

# Spiders of Pakitza (Madre de Dios, Perú): Species Richness and Notes on Community Structure

DIANA SILVA

Museo de Historia Natural  
Apartado 14-0434  
Lima 14, Peru

JONATHAN A. CODDINGTON

Dept. Entomology  
National Museum of Natural History  
Smithsonian Institution  
Washington, DC 20560

## RESUMEN

El muestreo cuantitativo realizado en Pakitza durante abril-mayo y setiembre-octubre de 1991 -sólo los ejemplares adultos (2616 arañas)- dio como resultado 498 especies de arañas distribuidas en 33 familias. El análisis de la estructura de la comunidad de arañas indica que el grupo de tejedoras de telas circulares es dominante en abundancia y diversidad de especies, seguido por el grupo de tejedoras de telas irregulares. Las familias numéricamente dominantes son Theridiidae y Araneidae, cada una representa el 28 % del total de ejemplares colectados; la tercera familia más abundante es Uloboridae (7.1 %). La mayoría de las especies colectadas (56 %) está representada sólo por uno o dos ejemplares, estas especies parecen tener una gran influencia en el estimado de la riqueza cuando se consideran las variaciones por estacionalidad o tipo de bosque -las diferencias no son significativas cuando se excluye las especies representadas sólo por un ejemplar. El mismo efecto se observa cuando los únicos se excluyen del estimado total de la riqueza de especies, el que es significativamente mayor a finales de la época seca. La araneofauna de la terraza aluvial antigua (OAT) parece ser más rica en especies que aquélla del bosque inundable alto (UFF), aunque puede ser un efecto del tamaño de la muestra. La evaluación de los métodos no-paramétricos utilizados para el estimado de la riqueza de especies demuestra que cada uno tiene sus ventajas y desventajas, aunque los intervalos de confianza superimponen. Quizá este rango de valores es suficiente para el estimado de la riqueza de especies. Cuando se compara los diferentes métodos usualmente se encuentra el siguiente orden, partiendo de aquellos que proporcionan los estimados más bajos hasta aquellos que indican los estimados más altos: lognormal, jackknife, Chao1, Chao2, y curva de acumulación de especies.

## ABSTRACT

A quantitative sampling protocol conducted in Pakitzá during early and late dry season (April-May and September-October, 1991) yielded 2616 adult spiders comprising 498 species and 33 families. For this sample, the orb weavers were the most abundant and diverse, followed by the sheet/line weavers. Species of Theridiidae and Araneidae were numerically dominant, each family accounting for approximately 28 % of the total collected specimens. The third most abundant family was Uloboridae comprising 7.1 % of the total collection. Most species (56%) were represented by only 1 or 2 individuals; these species strongly affect the richness estimate when variation due to season and type of forest are considered. There were more species in the late dry season than in the early dry season, but when the singletons (132 vs. 75) were excluded this effect disappears. The same effect is observed when all uniques were excluded from the total richness, which is substantially higher in the late dry season. The spider fauna of the old alluvial terrace forest (OAT) seems to be richer than that of the upper floodplain forest (UFF), although this may again be due to sample size. The assessment of non-parametric methods used to estimate the richness of spider species shows that each estimator has its strengths and weaknesses. Where available, the confidence intervals of all of the estimators overlap; perhaps this range of values is a sufficiently accurate estimate of species richness. Within any one comparison, the estimators often follow a set ranking from lowest to highest values: lognormal, jackknife, Chao1 and Chao2, species accumulation curve.

## INTRODUCTION

Tropical forests, especially Neotropical forests, include some of the most species-rich ecosystems in the world. Exactly how rich is a matter of some debate, partly because methods to estimate species richness are themselves debatable and little understood. Although richness can be determined for long-lived sessile organisms like trees by exhaustively enumerating all individuals, it is time-consuming, laborious, and expensive (e.g. Hubbell and Foster, 1983). Exhaustive enumeration is not a practical option for many animal groups, because it is impossible to census all individuals. The species composition of the ecosystem is dynamic and will change during the period of the huge census effort required. Although censussing may work well for obvious, large, species-poor groups such as birds or perhaps larger terrestrial vertebrates, it is manifestly impractical for megadiverse groups such as terrestrial arthropods. The latter taxa are generally small in size, short-lived, and vagile. Estimating the species richness of such groups at a point in time is no small problem.

The current study arose from the first author's long-term interest in the patterns of distribution and abundance of Peruvian spiders, and the second author's interest in the possibility of estimating species richness by extrapolation from sample data. The inventory reported here was not ideal for either task, but

it has taught us that Pakitzá's spider fauna is so rich that adequate point samples or studies that encompass the entire fauna are probably beyond the reach of single investigators, though possibly attainable by larger groups of collaborating workers.

This study contributes to the larger effort of designing methods to estimate species richness of very diverse groups by applying several quantitative richness estimation methods to a series of samples collected in the same way among a series of forest types (Colwell and Coddington, 1994; Heyer et al., 1994; Longino 1994). It also provides a data set that others interested in the same problem can use (to obtain the full data set please write the second author). While the true richness of a given site at a given time for a given group may be nearly impossible to verify empirically, we anticipate that the various estimators may behave similarly when applied to different data. Even without knowing the "true" answer in any one case, we can learn something about the circumstances under which they are reliable and when they are likely to give very misleading results.

Available methods include the classic lognormal (Preston, 1948), the jackknife (Heltshe and Forrester, 1983, 1985), the two estimators here called Chao1 and Chao2 (Chao, 1984, 1987) and species accumulation curves, here fitted to the Michaelis-Menten equation, a hyperbolic function that seems to fit species accumulation curves rather well (Lamas et al., 1991; see Soberón and Llorente (1993) and Colwell and Coddington (1994) for a review). Other methods exist (Colwell and Coddington, 1994) but they are mainly variants of the above estimators and give comparable results. The Chao2 estimator was originally designed to estimate population size when probability of capture and recapture varied among individuals (Chao, 1987). This seems formally equivalent to the estimation of total species richness when species vary in relative abundance (and thus in probability of capture), and so it seems reasonable to apply it to the current problem. To the extent the data permitted, we applied these five estimators to our total data set, and partitions of it by forest type and season (early versus late dry season).

We also seek to inventory and characterize the dynamics of the spider fauna of Pakitzá in at least a semi-quantitative way such that the resulting data will provide more than an annotated list of species and a museum collection to support tropical systematics, although both of those are worthwhile goals. Russell-Smith and Stork (1994) briefly review spider diversity studies from other tropical areas. We particularly focus on differences and abundance of the spider fauna between early and late dry season, and between forest types. These questions were approached in two ways, by looking at the effect these variables have on the number of adults and number of species per hourly sample, and also by examining their effect on the inventory viewed as a whole. We assume that an environment with more spiders or species will be reflected in how much a collector can catch in a unit of effort. We were also interested to explore the effect that rare species have on such analyses (Gaston, 1994).

While data collection protocols are usually designed for a specific purpose (as ours have been to estimate richness), these data may also be useful to other

investigators asking different questions (e. g. Huston, 1995; Rosenweig, 1995). The spider fauna of Pakitzá is only known from one previous qualitative sampling by Coddington and Silva (unpubl. data). During a period of three weeks in September-October, 1987, we collected 237 species. As of 1991, six new species have already been described from that inventory (Baert, 1990a; Levi, 1991b; Millidge, 1991).

## STUDY AREA

The study area is on the east side of the Manu River, among Pleistocene terraces up to 100 m above the present Manu river bed. The Biological Station of Pakitzá, 11° 56'S/71° 17'W, at an elevation of 356 m, includes approximately 4000 ha of lowland rain forest with an extremely irregular topography. Erwin (1991) provides a detailed description for Pakitzá.

*Weather.*- Data recorded in Cocha Cashu (approx. 21 km NE of Pakitzá) for ten years shows two distinct seasons based upon annual mean fluctuation in rainfall and temperature (Erwin, 1991). Four complete years of data indicate an average rainfall of about 2000 mm, seasonally distributed, most of it falling between November and May. Dry season months (May-October) normally receive less than 100 mm, though year-to year variation in the intensity and duration of the dry season is considerable (Terborgh, 1990). Dry seasons are also characterized by very strong winds and short cold periods, at this time the temperature may drop to 10-15 °C (Erwin, pers. comm.)

*Vegetation.*- Rio Manu presents an undisturbed rainforest flora (Foster, 1990). Generally, there is a one or two layer canopy forest with numerous super-emergents and varied amounts of herbaceous or shrubby understory (Erwin, 1991). In the BIOLAT Station Erwin (1991) identified twelve forest types, but only seven were sampled during this study. We describe these seven forest types, with their acronyms as listed in Appendix 1, following Erwin (1991).

### UPLAND SLOPE FOREST (USF).

This non-flooded forest type starts at stake 70 on Trail Tachigali and is found on reddish clay soil. There is no information on vegetation but according to Erwin (1991) the soil, drainage pattern, tree species, and associated microfauna are unique. The spiders were collected between stakes 80 and 100.

### OLD ALLUVIAL TERRACE FOREST (OAT).

This non-flooded forest type is found on sandy surface soil overlaying red lateritic soil. These soils are rapidly drained. BIOLAT Zone 3 is on this type of forest. This zone is dominated by Leguminosae (16%), Moraceae (15.5%), and

Palmae (14.1%); lianas are essentially absent. Our samples were taken outside zone 3 along Castañal and Troncal Tachigali trails; however these are not pure OAT collections since there are patches of dissected alluvial terrace forest mixed along these trails. Collections from Pacal (roughly, between stakes 5 to 25) and Zúngaro trails were also included in this forest type.

### **DISSECTED ALLUVIAL TERRACE FOREST (DAT).**

Well drained sandy surface soils characterize the non-flooded old alluvial terraces within 2 km of the Manu River. The dominant vegetation in this kind of forest are Violaceae (31.2%), Palmae (16.3 %), and Moraceae (10%). Samples are from Zone 1 and also along Tachigali trail, roughly between stakes 10 to 40. We may have mixed samples with a small patch of OAT.

### **LOWER FLOODPLAIN FOREST (LFF).**

Two zones occupy the lower, seasonally-flooded floodplain and different communities of plants occur in each of these zones. The lower zone, which floods and drains many times during the year, is covered with grasses and willows. Only one sample was taken here. The upper zone, on the other hand, may only flood once or twice per year. This is characterized by a forest with fewer and smaller trees (10-20m) than in other parts of Pakitzá. There are few palms and Zone 07 apparently is dominated by *Guarea* (29%) and *Sapium* (29%). The samples were taken inside this zone, and a few outside along Castañal trail.

### **UPPER FLOODPLAIN FOREST (UFF).**

The seasonally-flooded recent floodplain is on the richest alluvial soils. Parts of this forest are subject to yearly inundation, while other large areas are inundated by the highest floods, which may only occur once a century (Foster, 1990). The dominant trees, 25-35m tall, belong to Myristicaceae (11%), Bombacaceae (8%), and Meliaceae (7%). There are also many palms (21%) growing in this forest. We worked along the trails around Zone 2 and Caña Brava trail.

### **CLOSED RIPARIAN VEGETATION (RVF).**

A distinctive, seasonally-flooded streamside vegetation occupies certain stretches of the deeper stream courses along the main watersheds. This vegetation is overshadowed by the adjacent forest type. No surveys have been made to date. The samples were limited to Quebradas Picaflor, Trompetero, and Carpintero.

### **OXBOW LAKES (TGH).**

Through a special collecting permit, since they are not in the BIOLAT station, it was possible to take a few samples from the seasonally-flooded lagoons (cochas)

near Pakitza. The collections were made inside the forest, along the trails surrounding the oxbow lakes, and also from the aquatic herbs and shrubs in their exposed edges. The following information was taken from Ascorra et al. (1991): Cocha Juarez is on the east side of the Manu River, ca. 20 km river down from Pakitza. Cocha Otorongo is on the west side of the Manu River, between Salvador and Juarez lagoons. Cocha Salvador is also on the east side of Manu River, ca. 10 km river down to Pakitza. Cocha Totora is on the east side of Manu River, ca. 21 km NE Pakitza, in the Biological Station of Cocha Cashu.

## METHODS

Sampling occurred during two periods in the dry season of 1991. The first period, from April 21 to May 13, coincided with the early dry season. The second one was from September 26 to October 19, during the late dry season. Although we collected spiders with both non-quantitative and quantitative methods, this paper presents only the quantitative data.

The sampling protocol used elements of that of Coddington et al. (1991), but differed in significant respects. First, sampling was almost entirely done by the first author. Second, the sampling focussed almost entirely on the shrub, tree-trunk, and aerial web-spinning fauna; methods that accessed other components of the fauna were de-emphasized. The inventory thus was not intended to be representative of the total fauna, but that is in some ways a virtue because the lack of breadth may be compensated by depth--it is probably the largest and most detailed quantitative local list of web and cursorial spiders of the shrub and tree trunk zones from a lowland Neotropical site in the literature. Each sample was classified by three factors. Forest type was as noted above. Time of day of collection was classified either as day (0900-1600) or night (2000 to 2400). Methods of collection were as described below. The basic sampling unit was one hour of constant searching for spiders. Juvenile specimens were not purposely collected, since only adults can be only reliably identified to species. The full database thus contains sample number, forest type, season, month, date, collector name, method, time of day, replicate (if the same method was used by the same person within one time period and place), BIOLAT plot number if applicable, species code, genus, and family.

