of species in trails in the forest occurred at considerably higher rates than by the river margins (Figure 6). Estimates of the maximum number of species for the two kinds of environment, based on the Michaelis-Menten curve (Estimates 5: "MMMeans"; Colwell, 1997), were 68 species for trails in forest and 35 species for searches at the margins of rivers. These values are in good agreement with actual numbers of species found in each of these general kinds of environment with all methods, 65 and 32 species respectively. Fitting of Michaelis-Menten curves also makes possible estimation of the cost in samples of finding a certain number of additional species. Thus, adding the next species to each of the lists obtained in formal active searches is expected to require 2 samples more for trails, and 7 samples for the margins. The estimated (and observed) values give an idea of the chances of success in future searches, and indicate that while only a few rare species are yet to be encountered at the margins of rivers in the ECFPn, the expectation for searches in trails in the forest is for a comparatively much larger set of species.

Concluding Remarks

Of the 20 polistine genera with chances of being found in the region of Caxiuanã, only *Chartergellus*, *Marimbonda*, and *Nectarinella* are still unrecorded. Figure 7 shows the number of species by genus in the ECFPn and two other localities in Pará (Belém and Serra dos Carajás), as well as the number of species recorded in the literature or known to occur in that Brazilian state "before" the survey in the ECFPn (Cooper, 1996*a*, 1997*b*; Richards, 1978; unpublished information in the Museu Goeldi and INPA collections). The latter number is presented as a crude reference about the number of species that could