The collecting methods employed were 1) searching and picking by hand from the aerial vegetation and other surfaces, colloquially known as "looking up"; 2) searching and picking by hand both up in the vegetation and on the ground, or "looking up and down"; 3) searching and picking by hand on the ground surfaces, leaf litter or under logs, or "looking down"; 4) use of a beating try on the understory vegetation or lower branches of trees; and 5) pitfall traps located inside BIOLAT plots. Pitfall collections have not been included in the present study.

As noted above, both the methods used and the allocation of sampling effort

based against the ground and litter fauna. The spider fauna inhabiting the leaf litter or ground crevices, represented in Neotropical forests mostly by anapids, oonopids and small gnaphosids (Höfer, 1990; pers. obs.), was mainly evaluated by non-quantitative methods during both periods of field work. Because these groups and their ecological equivalents were almost entirely missed by the methods employed, this inventory pertains mainly to patterns within aerial web builders or other spiders that inhabit the shrub, tree trunk, aerial web zone, or other such "non-forest floor" zones.

Terms of relative abundance, like commonness or rarity, are based upon the general impression of the spider fauna throughout the field work and by personal experience with other Peruvian lowland forests.

## IDENTIFICATION

All specimens were sorted to morphospecies, but due to the scarcity of recent taxonomic revisions, many of the spiders can not be identified in a reasonable amount of time. Many Neotropical species are undescribed, and many of the known spider species were described without using modern taxonomic criteria, are based on juvenile specimens, or were described from only one sex.

We have gone to some lengths to include those taxonomic references most useful in identifying lowland Neotropical spiders. Ignorance of the literature is often a great obstacle to the study of spiders, and we hope that the bibliography presented here may help the beginning worker. Keyserling (1876-93), Pickard-Cambridge, F. O. (1897-1905), Pickard-Cambridge, O. (1889-1902), Simon (1892-1895, 1897-1903), Taczanowski (1872-79), in addition to papers by Baert and Maelfait (1986), Brignoli (1979), Bryant (1942, 1945), di Caporiacco (1947-1955), Chamberlin and Ivie (1942), Chickering (1937-1973), Jiménez (1988), Levi (1953-1993), Mello-Leitao (1939-1948), Nentwig (1993), Schenkel (1953), Schmidt (1971), Petrunkevitch (1925-1930), and Soares and Camargo (1955) are major works that describe Neotropical spiders and help to identify some species. However, only modern taxonomic revisions permit confident establishment of accurate names, and even then coverage is usually far from complete. References to genera that may occur in the Neotropics are cited under each family (Brignoli, 1983; Platnick, 1989, 1993). Families and genera are listed alphabetically, according to Platnick (1989), with a few exceptions.

Voucher specimens are deposited in the United States National Museum of Natural History, Smithsonian Institution. Duplicates and non-quantitative collections are kept in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (Peru).

## ANALYSIS

Any statistical procedure assumes that the sample is a random selection from the universe being investigated. In the present case, the universe being investigated

is that portion of the total spider fauna accessible by our collecting methods and present as adults in the seven forest types during the early and late dry season of 1991. "Accessible to the methods" is a crucially important qualifier. Obviously we can say very little about the portion of the spider community that exclusively abides in the canopy, burrows, or leaf litter because we made no concerted effort to collect them. How much of the spider community we thereby ignored is an interesting question. Judging from other studies (e.g. Young, 1992, Coddington unpubl. data), or virtually complete lists, e.g. Heimer and Nentwig, 1984; Kaston, 1948; Roberts, 1987), one may guess very roughly that the portion of the total fauna accessible to the methods applied here might be 50 - 85 % of the total. Litter inhabiting ground spiders such as erigonine linyphiids usually make up a large percentage of temperate communities, but they are unusually species-poor in the tropics. This taxon is replaced by groups like oonopids, pholcids, anapids, ochyroceratids, and other such cryptic forms. Typical values for the local richness of these tropical groups is at present unknown, although Höfer (1990) has presented some data for Amazonian terra firme forest. Another undercollected group is the Mygalomorphae, but these species constitute much less than 10% of the richness of a lowland tropical community. Presumably the largest omission is the canopy fauna. If current estimates of the low degree of overlap between canopy and subcanopy arthropod communities are correct, estimates based on subcanopy samples will be serious underestimated. In any case, if it is possible to estimate reliably the parametric value of the species richness of constrained samples, relationships such as the above can then be used to estimate the actual species richness.

We followed Magurran (1988) in fitting the data to a lognormal distribution. The area under the best-fit lognormal curve estimates the total species richness of the community. A shortcoming of the lognormal model is that no analytical formula for the confidence interval for the area under the curve exists and that the best method to fit discrete data to a continuous model is debatable (Colwell and Coddington, 1994; Ludwig and Reynolds, 1988; Pielou, 1975). However, it is the only model used here that permits a formal test of the fit of the data to the model.

Chao1, like the lognormal, does not require replicate samples and uses the relative abundance of species in the total sample to estimate richness (Chao, 1984). It works by augmenting the observed richness,  $S_0$ , by the square of the number of singletons  $n_1$  divided by twice the number of doubletons,  $n_2$ , thus  $S^* = S_0 + n_1^2 / 2n_2$ . Algebraically this is the same formula as Chao2 (see below), and Chao (in litt.) has suggested that the formula developed for the variance of Chao2 may also be used for Chao1 (see below). Chao (1984) was careful to emphasize that this estimator is really a lower bound on  $S^*$ . It should work best if most of the information in the sample is concentrated in the lowest frequencies, e.g. singletons and doubletons should predominate in the sample. As that is often the case in tropical work, this estimator deserves careful consideration.

The remaining techniques all require a series of replicate samples. We used least squares techniques combined with non-linear curve fitting (Wilkerson, 1991) to find the asymptote of the Michaelis-Menten equation,  $\text{cum}_n = S^* \cdot (S^* \cdot b) / (b + S_n)$ , where  $\text{cum}_n$  = the number of species accumulated by the nth sample,  $S_n$ ,  $S^*$  = total species richness, and  $b$  is a constant. To ascertain the effects of sample order on the asymptote, we randomized sample order 100 times, calculated an asymptote for each sample order, and computed the cumulative frequency distribution of these asymptotes. We then dropped the lowest and highest 2.5% of the cumulative distribution of asymptotes to approximate the interval within which 95% of asymptotes resulting from randomized sample orders should fall. This procedure is certainly not a technical 95% confidence interval on the species accumulation curve asymptote, but it does capture the variability in asymptotes due to sample order. We report the mean and the interval noted above as a measure of variability for the asymptote. Soberón and Llorente (1993) review the use of accumulation curves to estimate species richness. Of course, the accumulation curve technically reaches its asymptote only at infinity, but since decimal places in species richness estimates are biologically meaningless (we omit them throughout our results), the mathematical infinitude of an asymptote is not a serious objection to its practical use.

The jackknife estimator works by augmenting the observed number of species ( $S_0$ ) by the number of species ( $k_1$ ) unique to one sample, weighted by the number of samples,  $S$  (Heltshe and Forrester, 1983). Total species richness is  $S^* = S_0 + k_1(S-1)/S$ . In the limit in which all species occur in at least two samples, the jackknife accepts the observed number of species as the total richness. Its variance  $\text{var}(S^*) = (S-1)/S[\sum j^2 f(j) - k_1^2/n]$  is a function of the number of samples  $f(j)$  having  $j$  unique species. This is intuitively reasonable as well. If the unique species are distributed evenly across samples, the variance is low. If instead they are clumped in a few samples, their true total number is less certain, and the variance and confidence interval increase. Other higher order jackknife estimators also exist, but the results are largely the same as with the first order jackknife (Colwell and Coddington, 1994).

As noted above, Chao (1987) did not originally suggest Chao2 as an estimator of species richness, but rather to estimate population size when the capture probabilities vary among individuals. We trust that communities in which species differ in relative abundance is a formally equivalent problem. Chao2 works by augmenting observed richness,  $S_0$ , by the square of the number of unique species,  $k_1$ , divided by twice the number of species that occur in two samples only,  $k_2$ , thus  $S^* = S_0 + k_1^2 / 2k_2$ . The logic is in some senses "midway" between that of the jackknife, which also focusses on those species unique to particular samples, and Chao1, which is also sensitive to species that occur twice, albeit in abundance and not among samples. The variance of this estimator is  $\text{cvar} = k_2 * (.25 * (k_1 / k_2)^4) + (k_1 / k_2)^3 + 0.5 * (k_1 / k_2)^2$ . Like Chao1, the estimator should work well if species occur in only one or two samples, and as this is common in tropical samples, it also deserves careful consideration.

Unlike the lognormal and species accumulation curves, the non-parametric methods (jackknife, Chao1, Chao2) all have upper limits on the estimate they can provide for a given sample. If all observed species are unique to various samples, the jackknife reaches its maximum value of just under twice the observed richness. The upper limit for the Chao1 and Chao2 estimators is much higher, about half the square of the number of singletons or uniques, respectively (Colwell and Coddington, 1994). In practice, this ought to mean that Chao1 and Chao2 ought to escape undersampling bias sooner than the jackknife. If they work well, they ought to be able to do so with less data. Like the jackknife, if all species are represented by at least two individuals (or in two samples), the richness estimated by Chao1 and Chao2 will equal the observed richness. We used SYSTAT ver. 5.02 (Wilkerson, 1991) for all statistical analyses.

## RESULTS AND DISCUSSION

### GENERAL

Table 1 summarizes the results of the inventory for the total catch as well as partitioning it by forest type, season, time of day and collector.

A total of 2616 adults and 498 species were collected in the 109 quantitative samples. Viewed as a whole, the sample contained 207 species (41.6%) represented by only one individual (singletons), an additional 17 species that also occurred in only one hourly sample (for a total of 224 "uniques"), and the most abundant species numbered only 106 individuals. The sample is typically tropical, with many rare and few common species. Sampling efforts focussed primarily on two forest types (OAT, UFF) and to a much lesser extent on a third (DAT). The distinction between DAT and OAT was not always clear, and, as noted above, some OAT samples may have contained spiders collected from DAT and visa versa. The remaining 4 forest types were sampled too sparsely (< 10 samples each) to permit conclusions; generally they have been omitted from the quantitative analyses of results. Sampling also concentrated on one very productive method, aerial hand-picking, or "looking up," and to a lesser extent on a mixture of this method with ground sampling, or "looking down." The total sample probably reflects the fauna of the herb and shrub layer as well as a single collector could access it, but is almost certainly biased against the ground fauna, better sampled by "pure" looking down or trapping techniques (Höfer, 1990). Because of small sample size, this method and those involving beating were dropped from the analyses of the effects of seasonality, time of day, or forest type on composition of the samples. They have, however, been included in the estimate of overall species richness.

One simple measure of sampling completeness, density, or intensity is the ratio of individuals to species. The higher the ratio, the denser and more complete the

**Table 1:** Summary statistics for Pakitza samples.

Data Partition	Tot Ind	S	Tot Spp	Sampling Intensity	Nº Singletons	Fraction of Total Singletons	Nº Uniques	Fraction of Total Uniques	Fraction of Ind./sample mean (SD)
<b>FOREST TYPE</b>									
DAT	218	12	108	2.0	23	0.05	25	0.11	18.1 (8.1)
LFF	133	7	82	1.6	10	0.02	10	0.04	19.0 (6.7)
OAT	1199	45	324	3.7	90	0.18	95	0.42	26.6 (12.7)
RVF	36	2	26	1.4	3	0.01	4	0.02	18.0 (9.9)
TOH	167	6	99	1.7	20	0.04	22	0.10	27.8 (8.5)
UFF	797	32	250	3.2	58	0.12	64	0.29	24.91 (2.1)
USF	66	5	41	1.6	3	0.01	4	0.02	13.20 (2.4)
<b>SEASON</b>									
EARLY	1274	54	306	4.2	75	0.15	84	0.38	23.6 (11.4)
LATE	1342	55	368	3.7	132	0.27	140	0.63	24.4 (11.1)
<b>TIME OF DAY</b>									
DAY	824	43	254	3.2	68	0.14	77	0.34	19.16 (1.1)
NIGHT	1792	66	385	4.7	139	0.28	147	0.66	27.15 (1.3)
<b>METHOD</b>									
AERIAL SEARCHING	1997	79	442	4.5	171	0.34	182	0.81	25.38 (1.2)
AERIAL + GROUND SEARCHING	573	26	199	2.9	33	0.07	39	0.17	22.04 (2.7)
1 HOUR BEATS	22	2	15	1.5	0	0.00	0	0.00	11.00 (5.0)
1 HOUR BEATS GROUND	11	1	8	1.4	1	0.00	1	0.00	11.00 (na)
SEARCHING	13	1	8	1.6	2	0.00	2	0.01	13.00(na)
<b>TOTAL</b>	<b>2616</b>	<b>109</b>	<b>498</b>	<b>5.3</b>	<b>207</b>	<b>0.42</b>	<b>224</b>	<b>1.00</b>	<b>24.00 (1.1)</b>

sample. Sampling intensity (total ind./total spp.) for all of our samples together was 5.3, but when partitioned into samples from each of the forest types, sampling intensity ranged from 1.4 to 3.7. When partitioned by season, sampling intensity ranged from 3.7-4.2. In general, whenever a larger sample of a given sampling intensity is partitioned for analysis, sampling intensity drops and the ratio of rare to common species increases.

## SAMPLE COMPOSITION.

Most of the available methods to estimate species richness require data structured as replicate samples. Two aspects of such samples are important, number of species and abundance within samples (e.g. presence/absence, singletons or not; uniques or not). For example, in this study, collectors averaged about 24 adult specimens per hour of work and about 17 species, both slightly higher than any of the three Bolivian sites reported by Coddington et al. (1991). Comparison of the Peruvian to the Bolivian data is not yet complete, but it is likely that the

Spp./sample mean (SD)	Singletons portion of Partition Richness	Uniques portion of Partition Richness
12 (4.8)	0.21	0.23
15.7 (5.1)	0.12	0.12
19.2 (7.4)	0.28	0.29
13.1 (7.0)	0.12	0.15
21.2 (5.6)	0.20	0.22
18.2 (7.4)	0.23	0.26
9.8 (4.6)	0.07	0.10
16.4 (7.4)	0.25	0.27
18.6 (7.1)	0.36	0.38
12.7 (6.0)	0.27	0.30
20.6 (6.4)	0.36	0.38
19.1 (6.9)	0.39	0.41
14.0 (7.0)	0.17	0.20
8.0 (4.2)	0.00	0.00
8 (na)	0.13	0.13
8 (na)	0.25	0.25
17.5 (7.3)	0.42	0.45

difference will be significant. It accords with the general impression that Peruvian forests are richer both in species and number of individuals than the more temperate Bolivian forests. It is appropriate to examine the structure of the data used to estimate richness as well as any influences the sampling protocol may have on number of animals or species per sample. It also provides an opportunity to ask if cumulative differences due to seasonality or forest type seen in the total sample are also reflected in the hourly samples.

### EFFECT OF FOREST TYPE, SEASON, METHOD, TIME OF DAY, AND COLLECTOR

Viewing the data as replicate, hourly samples, forest type had a significant effect on richness but not on abundance within samples (Table 2). If the more poorly sampled forest types are included, the effect is less pronounced but generally the same. The dissected alluvial terraces (DAT forest) yielded significantly less rich hourly samples than either old alluvial terraces (OAT) or upland floodplains (UFF)( $p < 0.005$ ,  $p < 0.030$ , respectively, Tukey test). OAT and UFF were not different from each other. Although the difference between the forests may be real, it may

also be due to low sample size from the DAT forest, which received only 12 hours of sampling. The number of adults or species per sample was not different between early and late dry season (Table 2).

Because so few methods were used to sample the fauna, and because the most frequently employed methods overlapped (aerial hand-picking versus aerial and ground hand-picking), method of collection was unlikely to affect significantly the richness or abundance of spiders within samples, and it did not (Table 3). Collecting method usually does have a significant effect (e.g. ground hand-picking versus beating; Coddington et al., 1991; Young, 1992). Beating had to be dropped from the analysis due to small sample size (Table 1). Note that even if some methods are less productive in terms of individuals or species, they still have a role in estimating richness if they access different components of the fauna.

Time of day, however, significantly affected both abundance and richness of the hourly samples (Table 3). Both more species and more individuals are collected at night. The interaction between time of day and method was also

**Table 2.** Analysis of variance in abundance and species richness per sample by season and forest type (for three forest types with sample size > 10).

ABUN	N:	88	MULTIPLE R: 0.276	SQUARED MULTIPLE R: 0.076	
ANALYSIS OF VARIANCE					
SOURCE		SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO
FOREST		717.809	2	358.905	2.468
SEASON		41.651	1	41.651	0.286
FOREST*SEASON		247.614	2	123.807	0.851
ERROR		11924.444	82	145.420	0.431
NSP	N:	88	MULTIPLE R: 0.373	SQUARED MULTIPLE R: 0.139	
ANALYSIS OF VARIANCE					
SOURCE		SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO
FOREST		534.248	2	267.124	5.330
SEASON		127.132	1	127.132	2.537
FOREST*SEASON		50.228	2	25.114	0.501
ERROR		4109.460	82	50.115	0.608

significant. Hand-searching during the day is exceptionally unproductive, while hand-searching during the night is very productive. Collector identity had no significant effect on abundance or richness of the samples.

In summary, time of day strongly affected average richness of the hourly samples and to a lesser extent the average abundance of animals/sample. Forest type (DAT) affected richness, but not abundance (Table 2), perhaps due to differences in sampling effort.

## SPECIES RICHNESS ESTIMATES

Because the data were taken as a series of smaller, replicate samples that can

**Table 3:** Analysis of variance in abundance and richness of samples by time of day (day vs. night) and method (Aerial searching versus aerial and ground searching).

ABUN	N:	88	MULTIPLE R: 0.422	SQUARED MULTIPLE R: 0.178	
ANALYSIS OF VARIANCE					
SOURCE		SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO
TIME OF DAY		629.655	1	629.655	4.985
METHOD		7.049	1	7.049	0.056
TIME*METHOD		570.210	1	570.210	4.514
ERROR		10609.770	84	126.307	0.037*
NSP	N:	88	MULTIPLE R: 0.617	SQUARED MULTIPLE R: 0.380	
ANALYSIS OF VARIANCE					
SOURCE		SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO
TIME OF DAY		754.626	1	754.626	21.424
METHOD		2.523	1	2.523	0.072
TIME*METHOD		92.747	1	92.747	2.633
ERROR		2958.747	84	35.223	0.108

**Table 4.** N° individuals, samples, observed species, and mean and confidence interval (where available) of the jackknife, Chao1 Chao2 and species accumulation richness estimators for three forest types, two seasons and the total data set.

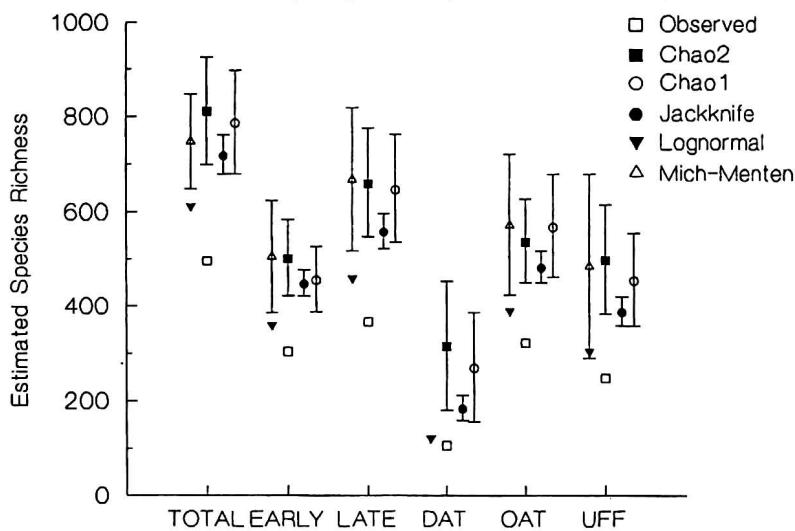
Partition	# Ind.	Samp.	# Obs	(1) JACKNIFE		(2) CHAO1		(3) CHAO2		(4) SPP.ACC.		LOG. NORMAL	Mean 1-4	Mean Obs.	Inventory Completeness
				Est.	CL	Est.	CL	Est.	CL	Est.	CL				
<b>FOREST</b>															
DAT	218	12	108	185	26	271	115	316	136	505	119	122	319	211	0.34
UFF	797	32	250	389	31	456	99	499	116	484	195	304	457	207	0.55
OAT	1199	45	324	483	34	570	109	538	89	572	149	389	541	217	0.60
<b>SEASON</b>															
EARLY	1274	54	306	449	28	457	70	503	81	661	114	358	518	212	0.59
LATE	1342	55	368	560	37	649	113	661	114	668	150	459	635	267	0.58
<b>TOTAL</b>															
TOTAL	2616	109	498	720	41	788	108	812	113	747	99	612	767	269	0.65

be pooled to calculate overall relative abundance of species, the five independent estimates of richness mentioned in the introduction can be applied. Due to the small sample sizes for forests LFF, RVF, TGH and USF, some or all of the methods failed to provide reasonable answers, and so these results are omitted from Table 4 and Fig. 1.

Estimates based on the complete sample range from the lognormal (612) to Chao2 (812). The confidence limits of the estimators for the complete sample range from a minimum of 648 to a maximum of 896 species, but broadly overlap (Table 4, Fig. 1). This range of richness values could thus be considered a rough interval estimate of the parametric richness of the particular component of the Pakitzá spider fauna sampled during that year. Nevertheless, it is still probably an underestimate (see below).

Although the fit of the total sample to the lognormal seems adequate graphically (Fig. 2), it can be rejected at the  $p < 0.05$  level ( $X^2 = 13.2$ ,  $df = 5$ ,  $0.2 < p < 0.05$ ). The data do not contain an observed mode, indicating that sample

Fig. 1.— Comparison of five methods of estimating species richness for 6 partitions of the data (see Table 4)



size may have been insufficient for a definitive test of the lognormal fit to the data. Insufficient sample size could also explain why the lognormal is consistently the lowest of the estimators for any given partition of the data (Table 4).

The lognormal clearly requires the

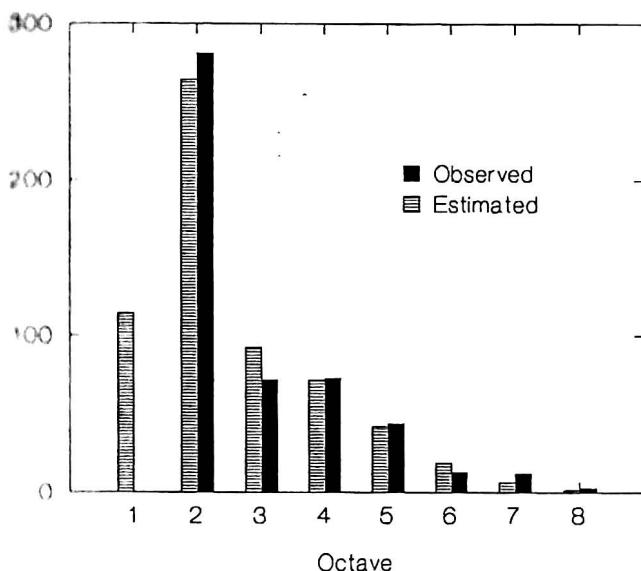


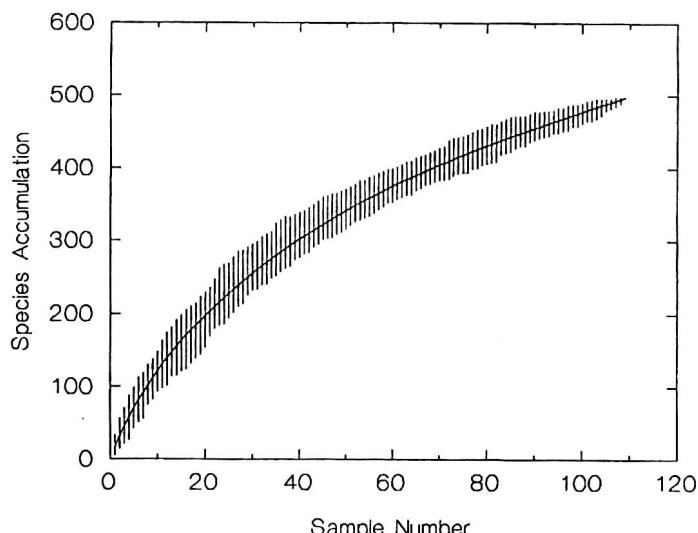
Fig. 3a. Fit of the total sample to the continuous lognormal model ( $\chi^2_{\text{obs}} = 13.24$ ,  $df=5$ ,  $p < 0.05$ )

most sampling effort to function well. Estimating the mean and variance of the normal distribution is chancy if the data lack an observed mode, but in large communities filled with rare species (=the tropics), "capturing the mode" requires a truly terrific sampling effort. Neither the complete sample nor any of its partitions contained a mode. The lognormal has the unique flaw that it depends to some extent on

the full relative frequency distribution of the community, which in turn dictates that even common species must continue to be collected. Of course, rightward octaves could be truncated as well, but then the goodness of fit test (and the fit itself) will be based on even fewer degrees of freedom. It is hard to envisage fitting the lognormal to a tropical sample with an observed mode that contained fewer than five or six octaves, in which case the most abundant species would number in the 100's anyway. Relative abundance is notoriously difficult to measure accurately and therefore the lognormal may be doomed to fixate on artifacts caused by various kinds of sampling bias.

The jackknife estimates for all partitions are fairly low, and the confidence intervals are small (Table 4, Fig. 1). As noted above, it has the flaw that it cannot produce an estimate of more than twice the number of observed species. With the possible exception of the IDAT forest partition, none of the jackknife estimates of richness in Table 4 are even close to double the observed value; perhaps this theoretical limit does not come

Fig. 3.- Plot of the minimum, maximum, and mean value (line) for 100 randomized samples orders for the total data set



into play for these data. On the other hand, the behavior of the jackknife as this limit is approached is unknown. Perhaps high estimates are increasingly "difficult" to achieve as the limit is approached. The small confidence intervals given by the jackknife are probably explained by the high proportion of singletons (usually about 30-40% for any partition, Tables 1 and 4), which by definition are unique to a sample. For the total sample, 207 singletons must "fit" into 109 samples. The actual number of uniques was 224, meaning that 17 species with abundances greater than one were also unique to single samples. At an average of 17 or 18 species per sample (Table 1), the distribution of uniques across samples must be fairly uniform and must therefore result in a rather low variance, and, consequently, a fairly narrow confidence interval.