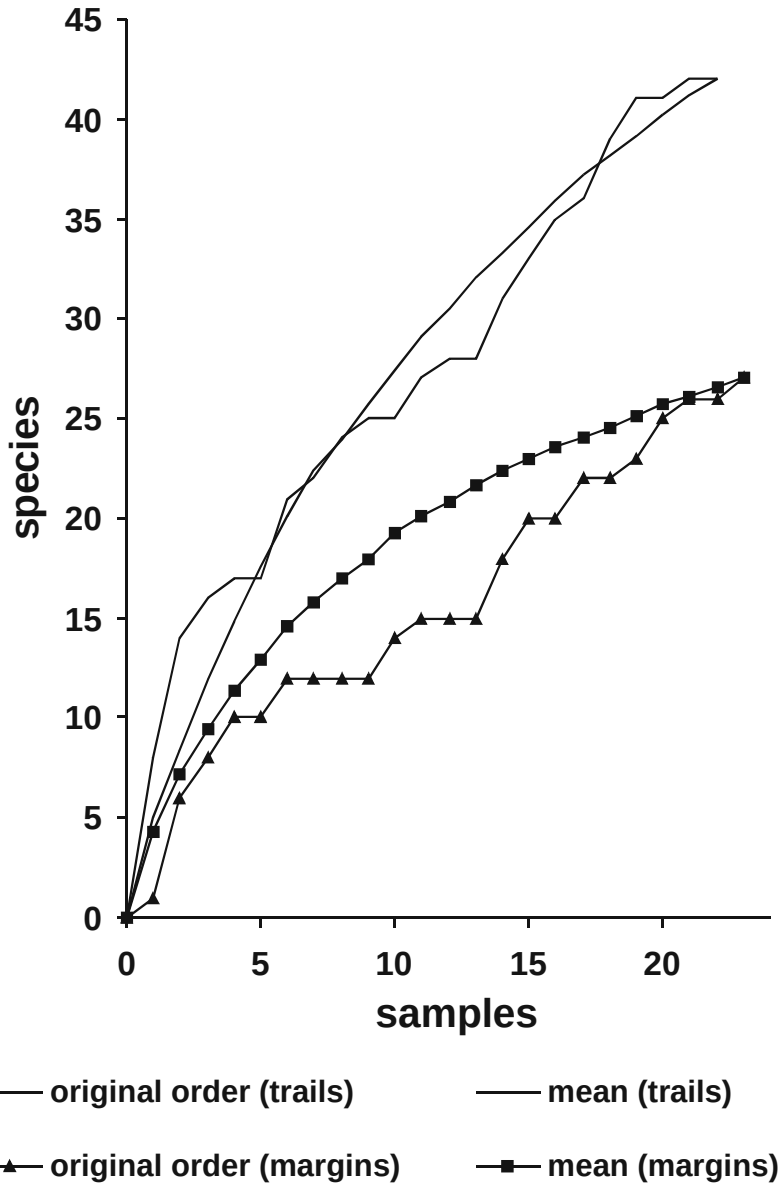

Figure 6. Species accumulation curves for social wasps collected in 45 searches (linear 1,000 m unity samples) in the ECFPn, in Caxiuanã, PA, Brazil. Curves without markers represent accumulation of 22 samples obtained in trails in forest. Curves with markers refer to 23 samples obtained by the margins of water bodies. Smooth curves are mean curves from 100 instances of randomization of sample accumulation order.