Chao (1984) carefully notes that Chao1 is a lower bound on the estimated richness, and further, that it should perform better in samples dominated by singletons and doubletons. For the complete Pakitzá sample, 281 of 498 species, or 56%, were singletons or doubletons. Information on substantial numbers of species were thus discarded by this estimator, which depends crucially on the relative abundance of the two rarest classes of abundance. Whether accurate data on these frequency classes are the easiest or the most difficult to obtain is an interesting question. The ease of assessing presence versus absence, or nearly that, is confounded by stochastic errors and bias in sampling.

Chao2 utilizes the analogous number of species that occurred in just one or two samples, thus also discarding substantial amounts of information. Because Chao2 requires only presence-absence data and may be robust to undersampling bias (Colwell and Coddington, 1994) it may be the most practical richness estimator currently available. The estimates it provides (Table 4, Fig. 1), although typically high, may be closest to the true values. Both of Chao's estimators should work well on relatively sparsely sampled tropical faunas. Although the values given by each overlap quite closely, this is probably due to the high frequency of "rare" species in the sample (most uniques are singletons and visa versa).

The fit of the mean of 100 accumulation curves with randomized sample orders

to the Michaelis-Menten model seems acceptable (Figs. 3, 4). It is disturbing, however, that the best fit curve ("Estimated" in Fig. 4) is more cupped and thus yields a lower asymptote than one might fit by eye to the observed curve. In many

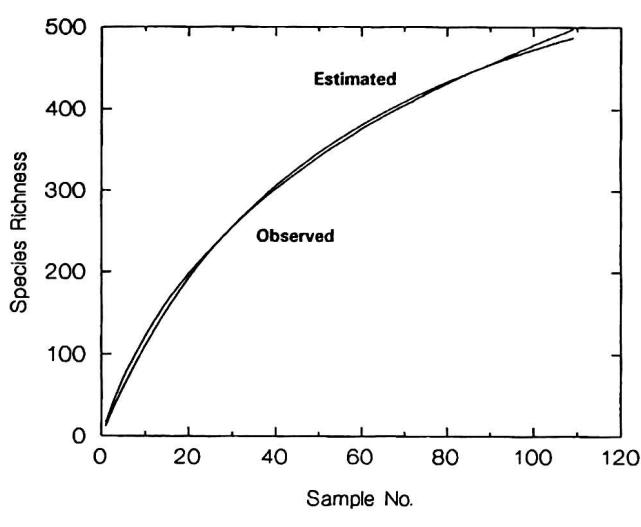


Fig. 4.— Plot of the least squares best fit curve against the mean curve for 100 randomized samples orders. The fit is good overall, but the Michaelis-Menten estimate is low at tails and high in the center of the sample range

of the 100 randomized accumulations the Michaelis-Menten model also appeared to be low at the tails but high in the center of the curve. If systematic, this bias will deflate richness estimates. The behavior of the Michaelis-Menten model is also quite erratic for small data sets that represent sparse sampling. In Table 4, the DAT value is quite out of line from the others, undoubtedly because so few samples were available. An advantage of the method used here, i.e. taking the mean of a large number of asymptotes resulting from randomized sample orders rather than accepting the best fit asymptote to the mean of those curves, is that some of these biases may be reduced.

Species accumulation curves are in some ways the most attractive technique to estimate richness. They are straightforward and lend themselves to graphical evaluation. The chief problem is the lack of justification for the Michaelis-Menten equation compared to other possible hyperbolic functions. Soberón and Llorente (1993) discuss other possible models that may better represent the biological realities implicit in accumulation curves. However, the Michaelis-Menten function has been widely used in the past for this purpose, and it fits data reasonably well. Some more than merely analogical relationship among biological variables posed by the Michaelis-Menten equation needs to be demonstrated. The most fundamental problem with accumulation curves is that the curve is extrapolated well beyond the last sample. If the fit between the model and the data is systematically skewed, the skew grows along with the extrapolation. Probably any approach that assumes a biologically realistic model will encounter the same problem for many data sets, if only because biological reality is diverse. An alternative approach might be to find a hyperbolic function complex and flexible enough to fit any accumulation curve extremely closely. At least then the extrapolation would depend as closely as possible on whatever biological situation the observed data represented.

Good estimators of species richness should provide confidence intervals. At the very least, confidence intervals should engender a healthy skepticism of overly exact "numbers" of species, whether of a park or the entire Earth. As sampling effort or sample size increases, the confidence intervals should narrow, until finally the true value is specified. More efficient estimators of species richness should have all of these virtues, but achieve higher accuracy and precision on the basis of relatively fewer data (Coddington et al., 1991).

The estimators used here do not fulfill the above criteria in all respects. For example, the richness estimated for any of the data partitions in Table 4 correlates well with sample size. For Chao1, Chao2, and the jackknife the reason is clear; all these estimators work by augmenting the observed richness by some moiety, itself usually a function of the "rare" species, whether numerically rare (Chao1) or the very related notion of rarity in space or time (Chao2, the jackknife). If tropical faunas are so large that early in the sampling effort the accumulation of species, and mainly rare species, is essentially constant with increasing sampling effort (as it sometimes seems to in this case, see below), then the number of rare species and the observed richness increase in lock step. It is not until the rate of

discovery of "new" species begins to drop, perhaps as evidenced by concavity in the accumulation curve, that any estimation procedure will begin to close in on the true value of richness.

For these data, the estimated richesses for various data partitions correlate with total number of specimens or samples, observed richness, and number of singletons (compare Tables 1 and 4). Fig. 5 juxtaposes the observed richness against the mean of the "unobserved" moieties as estimated by the jackknife, Chao1, Chao2, and Michaelis-Menten function for various partitions of the data. Although for small samples sizes such as the DAT forest, the unobserved moiety nearly doubles the observed richness, for all other partitions it is remarkably constant, adding about 200-270 species to the observed total. In effect, the fraction added to the observed richness by the estimators increases less with sample size than does the observed richness. This behavior seems rather odd. If an estimator has the undesirable behavior of correlation with sample size (Colwell and Coddington, 1994), one might expect the unobserved moiety to correlate as much or more than the observed fraction, given its "extrapolative" origins. On

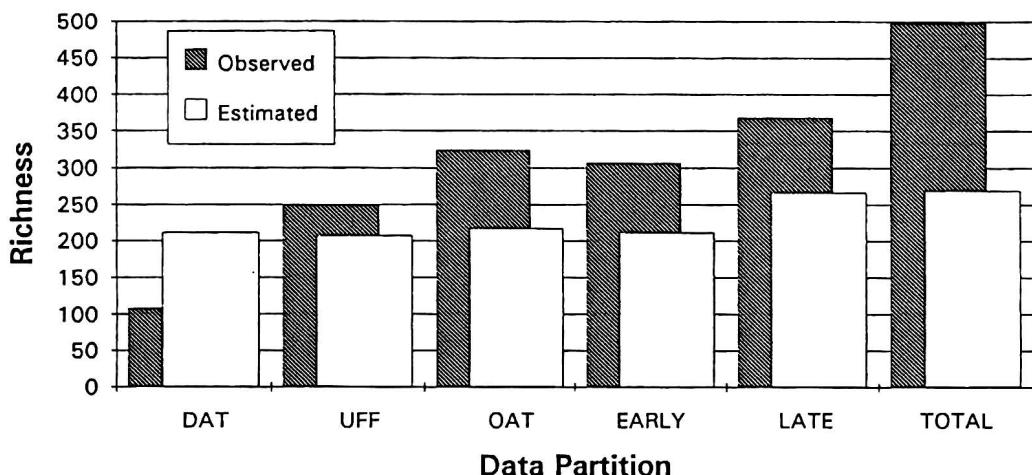


Fig. 5.— Histogram of the mean of the unobserved moieties for the jackknife, Chao1, Chao2, and Michaelis-Menten model estimators, plotted against the observed richness for each of the 6 partitions of the total sample.

the other hand, if species richness estimators behave "correctly," one should see a compensatory decrease in the unobserved moiety with increasing sample size such that the total richness estimate remains constant over a wide range in sample size. Fig. 5 shows that the behavior of the unobserved moiety for these data and estimators is intermediate. It does not increase much with sample size, which is good, but it does not decrease either, and so the net effect is correlation with sample size. If one considers the ratio of observed to mean estimated richness for any given partition of the data (Table 4), the "degree of completion" of the

inventory does rise with sample size. Perhaps the current data simply represent the relatively straight, early portion of the accumulation curve, but concavity is evident in Figs. 3 and 4. Given any reasonable frequency distribution, the estimators may have a practical upper bound that is a function of sampling effort. Until this upper bound exceeds the true parametric richness, procedures will always underestimate.

Within any one partition of the data, the estimators often have the same rank from low to high values: lognormal jackknife, Chao1, Chao2, Michaelis-Menten, although the rank of the latter is variable. Some of the reasons why this may be so in each case have been discussed above. Certainly the lognormal and the jackknife are usually lower, whereas the latter three are higher. The same pattern occurs in other data sets (Coddington, unpubl. data). As noted above, partitioning data into subsets tends to increase the numbers of rare species in the partitions compared to the whole dataset. If, as surmised above, Chao1 and Chao2 are more robust to undersampling bias than the jackknife or the lognormal, the disparity between the lower and higher estimators should be most obvious in the sparsest samples, and the effect should lessen as the sample approaches and then substantially surpasses half the total number of species.

Despite this expectation, the clusters of estimators for the six partitions of the data in Fig. 1 do not strongly support it. For the DAT forest, the lognormal and the jackknife are lower than Chao1 or Chao2, but this gap did not narrow greatly in the total data set. An alternative and highly possible explanation for this pattern is that even this sample, with 498 species comprising 2616 individuals, substantially undersamples the actual diversity at Pakitzá and so that even the most liberal estimators are still largely constrained by undersampling bias.

In summary, each estimator used here has its strengths and weaknesses from both theoretical and pragmatic points of view. One interesting result is that a really informed guess of the number of species "as yet unseen" may require a variety of estimators subjected to a variety of analytical techniques. For example, the concavity seen in Figs. 3 and 4 provide real evidence that progress towards a complete inventory has been made. On the other hand, species accumulation curves may be more affected by undersampling bias than other estimators, and thus yield poorer estimates. Chao1 and Chao2 seem like useful and handy techniques, but they are closely similar to each other and don't really represent dramatically different approaches to the problem. The jackknife has a good statistical pedigree, and is quite conservative. Close agreement between it and other estimators may be the hallmark of a robust estimate. Ironically, the one estimator that seems almost useless is the lognormal. It requires an immense amount of data, is "murky" to fit, is clearly not independent of sample size, and provides no confidence interval. Its main virtue seems to be the immense interest lavished on it in the ecological literature (e.g. May, 1975), and hence its use as a bridge or benchmark to link the results of more capable estimators to past work.

## SEASONALITY AND SPECIES RICHNESS

Estimated species richness for the late dry season community is greater than for the early dry season (Table 4, Fig. 1). Among forests, OAT is richer than UFF or DAT (Table 4, Fig. 1). Species tend to be more abundant in the late dry season than in the early dry season (Appendix 1,  $p < 0.033$ ,  $n = 498$  species, Wilcoxon signed rank test), but if singletons are excluded, the effect disappears ( $P < 0.623$ ,  $n = 291$  species, Wilcoxon signed rank test). The total observed richness was also significantly higher in the late dry season (Table 1,  $p < 0.000$ , sign test), but again, when the 224 uniques are excluded, the effect disappears ( $p < 0.139$ ).

## DISTRIBUTION OF SINGLETONS AND UNIQUES

Because of the weight given to singleton or unique species by richness estimators, their distribution in the sample merits special attention. Despite roughly similar sample sizes, judged both by numbers of samples and individuals, the late dry season had more singletons and uniques than the early dry season (132 or 140 vs. 75 or 84, respectively,  $p < 0.000$ , sign test). Females predominated over males among singletons (135 vs. 72,  $p < 0.000$ , sign test), a result at odds with the common wisdom that webless, wandering males will appear more frequently as singletons than the sedentary, more conspicuous females. However, the sex ratio of the total sample was also highly biased towards females (1669 vs. 947,  $p < 0.000$ , t test). In contrast, raw numbers of singletons and uniques among forest types, time of day, and method correlates positively with sample size (Table 1), but when viewed as a fraction of the richness for that partition remain roughly constant at 20-30 % over a wide range in sample sizes (Table 1). Chi-square tests on the proportion of singletons in these cases, assuming an expected frequency proportional to number of hourly samples, are all insignificant. Apparently the probability of encountering singletons does not drop dramatically across this range of sample sizes. One might have expected singletons to comprise a smaller percentage of a sample if the sampling intensity is higher, but if anything, it is larger. In sum, the effect of rare species (whether as singletons or uniques) is dramatic on comparisons between partitions of the data.