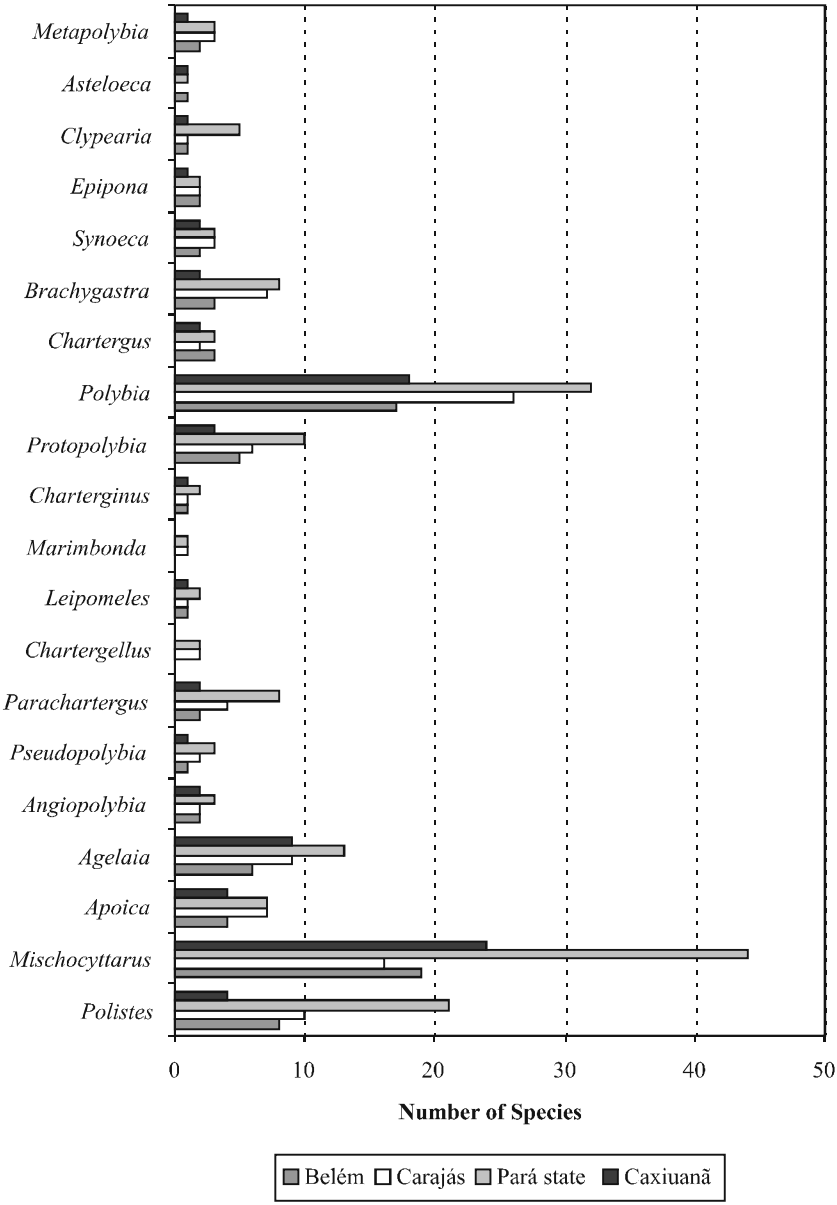

Figure 7. Numbers of species by genus known to occur in Caxiuanã and two other localities in the Brazilian state of Pará (Belém and Serra dos Carajás). It is also presented the number of species recorded in the literature (or known to occur) in Pará "before" the survey in the ECFPn (Cooper, 1996*a*, 1997*b*; Richards, 1978; unpublished information in the Museu Goeldi and INPA collections).

possibly be encountered in the ECFPn. Regarding the three largest genera, Caxiuanã presented high species richness in *Mischocyttarus* and *Polybia*, but a comparatively low number of *Polistes* species. It also revealed few species in the medium-sized genera *Parachartergus*, *Protopolybia*, and *Brachygastra*. Genera and species from Caxiuanã are fewer than those known from Serra dos Carajás, and this is probably not just consequence of unequal collecting efforts, but has both historical and ecological causes. The Carajás region is well within the zone of contact between Amazonia and the "Cerrado" of central Brazil, and is particularly rich in natural open vegetation habitats.

None of the formal methods used in the survey in Caxiuanã showed more than reasonable performance. Malaise traps failed to find 64% of the species encountered in the forest interior habitats in the ECFPn, and active searches in trails and by river margins still missed considerable 30% of the total 79 species known to occur in the area. Table 1 presents information on the circumstances in which the species were recorded. One sees that 4 species were found exclusively through the information given by people resident in the ECFPn. Another 9 species were encountered in different kinds of situations, in informal searches or quite fortuitously. These 13 species comprise expressive 16% of the total species found in Caxiuanã, and from a qualitative viewpoint they include two undescribed species. This demonstrates that inventories of social wasps in Amazonia must be based on a variety of procedures. Ideally, the collecting methods should be efficient in finding species, and accurate in respect of correctly depicting their relative abundance. The efficiency of Malaise traps, however, by their passive mechanism, is certainly more strongly dependent on general abundance and size of colonies, and probably also on the species foraging behavior. The spectrum of locally "available" species thus seems to be considerably reduced, and a majority of the rare ones will only be recorded at much lower rates (see Fig. 2). The frequencies obtained in TMM traps installed in the ECFPn indeed may assess with some degree of accuracy the most common species in the forest interior habitats, but representation of the more rare species is quite inadequate since most of them were simply not collected in traps (but see Kojima and van Achterberg, 1997).

Considering the general inventory of the species, the active search method was far more efficient than Malaise traps. However, there was an important difference between searching on land and by the margins regarding the level of mobility of collectors. In the case of species with cryptic nests, collecting will strongly depend on the capture of foraging individuals, and this resulted to be less efficient in searches made by boat along river margins. This has been certainly influential on the virtual absence of *Agelaia* species in samples from the margins (Fig. 5B). Another point regarding bias defects of both search procedures is that they would hardly be effective in finding colonies of species that show preference for nesting on higher branches and trees.

The 22 samples obtained in trails in the forest proved to be insufficient in face of the great species richness. Even the visual inspection of the curve in Figure 6 shows that the process of species discovery in trails is still considerably removed from the asymptote, and that more samples would be desirable. The number of additional samples that would be necessary to reach the actual 65 species found (with all methods) in the forest interior habitats is estimated to be 240 samples, which is roughly ten times larger than the effort used in trails. However, the small difference between the estimated asymptotic value (68) and the observed number of 65 species indicates that Malaise traps and other modes of collecting have already diminished the deficit projected for searches in trails. This is also suggested in general terms by (*1*) the total number of species added at each expedition with all collecting methods (45, 12, 16, and 6 species) and (*2*) the numbers of species known from other localities in Pará state. The number of 105 species known from Carajás probably serves as a good approximation of an upper limit for the size of local faunas in Brazilian Amazonia.

Acknowledgments

This work received financial support (grant 0305972) from the "Fundação O Boticário de Proteção à Natureza". It was also supported by the "Departamento de Zoologia" and "Estação Científica Ferreira Penna (ECFPn)" of the "Museu Paraense Emílio Goeldi". Dr. Pedro L. B. Lisboa, coordinator of the ECFPn, facilitated conditions for the field work. I am also grateful to Dr. Carlos R. F. Brandão and Dr. James M. Carpenter for their comments on an earlier manuscript. Dr. Robert K. Colwell helped by e-mail on the use of Estimates 5.

References

Almeida, S.S., P.L.B. Lisboa & A.S.L. Silva. 1993. Diversidade florística de uma comunidade arbórea da Estação Científica Ferreira Penna, em Caxiuanã (Pará). Bol. Mus. Para. Emílio Goeldi, ser. Bot. 9:93-188.

Archer, M.E. 1985. Population dynamics of the social wasps *Vespula vulgaris* and *Vespula germanica* in England. Journal of Animal Ecology 54:473-485.

Archer, M.E. 1990. Seasonal flight activity of social Vespinae (Hym., Vespidae) as monitored by Malaise trap catches. Entomologist's Monthly Magazine 126:179-184.

Carpenter, J.M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. in: "The Social Biology of Wasps" (K. G. Ross H. W. Matthews, eds.), pp. 7-32, Cormell Universery Press, Ithaca, New York and London, 678p.

Carpenter, J.M., 1999. Taxonomic Notes on Paper Wasps (Hymenoptera: Vespidae; Polistinae). Am. Mus. Novitates 3259:44 pp.

Carpenter, J.M., J. Kojima & J.W. Wenzel. 2000. *Polybia*, Paraphyly, and Polistine Phylogeny. Am. Mus. Novitates 3298:24 p.

Carpenter, J.M. & J.W. Wenzel. 1999. The relative abundance of swarm-founding social wasps in the Congo Basin (Insecta: Hymenoptera; Vespidae, Polistinae). Nat. Hist. Bull. Ibaraki Univ. 3:9-14.

Carpenter, J.M., J.W. Wenzel & J. Kojima. 1996. Synonymy of the Genus *Occipitalia* Richards, 1978, with *Clypearia* de Saussure, 1954 (Hymenoptera: Vespidae; Polistinae, Epiponini). J. Hym. Res. 5:157-165.

Colwell, R.K. 1997. Estimates: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Colwell R.K. & J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Trans. R. Soc. Lond. B 345:101-118.

Cooper, M. 1996*a*. The subgenus *Monogynoecus* Richards of *Mischocyttarus* de Saussure (Hym., Vespidae, Polistinae) with descriptions of two new species. Entomologist's mon. Mag. 132:23-28.

Cooper, M. 1996*b*. The *mendax* group of *Mischocyttarus* (Hym., Vespidae, Polistinae) with descriptions of new species. Entomologist's mon. Mag. 132:273-280.

Cooper, M. 1997*a*. A new subgenus of *Mischocyttarus* de Saussure (Hym., Vespidae). Entomologist's mon. Mag. 133:117-129.

Cooper, M. 1997*b*. The subgenus *Megacanthopus* Ducke of *Mischocyttarus* de Saussure (Hym., Vespidae), with a key and three new species. Entomologist's mon. Mag. 133:217-223.

Cooper, M. 1998*b*. New species of the *artifex* group of *Mischocyttarus* de Saussure (Hym., Vespidae) with a partial key. Entomologist's mon. *Mag.* 134:293-306.

Diniz, I.R. & K. Kitayama. 1998. Seasonality of vespid species (Hymenoptera: Vespidae) in a central Brazilian cerrado. Rev. Biol. Tropical 46:109-114.