## COMMUNITY STRUCTURE

It is clear that spiders are numerically abundant and represented by a large number of species in many kinds of microhabitats. It is also clear that spiders can provide clues to understand better the importance of habitat structure on the composition of terrestrial invertebrate communities. Apparently, the diversity of spider communities is positively correlated with microhabitat complexity (Uetz, 1991). However, the nature of interactions in Neotropical spider communities is relatively unknown, and, in general, information about the effects of physical

## *Spiders of Pakitzá. Species Richness and Notes on Community Structure*

variables such as microhabitat structure on the occurrence patterns of spiders is still scarce (Gertsch and Riechert, 1976; Post and Riechert, 1977; Uetz, 1990; Rypstra, 1983; Jocqué 1984; Döbel et al., 1990).

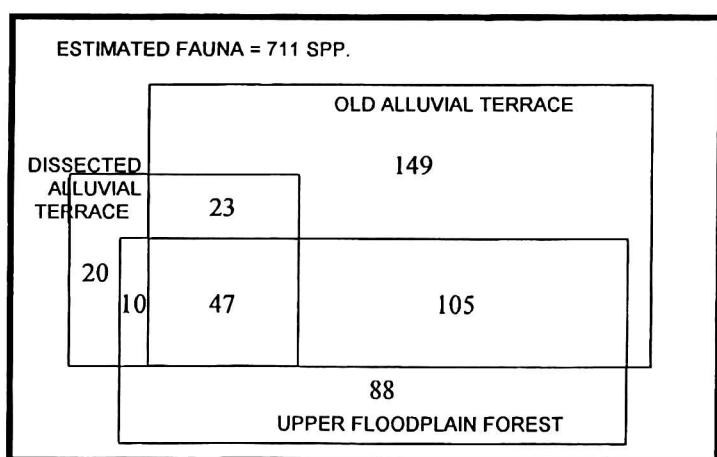
Our data shows that species composition, density and diversity may differ from one period of sampling to the other and also in different types of forest. Whether this effect is due to differences in sampling hours among forests, or seasons, or whether it reflects a natural phenomenon related to microhabitat qualities, will be clarified only with additional studies involving the phylogenetic history and ecological relationships within the whole community.

Our data suggest that spiders were more abundant and diverse in the late dry season than in the early dry season. The study presented by Lubin (1978), based on a year's census of web-building spiders on Barro Colorado Island, shows a sharp decrease in abundance of spiders throughout the dry season. Lubin found two population peaks, one in the late wet season and the second in the mid wet season; but a smaller increase in total numbers may occur after the first rains at the end of the dry season, followed by a decrease at the beginning of the wet season (Lubin, 1978).

Lubin has also shown a clear effect of forest type on the distribution of web-building spiders and she indicates that whereas the adults of some species are very restricted in time, the immatures can occur nearly year-round, defining two reproductive strategies: 1) a year-round emergence of immatures coupled with complete overlap of generations, and/or 2) the occurrence of long development periods of young, spanning seasons which are unfavorable for adults. These hypotheses may help to explain the existence of the large number of species represented by single adult specimens throughout a long period of sampling, and why they are overrepresented in the late dry season, especially when the great majority are web-building spiders.

Over 90% of the species in our sample occurred in the three Pakitzá forests (DAT, OAT, and UFF) for which we have more than 10 hours of sampling (450 of 498 species, Table 1). Considering just the species from these three forest types, 370 were unique to one forest or another (Table 1), 23 were common to DAT

A Venn-like diagram of the diversity and overlap between dissected alluvial terrace forest (DAT), old alluvial terrace forest (OAT), and upland floodplain forest (UFF). Size of rectangles is proportional to the observed (not estimated) richness of each forest, and the area of overlap between any two or all three areas is proportional to the species in common.



and OAT, 10 were common to DAT and UFF, 105 were common to OAT and UFF, and 47 occurred in all three forests (Fig. 6). The question naturally arises of how dissimilar or distinct these forests are. Colwell and Coddington (1994) suggested "complementarity" as the distinctness or dissimilarity of two assemblages in any ecological dimension (e.g. species lists, host-parasite relations, pollinator-plant relationships, etc.), and proposed a simple statistic to measure it: the proportion of all members in two lists that occurs in only one or the other of them. Thus, the complementarity of two lists  $j$  and  $k$  is  $C_{jk} = (S_j + S_k - V_{jk}) / (S_j + S_k - 2*V_{jk})$ , where  $S_j$  is the number of species from site  $j$ ,  $S_k$  is the number from site  $k$ , and  $V_{jk}$  is the number in common. Using this statistic to compare the species lists from these three forest types, the DAT-OAT complementarity is 0.81, that of DAT-UFF is 0.85, and that of OAT-UFF is 0.64. Old alluvial forest is most distinct from upper floodplain forest, and not surprisingly, the alluvial terrace forests are quite similar.

In the following analysis we present an initial insight into the spider community of Pakitza. Apparently, in this community a highly heterogeneous environ-

**Table 5.-** Guild composition and abundance of the spider community at Pakitza.

Family	Spp. early	Spp. late	Spp. total	Ind. early	Ind. late	Ind. total	% spp.	% ind.
<b>ORB-WEAVERS</b>								
Anapidae	1	0	1	2	0	2	0.4	0.2
Araneidae	85	112	145	319	424	743	61.7	59.8
Deinopidae	1	2	2	2	5	7	0.9	0.6
Mysmenidae	9	1	9	33	3	36	3.8	2.9
Tetragnathidae	22	26	35	82	50	132	14.9	10.6
Theridiosomatidae	18	5	19	130	7	137	8.1	11.0
Uloboridae	16	21	24	77	108	185	10.2	14.9
<b>SCHEET-WEB WEAVERS</b>								
Dictynidae	0	1	1	0	1	1	0.9	0.1
Linyphiidae	5	4	6	17	8	25	5.4	2.9
Pholcidae	11	8	12	56	28	84	10.8	9.6
Scytodidae	2	2	2	8	11	19	1.8	2.2
Theridiidae	63	65	90	400	347	747	81.1	85.3
<b>CURSORIAL HUNTERS</b>								
Anypheenidae	6	9	13	13	16	29	15.3	11.1
Aphantochilidae	1	1	1	2	3	5	1.2	1.9
Caponiidae	1	0	1	1	0	1	1.2	0.4
Clubionidae	0	3	3	0	3	3	3.5	1.1
Corinnidae	5	11	13	9	17	26	15.3	10.0
Gnaphosidae	0	1	1	0	1	1	1.2	0.4
Lycosidae	5	3	6	17	5	22	7.1	8.4
Miturgidae	2	3	3	2	6	8	3.5	3.1
Oonopidae	2	3	3	2	4	6	3.5	2.3
Salticidae	18	35	41	33	127	160	48.2	61.3
<b>AMBUSH PREDATORS</b>								
Ctenidae	8	11	16	18	27	45	12.0	19.0
Hersiliidae	2	2	2	5	9	14	1.5	5.9
Heteropodidae	2	4	5	3	10	13	3.7	5.5
Mumidae	6	10	11	14	45	59	8.2	24.9
Oxyopidae	3	6	8	5	24	29	6.0	12.2
Philodromidae	1	0	1	1	0	1	0.7	0.4
Pisauridae	1	3	3	4	23	27	2.2	11.4
Selenopidae	0	1	1	0	2	2	0.7	0.8
Senoculidae	2	4	4	4	14	18	3.0	7.6
Thomisidae	6	9	12	12	10	22	9.0	9.3
Trechaleidae	1	4	4	2	5	7	3.0	3.0

ment is causing the extreme temporal and spatial partitioning of microhabitats by the spiders. Although our data seem to support the hypothesis that guild formation tends to minimize competition (Post and Riechert, 1977) and that this high specialization may promote a greater species richness, there is not enough information about many other factors (Pielou, 1975) that may help to explain the high number of coexisting spider species in Pakitzá.

We present this classification only as a first attempt that can be used in further comparisons with other spider communities to help understand species diversity patterns. Our guild categories primarily represent similarities in prey-capture strategy, although within any guild there is much variation in the details of prey capture. We recognized four guilds: orb-weavers, sheet/line weavers, ambush predators, and cursorial hunters (Table 5).

In Appendix 1 we present a complete list of species and their abundance in different forest types and seasons.

## ORB WEAVERS

In Pakitzá these comprise the richest (235 species) and most abundant (48 %) spider guild. Most species of this guild make an orb web, usually a two-dimensional structure, that captures mainly flying insects. Some species construct a highly modified structure, ranging from a three-dimensional web to only one silk line. Araneidae are the dominant spiders in this guild. In the following sections, useful taxonomic references are grouped at the end of each section.

### ANAPIDAE, 1 SP (ANA)

These tiny spiders inhabit the leaf litter or fallen tree trunks of some tropical forests where they are relatively common (Höfer, 1990; pers. obs.). We collected two specimens of *Pseudanapis* in the early dry season. In spite of exhaustive searching for anapids, no additional specimens were found; however it is possible that during the dry season they seek refuge in inaccessible humid microhabitats. Only one other specimen was collected in 1987 (*Anapisona* sp.); we suspect that anapids are rare at Pakitzá, although they may be present in the still unsorted canopy fogging samples, as is the case in other Peruvian lowland forests (pers. obs.). Balogh and Loksa (1968), Forster (1958), Forster and Platnick (1977), Georgescu (1987), Gertsch (1960), Müller (1987d), Platnick and Forster (1990), Platnick and Shadab (1978b, 1979a).

### ARANEIDAE, 145 spp (ARA)

In our samples araneids (the typical orb-weavers) were the richest and second most abundant family (743 ind.). These common spiders are found in a great variety of microhabitats from the ground up to the trees. *Eustala* was the richest (33 spp.) and most abundant genus (112 ind.). Most species (55 %) were

represented by single specimens. Most individuals were taken in the late dry season and it appears that the dominant species have no preferences for forest types.

Some of the four species of *Mangora*, the second most abundant genus (106 ind.), were found only in certain types of forests. Species 1 (38 ind.) was dominant during the early season in OAT forest, while species 4, the second most dominant araneid (51 ind.), was more or less equally distributed during the dry season in all forest types.

*Micrathena* is the second most diverse (18 spp.) araneid but most species are represented by few individuals.

Most specimens of *Cyclosa* (13 spp.), the third most abundant (74 ind.) araneid, were collected during the early dry season in OAT forest.

*Parawixia kochi* (Tacz.), species 94, is the dominant araneid in Pakitzá (53 ind.). It is broadly distributed in the Neotropics (Levi, 1992) and very abundant in Peruvian lowland forests; however, it was dominant only during the late dry season (47 ind.).

*Alpaida delicata* (Keys.), species 24, is the third most common araneid in Pakitzá (47 ind.). It is widely distributed in the Neotropics (Levi, 1988) and lowland forests in Peru. Most individuals (62 %) were collected in OAT forests.

*Araneus venatrix* (C.L. Koch), species 92, is another common species with a very broad distribution throughout the Neotropics (Levi, 1991a). In Pakitzá, most species were found during the late dry season (15 ind.) in UFF forests (61 %). Berman and Levi (1971), Bryant (1945), Chickering (1954, 1955), Gertsch (1955), Harrod et al. (1990), Levi (1968, 1970, 1972, 1980, 1985, 1986a, 1988, 1989, 1991-1993), Mello-Leitao (1945b).

## DEINOPIDAE, 2 SPP. (DEI)

Most of these nocturnal spiders were found hanging from dry twigs. In the daytime they were collected by beating clusters of dry leaves, mainly during the late dry season. Coddington (1990).

## MYSMENIDAE, 9 SPP. (MYS)

The peculiar three-dimensional web of these very tiny spiders (about 1 mm in size) is commonly found in the leaf litter, crevices of logs or tree trunks. Some species of *Mysmenopsis* are found as kleptoparasites of larger web spiders such as the araneid *Cyrtophora* or the diplurid *Linothele*. The dominant mysmenid, species 43, was collected only during the early dry season. Baert (1990a), Baert and Maelfait (1983), Coyle and Meigs (1989), Georgescu (1987), Gertsch (1960), Levi (1956a), Müller (1987e), Platnick and Shadab (1978a).

## TETRAGNATHIDAE, 35 SPP. (TET)

In terms of abundance this family ranked sixth (132 ind.). Tetragnathids are frequently found in horizontal orb webs in various microhabitats from the ground

layer up to the trees. *Glenognatha* and *Metabus*, the latter recorded from non-quantitative collections, are restricted to streams where they live in colonies. *Tetragnatha* are most common along streams but are also found inside the forest. The most abundant tetragnathid, *Leucauge* species 191, was mainly collected in the early dry season. Baert (1987), Chickering (1957, 1962), Hormiga and Döbel (1990), Levi (1980, 1981, 1986b), Levi and Eickstedt (1989), Okuma (1992).

### **THERIDIOSOMATIDAE, 19 spp. (THS)**

It ranked fifth (137 ind.) in terms of abundance. The two or three-dimensional webs of these tiny spiders are found in a variety of microhabitats from the leaf litter up to the trees. Because they prefer wet microhabitats, dryness appears to have a strong effect on their richness and abundance.

Most species (95 %) were collected in the early dry season. *Epeirotypus* species 12, numerically dominant (50 ind.), was collected in the early period from webs on spiny palm trunks; whereas the second most abundant theridiosomatid (31 ind.), *Theridiosoma* species 34, was found during the same period in webs scarcely above the ground layer. Coddington (1986), Georgescu (1987).

### **ULOBORIDAE, 24 spp. (ULO)**

This family ranked third in terms of abundance (185 ind.). Solitary foragers may be found under leaves or very well camouflaged among the vegetation, others form colonies among shrubs, while others are kleptoparasites of various weaver spiders. Uloborids like *Miagrammopes* species have reduced the orb web to only one line. Most species are represented by few individuals. The two most common species, *Uloborus* 15 (50 ind.) and *Philoponella* 14 (41 ind.) do not exhibit major differences between early and late dry season; on the other hand, most individuals of one common species of *Miagrammopes* 214 (14 ind.) were collected only in the late dry season. Chickering (1968a), and Opell (1979, 1981, 1982, 1984, 1987).

### **SHEET/LINE WEAVERS**

In this guild prey are detected by vibratory signals transmitted through sheet/line webs chiefly designed for walking arthropods. In terms of diversity (111 spp.) and abundance (34%) it ranked second in Pakitza. In this guild the dominant family is Theridiidae.

### **DICTYNIDAE, 1 sp (DIC)**

These small spiders were collected under roughened bark of a large tree trunk during non-quantitative sampling and only one male was collected while looking up at night in an UFF forest. Dictynids are probably not this rare at Pakitza; we probably overlooked the appropriate microhabitat. Gertsch (1945, 1946).

## LINYPHIIDAE, 6 spp. (LIN)

Although these small spiders are commonly found in temperate zones, they are uncommon in lowland Neotropical forests. Linyphiids inhabit various microhabitats from the ground layer up to the trees. Most species are represented by few individuals. Baert (1987a, 1990b), Müller and Heimer (1991b), Millidge (1985, 1991).

## PHOLCIDAE, 12 spp. (PHO)

The conspicuous webs of these small spiders are found in different microhabitats from the ground layer up to the trees. This is the seventh most abundant family (84 ind.). Some species appear to prefer the early dry season; although the dominant species, no. 21, (33 ind.) does not show a major difference between the early and late dry season. Brignoli (1981), Gertsch (1939, 1982, 1986), Gertsch and Peck (1992), Kraus (1957), Mello-Leitao (1918, 1946-1947b).

## SCYTODIDAE, 2 spp. (SCY)

These spiders were associated with dry leaves suspended in various understory microhabitats. Most individuals were collected at night from spiny palm trunks in the late dry season. Mello-Leitao (1918), Valerio (1971, 1981).

## THERIDIIDAE, 90 spp. (THD)

These small to medium-sized spiders were the most abundant (747 ind.) and second most diverse family at Pakitza. Theridiids may be found as solitary foragers, in colonies, or as kleptoparasites of other weaver spiders, inhabiting various microhabitats from the ground layer up to the trees.

The dominant theridiid was *Episinus erythrophthalmus* (Simon), species 56, (106 ind.), widely distributed throughout the Neotropics (Levi, 1964). It showed a preference for UFF forests in the early dry season.

*Argyrodes amplifrons* O.P.C., species 9, is fairly common in lowland rainforests in Peru. It was the second most abundant theridiid (71 ind.) at Pakitza and was most common in the early dry season.

*Thwaitesia bracteata* (Exline), species 76, the third most common theridiid in Pakitza (66 ind.) and broadly distributed in lowland forests of Peru, was collected mainly during the late dry season in UFF forests.

*Argyrodes metalissimus* (S. & C.), species 75, is another common spider in Pakitza (44 ind.). It is a kleptoparasite in the webs of the social theridiid *Anelosimus eximius* (Keys.), but solitary foragers may also be found underside leaves. This species is slightly more common in the late dry season. Archer (1950), Buckup and Marques (1991-1992), Exline and Levi (1962, 1965), Fowler and Levi (1979), Georgescu (1987), González (1991), Heimer and Müller (1991), Levi (1953-1955,

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1956b-1957, 1959-1960, 1962-1967, 1968b), Levi and Levi (1962), Levi and Randolph (1975), Levi and Smith (1983), Marques and Buckup (1989, 1992), and Müller and Heimer (1990, 1991a).

### **CURSORIAL HUNTERS.**

These spiders do not use webs for prey-capture and tend to move slowly (brief advances separated by long or short pauses) through the environment searching for prey. This guild ranked fourth in richness (85 spp.), although it is the third most abundant (10 %) in Pakitza. The dominant family is Salticidae (Table 5).

#### **APHANTOCHILIDAE, 1 SP. (APH)**

These ant-mimics spent most of their time on the vegetation or tree trunks searching for prey. Two genera (*Aphantochilus* and *Bucranium*) were collected in Pakitza, but only one is represented in our time based samples and more or less equally distributed in both early and late dry season. Gerschman and Pikelin (1964), Mello-Leitao (1946).

#### **ANYPHAENIDAE, 13 SPP. (ANY)**

These nocturnal spiders often seek refuge in the curled dry leaves of shrubs or suspended dry leaves clusters in the daytime. The two most common species are about as abundant in the early as in the late dry season. Brescovit (1991, 1992), Brescovit and Lise (1989), Gerschman and Schiapelli (1970), Platnick (1974).

#### **CAPONIIDAE, 1 SP. (CAP)**

These spiders are rare at Pakitza, but we expect to find more individuals in the canopy fogging samples, as is the case in other Peruvian lowland forests. A single male specimen was taken from the ground layer along a narrow stream of black water, near BIOLAT Zone 05 (early dry season). Alayón García (1986), Birabén (1954a, 1951), Brignoli (1977), Chickering (1967), Platnick (1993b).

#### **CLUBIONIDAE, 3 SPP. (CLU)**

Three clubionid specimens were collected at night, all from the vegetation during the late dry season. Brescovit and Bonaldo (1992), Chickering (1937), Müller and Heimer (1988).

#### **CORINNIDAE, 13 SPP. (COR)**

Most corinnids are ant-mimics and are found searching for prey in various microhabitats from the ground layer up to the trees. Most species were collected in the late dry season. All species were uncommon. Chickering (1972), Reiskind (1969, 1971), Bauab Vianna (1979), Müller and Heimer (1989), Platnick and Shadab (1974), Platnick (1975b, 1979a).

## **GNAPHOSIDAE, 1 SP. (GNA)**

A single female was collected from the vegetation in the early dry season. Baert and Maelfait (1986), Müller (1987a-c, 1988), Platnick (1975a, 1983a, 1983b), Platnick and Höfer (1990), Platnick and Shadab (1975-1976, 1979b-1988), Platnick and Murphy (1984).

## **LYCOSIDAE, 6 SPP. (LYC)**

These diurnal spiders, which are often found wandering on the ground layer, occurred at low densities during the dry season at Pakitza. The dominant lycosid, species 17 (12 ind.), was collected in the early dry season. Capocasale (1982, 1990-91), and Dondale (1986), Maelfait and Baert (1986), Zimber (1963).

## **MITURGIDAE, 3 SPP. (MIT)**

These uncommon spiders are found in the understory vegetation. Most individuals of these nocturnal spiders were found during the late dry season. Bonaldo (1992), Platnick and Shadab (1989), Platnick and Ramirez (1991).

## **SALTICIDAE, 41 SPP. (SAL)**

The jumping spiders ranked fourth in terms of abundance (160 ind.) in Pakitza. They were found in all microhabitats, more often in the daytime. Most species were collected in the early dry season (71 %), but the two most abundant species (34 and 22 ind., respectively) were found in the late dry season. Another common salticid, species 23 (21 ind.), was collected in both early and late dry season. Bauab-Vianna (1979b, 1980, 1983), Bauab and Soares (1978, 1980, 1982-83), Cutler (1981, 1982, 1985, 1988), Cutler and Müller (1991), Galiano (1960-1991), Müller and Cutler (1989), Proszynski (1971).

## **AMBUSH PREDATORS.**

The species in this guild tend to remain stationary for long periods of time waiting for prey. This group is represented by 134 species and they accounted for approximately 9 % of the total abundance. Ctenids are the most abundant (Table 5).

## **CTENIDAE, 16 SPP. (CTE)**

These typical nocturnal spiders live in various microhabitats from the ground layer up to the trees; they also occur on stream banks or near the water's edge of the river. Most species were uncommon and were collected in the late dry season. Bücherl et al. (1969), Chickering (1960), Eickstedt (1975, 1978, 1981, 1983), Eickstedt et al. (1969), Lachmuth et al. (1985), Mello-Leitao (1936), Peck (1981), Schiapelli and Gerschman (1972), Simo (1992).

## **HERSILIIDAE, 2 spp. (HER)**

These nocturnal spiders are found well camouflaged on the bark of large tree trunks. Few hersiliids were collected at Pakitzá, mainly in the late dry season. No revisions for a Neotropical fauna.

## **HETEROPODIDAE, 5 spp. (HET)**

These nocturnal spiders were often found inside curled leaves in the daytime or sitting on the vegetation at night. All species were uncommon, and most of them were collected during the late dry season. Baert and Maelfait (1986).

## **MIMETIDAE, 11 spp. (MIN)**

These specialized predators of other spiders are commonly found on the underside of leaves or hanging from the vegetation at night. The dominant mimetid (23 ind.), species 96, had higher densities in the late dry season. Archer (1950), Baert and Maelfait (1984), Chickering (1947, 1956), Mello-Leitao (1929), Platnick and Shadab (1993), Shear (1981).

## **OONOPIDAE, 3 spp. (OON)**

These very small spiders are frequently found in the leaf litter or under logs. Some specimens were collected at night in the late dry season from the vegetation. This is a family we expect to be more abundant in the canopy fogging samples, as it happens in Tambopata and Samiria forests (unpubl. data). Birabén (1954b), Brignoli (1978, 1979), Chickering (1951, 1968b-1970, 1972, 1973), Cooke (1972), Dumitrescu and Georgescu (1987).

## **OXYOPIDAE, 6 spp. (OXY)**

These spiders are known to be more active in the daytime when they are found in various microhabitats of the understory vegetation. The majority of our specimens were collected at night, from shrubs, in the late dry season. Brady (1964, 1969, 1970, 1975), Garcia-Neto (1989), Griswold (1983), Lourenço (1990), Mello-Leitao (1929).

## **PHILODROMIDAE, 1 sp. (PHI)**

A single female was collected in Cocha Otorongo, from the vegetation (early dry season). Dondale and Redner (1969, 1976), Jiménez (1987), Sauer and Platnick (1972).

### PISAURIDAE, 3 spp. (PIS)

These diurnal spiders are found in various types of microhabitats of the understory vegetation. Some species may also occur in marshy environments. The dominant pisaurid (18 ind.), *Architis cymatilis* Carico, species 95, was found only during the late dry season. Carico (1976, 1981, 1989, 1993a), Sierwald (1990).

### SELENOPIDAE, 1 sp. (SEL)

Only two of these nocturnal spiders were collected from tree trunks (late dry season). Alayón García (1992), Birabén (1953), Corronca (1990, 1991), Lins (1980), Muma (1953).

### SENOCULIDAE, 4 spp. (SEN)

These nocturnal spiders may be found in the daytime very well camouflaged in dry leaves or twigs. At night, they hang from the vegetation and resemble small pieces of dry leaves. Females with eggsacs were frequently seen in the late dry season. Our data indicate a slightly increase in the number of species and individuals in the late dry season. No recent revisions.

### THOMISIDAE, 12 spp. (THO)

Only few thomisids were collected from the vegetation, mainly in daytime. Birabén (1955), Chickering (1965), Dondale and Redner (1975) Garcia-Neto (1991), Jiménez (1992), Lise (1973, 1979, 1980a, 1980b, 1981), Mello-Leitao (1943), Rinaldi (1983, 1984, 1988).

### TRECHALEIDAE, 4 spp. (TRE)

These spiders, are mainly active in the daytime and occur in various microhabitats of the understory vegetation and also along the river, streams or marshy areas. Most species were collected in the late dry season. Carico (1993b), Carico et al. (1985), Sierwald (1990, 1993).

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**Appendix 1.** Species list of spiders collected from Pakitzá during 1991, partitioned by abundance within forest type and again within season.