Faith, D.P. 1995. Phylogenetic pattern and the quantification of organismal biodiversity. in: "Biodiversity. Measurement and Estimation" (D. L. Hawksworth ed.), pp. 45-58, Chapman & Hall.

Jeanne, R.L. 1991. Swarm-founding Polistinae. in: "The Social Biology of Wasps" (K.G. Ross and H.W. Matthews, eds.) pp. 191-231, Cormell Universery Press, Ithaca, New York and London, 678p.

Kojima, J. 1993. Relative abundance of swarm-founding *Ropalidia* in the eusocial wasps (Hymenoptera: Vespidae) in tropical Australia. New Entomol. 42:4-7.

Kojima, J. & K. van Achterberg. 1997. Social wasps collected by Malaise trapping in Southeast Asia, with a note on relative abundance of swarm-founding species (Insecta: Hymenoptera: Vespidae). Nat. Hist. Bull. Ibaraki Univ. 1:1-13.

Kitayama, K., I.R.D. Rocha & B.M. Bulhões. 1989. Densidade de ninhos de vespídeos em diversos habitats de Mato Grosso. in: I Simpósio Latinoamericano sobre Insetos Sociais Neotropicais, Rio Claro, São Paulo.

Lisboa, P.L.B., A.S.L. Silva & S.S. Almeida. 1997. Florística e Estrutura dos Ambientes. in: Caxiuanã (P.L.B. Lisboa, org.) pp. 163-193, Museu Paraense Emílio Goeldi, Belém, 446p.

O'Donnell, S. 1995. Necrophagy by Neotropical Swarm-Founding Wasps (Hymenoptera: Vespidae, Epiponini). Biotropica 27:133-136.

Ohgushi, R.I., S. Yamane & F. Sakagami. 1988. Ecological distribution and habitat-linked density of colonies of stenogastrine wasps in tropical S.E. Asia. Zoological Science 5:869-874.

Rafael, J.A. & I.S. Gorayeb. 1982. Tabanidae (Diptera) da Amazônia. I – Uma armadilha suspensa e primeiros registros de mutucas de copas de árvores. Acta Amazônica 12:232-236.

Raw, A. 1998. Population densities and biomass of neotropical social wasps (Hymenoptera, Vespidae) related to colony size, hunting range and wasp size. Revta. bras. Zool. 15:815-822.

Richards, O.W. 1971. The biology of the social wasps (Hymenoptera, Vespidae). Biol. Rev. (Cambridge) 46:483-528.

Richards, O.W. 1978. The social wasps of the Americas excluding the Vespinae. British Museum (Natural History), London, 580p.

Rocha, I.R.D., K. Kitayama & B.M. Bulhões. 1989. Densidade, local de nidificação e descrição do ninho de *Polistes subsericeus*. in: I Simpósio Latinoamericano sobre Insetos Sociais Neotropicais, Rio Claro, São Paulo.

Roth, R. & W.D. Lord. 1987. Cycles of queen size and abundance in a population of *Vespula maculifrons* (Hymenoptera: Vespidae). Environ. Entomol. 16:649-652.

Silveira, O.T. 2000. Relações Filogenéticas dos Subgêneros de *Mischocyttarus* Saussure e Revisão Taxonômica do Subgênero *Kappa* Saussure (Hymenoptera, Vespidae, Polistinae). Tese de doutorado, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, 295p.

Williams, P.H., R.I. Vane-Wright & C.J. Humphries. 1993. Measuring biodiversity for choosing conservation areas. in: "Hymenoptera and Biodiversity" (J. LaSalle, and I.D. Gauld, eds.), CAB International, Wallingford, UK, 348p.

CREDENCIAMENTO E APOIO FINANCEIRO DO
PROGRAMA DE APOIO AS PUBLICAÇÕES CIENTÍFICAS PERIÓDICAS DA USP
COMISSÃO DE CREDENCIAMENTO