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
ANY	Pseudanapis	325	0	0	1	0	0	1	0	2	0	2
ANY	Anyphaenid B	113	0	1	0	0	0	6	1	5	3	8
ANY	Anyphaenid B	358	0	0	6	0	0	1	0	3	4	7
ANY	Anyphaenid B	402	0	0	0	0	0	1	0	0	1	1
ANY	Anyphaenid C	114	0	0	0	0	0	1	0	0	1	1
ANY	Anyphaenid D	154	0	0	1	0	0	1	0	2	0	2
ANY	Anyphaenid D	475	0	0	0	0	0	1	0	1	0	1
ANY	Anyphaenid E	276	0	0	1	0	0	0	0	0	1	1
ANY	Anyphaenid F	277	0	0	1	0	0	0	0	0	1	1
ANY	Anyphaenid F	375	0	0	0	0	0	0	1	1	0	1
ANY	Anyphaenid G	295	0	0	3	0	0	0	0	0	3	3
ANY	Anyphaenid H	306	0	0	1	0	0	0	0	1	0	1
ANY	Anyphaenid I	397	0	0	1	0	0	0	0	0	1	1
ANY	Anyphaenid J	412	0	0	1	0	0	0	0	0	1	1
MIL	Bucranium	371	0	2	2	0	0	1	0	2	3	5
ARA	Alpaida	467	0	0	0	0	0	2	0	2	0	2
ARA	Acacia	149	0	0	3	0	0	0	0	1	2	3
ARA	Acacia	152	1	1	4	0	2	3	0	5	6	11
ARA	Aculepeira	265	0	0	1	0	0	0	0	0	1	1
ARA	Alpaida	24	10	0	29	0	0	8	0	15	32	47
ARA	Alpaida	25	0	0	4	0	0	2	0	4	2	6
ARA	Alpaida	26	2	1	3	1	0	7	0	11	3	14
ARA	Alpaida	141	0	1	5	0	2	0	0	2	6	8
ARA	Alpaida	233	0	0	2	0	1	1	0	3	1	4
ARA	Alpaida	323	1	0	1	0	0	0	0	0	2	2
ARA	Alpaida	393	1	0	0	0	0	0	0	0	1	1
ARA	Alpaida	448	0	0	1	0	0	0	0	0	1	1
ARA	Alpaida	464	1	0	0	0	0	0	0	0	1	1
ARA	Alpaida	478	6	0	0	0	0	0	0	6	0	6
ARA	Araneinae K	33	0	0	1	0	0	0	0	1	0	1
ARA	Araneinae L	79	0	0	0	0	0	3	0	2	1	3
ARA	Araneinae M	209	2	1	0	0	0	2	1	2	4	6
ARA	Araneinae N	227	1	0	0	0	0	0	0	1	0	1
ARA	Araneinae O	275	0	0	2	0	0	0	0	0	2	2
ARA	Araneinae P	331	0	0	1	0	0	0	0	1	0	1
ARA	Araneinae Q	335	1	0	0	0	0	0	0	0	1	1
ARA	Araneinae R	392	1	0	0	0	0	1	0	0	2	2
ARA	Araneinae S	409	0	0	0	0	0	1	0	0	1	1
ARA	Araneinae T	437	0	0	1	0	0	1	0	0	2	2
ARA	Araneinae U	439	0	0	2	0	0	0	0	1	1	2
ARA	Araneinae V	477	0	0	1	0	0	0	0	0	1	1
ARA	Araneinae W	481	0	0	0	0	0	0	1	1	0	1
ARA	Araneinae X	487	0	0	1	0	0	0	0	1	0	1
ARA	Araneinae Y	498	1	0	0	0	0	0	0	0	1	1

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
ARA	Araneus	92	0	4	0	0	3	11	0	3	15	18
ARA	Araneus	314	0	0	1	0	0	1	0	1	1	2
ARA	Araneus	494	1	0	0	0	0	0	0	1	0	1
ARA	Argiope	179	0	0	0	0	1	1	0	0	2	2
ARA	Aspidolasius	64	0	3	2	0	2	2	0	1	8	9
ARA	Bertrana	282	0	0	2	0	0	2	1	5	0	5
ARA	Chaetacis	5	2	1	8	0	1	0	1	10	3	13
ARA	Cyclosa	6	0	1	1	0	3	1	0	2	4	6
ARA	Cyclosa	29	1	0	6	0	0	2	0	7	2	9
ARA	Cyclosa	86	1	0	9	0	1	6	1	16	2	18
ARA	Cyclosa	100	0	0	11	0	0	1	0	7	5	12
ARA	Cyclosa	122	0	0	0	0	2	0	1	1	2	3
ARA	Cyclosa	170	0	0	0	0	1	0	0	0	1	1
ARA	Cyclosa	212	1	0	4	0	1	7	1	6	8	14
ARA	Cyclosa	220	0	1	0	0	1	0	0	0	2	2
ARA	Cyclosa	221	0	2	1	0	0	1	0	1	3	4
ARA	Cyclosa	297	0	0	0	0	0	1	0	0	1	1
ARA	Cyclosa	320	0	0	1	0	0	1	0	1	1	2
ARA	Cyclosa	385	0	0	0	0	0	1	0	0	1	1
ARA	Cyclosa	398	0	0	1	0	0	0	0	0	1	1
ARA	Cyrtophora	63	0	3	0	0	2	2	0	0	7	7
ARA	Cyrtophora	228	1	0	0	0	0	0	0	1	0	1
ARA	Cyrtophora	399	0	0	0	0	0	1	0	0	1	1
ARA	Dubiepeira	65	0	1	2	0	0	2	0	1	4	5
ARA	Dubiepeira	359	0	0	0	0	2	0	0	0	2	2
ARA	Enacrosoma	142	0	0	4	0	0	0	0	3	1	4
ARA	Enacrosoma	255	0	0	1	0	1	0	0	2	0	2
ARA	Enacrosoma	319	0	0	0	0	0	1	0	0	1	1
ARA	Eriophora	73	0	3	1	0	0	6	0	4	6	10
ARA	Eustala	355	0	0	0	0	0	2	0	0	2	2
ARA	Eustala	27	0	0	1	0	0	1	0	2	0	2
ARA	Eustala	28	0	0	1	0	0	0	0	1	0	1
ARA	Eustala	58	0	1	3	0	0	7	0	9	2	11
ARA	Eustala	68	0	1	0	0	0	0	0	0	1	1
ARA	Eustala	105	0	0	1	0	0	2	0	0	3	3
ARA	Eustala	106	0	0	15	0	1	17	3	14	22	36
ARA	Eustala	107	0	0	1	0	0	1	0	1	1	2
ARA	Eustala	140	0	0	1	0	0	0	0	1	0	1
ARA	Eustala	153	0	0	1	0	0	0	0	1	0	1
ARA	Eustala	251	0	0	1	0	0	0	0	0	1	1
ARA	Eustala	254	0	0	1	0	0	0	0	0	1	1
ARA	Eustala	268	1	0	0	0	0	0	0	0	1	1
ARA	Eustala	300	0	0	0	0	0	1	0	0	1	1
ARA	Eustala	312	1	0	4	0	0	0	0	2	3	5
ARA	Eustala	321	0	0	1	0	0	0	0	0	1	1
ARA	Eustala	338	0	0	2	0	0	1	0	3	0	3
ARA	Eustala	366	0	0	0	0	2	0	0	0	2	2
ARA	Eustala	401	0	0	0	0	0	1	0	0	1	1
ARA	Eustala	418	3	0	0	0	0	0	0	0	3	3

*Spiders of Pakitzá. Species Richness and Notes on Community Structure*

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
ARA	Eustala	421	0	0	0	0	1	0	0	1	0	1
ARA	Eustala	422	0	0	0	1	0	0	0	1	0	1
ARA	Eustala	426	0	0	0	0	1	0	0	0	1	1
ARA	Eustala	427	0	0	0	0	1	0	0	0	1	1
ARA	Eustala	431	0	0	1	0	0	0	0	0	1	1
ARA	Eustala	433	0	0	1	0	0	0	0	0	1	1
ARA	Eustala	434	0	0	1	0	0	0	0	1	0	1
ARA	Eustala	442	1	0	0	0	0	1	0	1	1	2
ARA	Eustala	443	0	0	0	0	0	1	0	1	0	1
ARA	Eustala	444	3	0	7	0	0	6	0	1	15	16
ARA	Eustala	461	0	0	1	0	4	0	0	0	5	5
ARA	Eustala	463	0	0	1	0	0	0	0	0	1	1
ARA	Eustala	465	1	0	0	0	0	0	0	0	1	1
ARA	Hypognatha	171	0	0	3	0	0	3	1	3	4	7
ARA	Kaira	479	0	0	0	0	0	1	0	1	0	1
ARA	Mangora	1	3	1	24	0	0	6	4	29	9	38
ARA	Mangora	4	5	2	22	1	1	20	0	23	28	51
ARA	Mangora	187	0	0	0	0	0	1	0	1	0	1
ARA	Mangora	192	0	0	2	0	0	0	0	0	2	2
ARA	Mangora	219	0	4	9	0	0	1	0	4	10	14
ARA	Mecynogea	3	4	3	5	0	0	2	1	5	10	15
ARA	Metazygia	115	0	0	2	0	0	3	0	2	3	5
ARA	Metazygia	330	0	0	3	0	0	1	0	1	3	4
ARA	Micrathena	2	0	0	0	0	0	0	2	2	0	2
ARA	Micrathena	7	2	0	8	0	0	2	0	8	4	12
ARA	Micrathena	55	0	0	4	0	0	3	0	6	1	7
ARA	Micrathena	67	0	1	1	0	0	7	0	8	1	9
ARA	Micrathena	74	1	0	0	0	0	2	0	2	1	3
ARA	Micrathena	78	0	0	3	0	0	3	0	4	2	6
ARA	Micrathena	162	0	1	2	0	1	3	0	5	2	7
ARA	Micrathena	180	0	0	1	0	3	2	0	2	4	6
ARA	Micrathena	186	0	0	1	0	0	0	0	1	0	1
ARA	Micrathena	193	0	0	2	0	0	0	0	0	2	2
ARA	Micrathena	230	0	0	0	0	1	0	0	1	0	1
ARA	Micrathena	246	0	0	0	0	0	1	0	1	0	1
ARA	Micrathena	267	0	0	1	0	0	0	0	0	1	1
ARA	Micrathena	270	0	0	2	0	0	1	0	0	3	3
ARA	Micrathena	286	0	0	0	0	0	1	0	1	0	1
ARA	Micrathena	364	0	0	0	0	1	0	0	0	1	1
ARA	Micrathena	417	0	0	2	0	0	0	0	0	2	2
ARA	Micrathena	484	0	0	1	0	0	0	0	1	0	1
ARA	Ocrepeira	80	0	0	0	0	0	1	0	1	0	1
ARA	Ocrepeira	104	0	0	8	0	0	10	0	10	8	18
ARA	Parawixia	94	5	5	23	0	3	17	0	6	47	53
ARA	Parawixia	110	0	0	3	0	0	2	0	1	4	5
ARA	Parawixia	287	0	0	0	0	1	0	0	0	1	1
ARA	Parawixia	302	1	0	1	0	0	0	0	0	2	2
ARA	Parawixia	389	0	0	0	0	0	1	0	0	1	1
ARA	Parawixia	449	0	0	1	0	0	0	0	0	1	1

D. Silva and J. A. Coddington

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
ARA	Pronous	483	0	0	1	0	0	0	0	1	0	1
ARA	Scoloderus	198	0	0	0	0	1	0	0	0	1	1
ARA	Spilasma	158	0	0	3	0	1	1	0	5	0	5
ARA	Testudinaria?	93	0	0	0	0	0	1	0	0	1	1
ARA	Testudinaria?	341	0	0	5	0	0	0	0	0	5	5
ARA	Testudinaria?	373	0	0	1	0	0	0	0	1	0	1
ARA	Verrucosa	382	0	0	0	0	0	1	0	0	1	1
ARA	Wagneriana	116	0	1	1	0	1	4	1	3	5	8
ARA	Wagneriana	156	0	0	1	0	0	0	0	1	0	1
ARA	Wagneriana	272	0	0	4	0	0	0	0	1	3	4
ARA	Wagneriana	311	0	0	3	0	0	1	0	3	1	4
ARA	Wagneriana	388	0	1	3	0	0	4	0	0	8	8
ARA	Wagneriana	406	0	0	0	0	0	1	0	0	1	1
ARA	Wagneriana	407	0	0	1	0	0	0	0	0	1	1
ARA	Wagneriana	413	0	0	1	0	0	0	0	0	1	1
ARA	Wagneriana	438	0	0	1	0	0	0	0	0	1	1
ARA	Xylethrus	139	0	1	3	0	0	1	0	3	2	5
ARA	Xylethrus	290	4	1	0	0	0	1	0	0	6	6
CAP	Nops?	125	0	0	0	1	0	0	0	1	0	1
CLU	Clubionid AA	259	0	0	1	0	0	0	0	0	1	1
CLU	Clubionid AA	471	0	0	0	0	0	1	0	0	1	1
CLU	Clubionid Z	395	0	0	1	0	0	0	0	0	1	1
COR	Castianeira	278	1	0	0	0	0	0	0	0	1	1
COR	Corinna?	88	0	0	2	0	0	1	0	0	3	3
COR	Corinna?	133	0	0	4	1	0	0	0	2	3	5
COR	Corinnid AB	159	0	0	1	0	0	2	0	2	1	3
COR	Corinnid AB	231	0	0	0	0	0	1	0	0	1	1
COR	Corinnid AC	269	0	0	1	0	0	0	0	0	1	1
COR	Corinnid AD	283	0	0	0	0	0	1	0	1	0	1
COR	Corinnid AE	344	0	0	1	0	0	0	0	1	0	1
COR	Myrmecium	210	1	0	0	0	0	1	0	0	2	2
COR	Myrmecotypus	298	1	0	0	0	0	0	0	0	1	1
COR	Sphecotypus	316	0	0	0	0	0	1	0	0	1	1
COR	Trachelas	235	0	0	1	0	0	0	0	0	1	1
COR	Trachelas	236	0	0	3	0	0	1	1	3	2	5
CTE	Acanthocetus	488	0	0	1	0	0	1	0	2	0	2
CTE	Ancylometes	71	0	0	0	0	0	1	0	1	0	1
CTE	Ctenus	48	0	0	4	0	1	1	0	3	3	6
CTE	Ctenus	49	0	0	5	0	0	4	0	4	5	9
CTE	Ctenus	203	1	0	3	0	0	2	0	3	3	6
CTE	Ctenus	216	1	1	0	0	0	0	0	0	2	2
CTE	Ctenus	288	0	0	0	0	1	0	0	0	1	1
CTE	Ctenus	466	0	0	0	0	0	1	0	1	0	1
CTE	Ctenus?	47	0	0	1	0	0	0	0	1	0	1
CTE	Ctenus?	357	0	0	1	0	0	0	0	0	1	1
CTE	Ctenus?	451	0	0	0	0	0	1	0	0	1	1
CTE	Cupiennius	258	0	0	3	0	1	4	0	0	8	8
CTE	Enoploctenus	138	0	0	1	0	0	2	0	3	0	3
CTE	Isoctenus?	374	0	0	1	0	0	0	0	0	1	1

*Spiders of Pakitzá. Species Richness and Notes on Community Structure*

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
CTE	Phoneutria	148	0	0	1	0	0	0	0	0	1	1
CTE	Phymatocerus?	410	0	0	1	0	0	0	0	0	1	1
DEI	Deinopis	322	1	0	3	0	0	0	0	0	4	4
DEI	Deinopis	356	0	0	0	0	0	3	0	2	1	3
DIC	Dictynid AF	453	0	0	0	0	0	1	0	0	1	1
GNA	Gnaphosid AG	491	0	0	1	0	0	0	0	1	0	1
HIER	Tama	245	0	2	3	0	0	4	0	4	5	9
HER	Tama	339	0	0	3	0	0	2	0	1	4	5
HET	HeteropodidAH	242	0	1	0	0	0	1	0	0	2	2
HET	HeteropodidAI	347	0	0	0	0	0	1	0	0	1	1
HET	HeteropodidAJ	386	0	1	1	0	0	0	0	0	2	2
HET	Olios?	54	0	0	2	0	0	0	0	2	0	2
HET	Olios?	87	0	0	1	0	0	5	0	1	5	6
LIN	Meioneta	37	0	0	3	1	1	1	0	5	1	6
LIN	Meioneta	38	0	0	1	0	1	1	0	2	1	3
LIN	Meioneta	243	0	0	1	0	0	0	0	1	0	1
LIN	Meioneta	369	0	0	0	0	1	0	0	0	1	1
LIN	Meioneta?	472	3	0	5	0	0	0	0	8	0	8
LIN	Novafrontina	370	0	1	0	0	3	2	0	1	5	6
LYC	Lycosa?	17	1	0	9	0	0	1	1	12	0	12
LYC	Lycosid AM	131	0	0	0	1	0	0	0	1	0	1
LYC	Lycosid AM	132	0	0	0	2	0	0	0	2	0	2
LYC	Lycosid AN	457	0	0	0	0	1	0	0	0	1	1
LYC	Porrímosa	247	0	0	2	0	0	0	0	1	1	2
LYC	Schizocosa?	299	0	2	0	0	0	2	0	1	3	4
MIM	Ero	96	0	1	13	0	1	8	0	4	19	23
MIM	Ero	111	1	1	3	0	1	3	0	1	8	9
MIM	Ero	112	0	0	0	1	0	4	0	3	2	5
MIM	Ero	163	0	0	1	0	0	0	0	1	0	1
MIM	Ero	253	3	0	1	0	0	0	0	0	4	4
MIM	Ero	340	1	0	7	0	0	1	0	4	5	9
MIM	Ero	408	0	1	0	0	0	0	0	0	1	1
MIM	Ero	440	0	0	2	0	0	0	0	0	2	2
MIM	Ero	445	0	0	1	0	0	0	0	0	1	1
MIM	Gelanor	411	0	0	1	0	0	0	0	0	1	1
MIM	Mimetus	271	0	0	3	0	0	0	0	1	2	3
MIT	Eutichurus?	50	0	0	2	0	0	1	0	1	2	3
MIT	Miturgid AO	260	0	1	3	0	0	0	0	1	3	4
MIT	Miturgid AO	292	0	0	0	0	0	1	0	0	1	1
MYS	Maymena?	41	0	0	3	0	0	0	0	3	0	3
MYS	Mysmena	42	0	0	1	0	0	0	0	1	0	1
MYS	Mysmena	43	5	0	5	0	0	0	0	10	0	10
MYS	Mysmena	45	0	0	1	0	0	0	0	1	0	1
MYS	Mysmena	420	0	0	1	0	0	0	0	1	0	1
MYS	Mysmenopsis	18	4	0	2	0	0	0	0	6	0	6
MYS	Mysmenopsis	19	1	0	2	0	0	2	0	2	3	5
MYS	Mysmenopsis	249	2	0	4	0	0	0	0	6	0	6
MYS	Mysmenopsis	480	2	0	1	0	0	0	0	3	0	3
OON	Oonopid AP	160	1	0	3	0	0	0	0	1	3	4

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
OON	Oonopid AQ	178	0	0	0	0	0	1	0	0	1	1
OON	Oonopid AQ	185	0	0	1	0	0	0	0	1	0	1
OXY	Oxyopes	256	2	5	5	0	0	4	0	2	14	16
OXY	Oxyopes	362	0	0	0	0	0	1	0	0	1	1
OXY	Oxyopes	492	0	0	5	0	0	0	0	0	5	5
OXY	Oxyopid AR	176	0	0	1	0	0	0	0	1	0	1
OXY	Oxyopid AR	415	0	1	0	0	0	0	0	0	1	1
OXY	Tapinillus	165	0	0	2	0	0	0	0	0	2	2
OXY	Tapinillus	223	0	0	1	0	0	0	0	0	1	1
OXY	Tapinillus	301	0	0	1	0	1	0	0	2	0	2
PHI	Ebo?	161	0	0	0	0	1	0	0	1	0	1
PHO	Metagonia?	90	0	0	4	0	0	4	0	5	3	8
PHO	Metagonia?	378	0	0	1	0	0	0	0	1	0	1
PHO	Micromerys	189	0	0	3	0	0	2	0	2	3	5
PHO	Modisimus?	22	1	0	3	2	0	1	0	7	0	7
PHO	Modisimus?	166	0	1	0	0	7	7	0	12	3	15
PHO	Physocyclus?	21	2	2	11	0	4	13	1	18	15	33
PHO	Physocyclus?	195	0	0	1	0	0	0	0	1	0	1
PHO	Physocyclus?	196	0	0	7	0	0	0	0	6	1	7
PHO	Physocyclus?	285	0	0	0	0	0	2	0	1	1	2
PHO	Physocyclus?	296	0	0	2	0	0	0	0	1	1	2
PHO	Physocyclus?	349	0	0	0	0	0	1	0	0	1	1
PHO	Physocyclus?	470	1	0	0	0	0	1	0	2	0	2
PIS	Architis	95	1	2	7	0	5	3	0	0	18	18
PIS	Dossenus	109	1	0	1	0	0	2	0	0	4	4
PIS	Thaumasia	130	0	0	2	2	0	1	0	4	1	5
SAL	Lyssomanes	119	6	2	11	0	1	2	0	0	22	22
SAL	Lyssomanes	199	3	6	18	0	1	6	0	0	34	34
SAL	Lyssomanes	313	0	0	0	0	0	6	0	0	6	6
SAL	Lyssomanes	400	0	0	0	0	0	1	0	0	1	1
SAL	Lyssomanes	441	0	0	1	0	0	0	0	0	1	1
SAL	Peckhamia	194	0	0	2	0	0	0	1	1	2	3
SAL	Salticid BL	16	1	0	0	0	0	0	0	1	0	1
SAL	Salticid BL	425	0	0	1	0	0	0	0	0	1	1
SAL	Salticid BM	20	0	2	1	0	0	0	0	1	2	3
SAL	Salticid BM	81	0	0	0	0	0	1	0	1	0	1
SAL	Salticid BM	303	0	0	1	0	0	0	0	0	1	1
SAL	Salticid BN	23	2	0	2	0	3	9	5	10	11	21
SAL	Salticid BO	82	0	0	2	0	0	1	0	3	0	3
SAL	Salticid BP	91	0	0	2	0	0	0	0	0	2	2
SAL	Salticid BQ	101	1	0	3	0	2	3	0	1	8	9
SAL	Salticid BQ	102	0	0	0	0	0	1	0	0	1	1
SAL	Salticid BR	126	0	1	1	0	0	1	0	0	3	3
SAL	Salticid BR	350	0	0	0	0	0	1	0	0	1	1
SAL	Salticid BS	134	0	0	0	1	0	1	0	1	1	2
SAL	Salticid BT	135	0	0	1	0	0	0	0	0	1	1
SAL	Salticid BT	208	1	0	1	1	1	3	0	3	4	7
SAL	Salticid BT	289	1	0	1	0	1	0	0	1	2	3
SAL	Salticid BU	147	0	0	1	0	0	0	0	1	0	1

*Spiders of Pakitzá. Species Richness and Notes on Community Structure*

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	<b>TOTAL</b>
SAL	Salticid BU	167	0	0	0	0	2	0	0	1	1	2
SAL	Salticid BU	190	0	0	0	0	0	2	1	2	1	3
SAL	Salticid BV	168	0	0	0	0	1	0	0	1	0	1
SAL	Salticid BW	177	0	0	2	0	0	4	0	2	4	6
SAL	Salticid BW	205	0	0	1	0	0	0	1	1	1	2
SAL	Salticid BW	211	0	0	1	0	0	1	0	0	2	2
SAL	Salticid BX	206	0	0	3	0	0	0	0	0	3	3
SAL	Salticid BX	207	0	0	1	0	0	0	0	0	1	1
SAL	Salticid BX	213	0	1	0	0	0	0	0	0	1	1
SAL	Salticid BY	224	1	0	0	0	0	0	0	1	0	1
SAL	Salticid BZ	280	1	0	0	0	0	0	0	0	1	1
SAL	Salticid CA	351	0	0	0	0	0	1	0	0	1	1
SAL	Salticid CB	363	0	1	0	0	1	0	0	0	2	2
SAL	Salticid CC	368	0	0	0	0	1	0	0	0	1	1
SAL	Salticid CD	458	0	0	0	0	1	0	0	0	1	1
SAL	Salticid CE	459	1	0	0	0	1	0	0	1	1	2
SAL	Salticid CF	496	0	1	0	0	0	0	0	0	1	1
SAL	Synemosina	279	1	0	0	0	0	0	0	0	1	1
SCY	Scytodes	69	0	0	8	0	0	1	0	5	4	9
SCY	Scytodes	348	1	1	2	1	0	5	0	3	7	10
SEL	Selenops	294	0	0	2	0	0	0	0	0	2	2
SEN	Senoculus	108	0	1	3	0	0	3	0	2	5	7
SEN	Senoculus	151	0	0	5	0	0	1	0	2	4	6
SEN	Senoculus	334	1	0	0	0	0	0	0	0	1	1
SEN	Senoculus	436	0	0	4	0	0	0	0	0	4	4
TET	Dolichognatha	31	1	0	4	0	1	6	1	7	6	13
TET	Azilia	217	2	1	0	0	0	0	0	2	1	3
TET	Azilia	237	0	0	4	0	1	3	0	7	1	8
TET	Azilia	361	0	0	0	0	0	1	0	0	1	1
TET	Azilia?	66	0	2	0	0	0	0	0	0	2	2
TET	Chrysometa	30	2	0	3	0	0	0	0	2	3	5
TET	Chrysometa	70	0	1	0	0	0	0	0	0	1	1
TET	Chrysometa	261	0	1	2	0	0	1	0	0	4	4
TET	Chrysometa	308	0	0	2	0	0	0	0	2	0	2
TET	Chrysometa	403	0	0	0	0	0	1	0	0	1	1
TET	Chrysometa	430	0	0	1	0	0	0	1	1	1	2
TET	Dolichognatha	85	1	1	4	0	0	4	1	7	4	11
TET	Dolichognatha	345	0	0	2	0	0	1	0	1	2	3
TET	Dolichognatha	346	0	1	1	0	1	1	0	1	3	4
TET	Dolichognatha	352	1	0	0	0	1	1	0	0	3	3
TET	Glenognatha	129	0	0	1	2	0	0	0	3	0	3
TET	Homalometra?	324	0	0	0	0	0	2	0	1	1	2
TET	Leucauge	84	0	0	3	0	0	1	0	3	1	4
TET	Leucauge	127	0	0	0	3	5	1	0	9	0	9
TET	Leucauge	191	0	0	9	0	1	3	3	12	4	16
TET	Leucauge	326	0	0	1	0	0	1	1	3	0	3
TET	Leucauge	353	0	0	0	0	0	1	0	0	1	1
TET	Leucauge	365	0	0	0	0	2	0	0	0	2	2
TET	Leucauge	383	0	0	0	0	0	2	0	0	2	2

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
TET	Leucauge	394	0	0	1	0	0	0	0	0	1	1
TET	Leucauge	404	0	0	0	0	0	1	0	0	1	1
TET	Leucauge	423	0	0	1	0	0	2	0	3	0	3
TET	Leucauge	454	0	0	1	0	1	0	0	1	1	2
TET	Leucauge	455	0	0	0	0	1	0	0	0	1	1
TET	Leucauge	456	0	0	0	0	1	0	0	0	1	1
TET	Mecynometa	183	0	0	3	0	0	0	1	4	0	4
TET	Nephila	72	0	0	0	0	2	2	0	3	1	4
TET	Prionolaema?	181	0	0	3	2	0	0	0	5	0	5
TET	Tetragnatha	128	0	0	1	2	1	0	0	4	0	4
TET	Tetragnatha	473	0	0	0	0	0	1	0	1	0	1
THD	Achaearanea	8	3	0	1	0	1	2	1	8	0	8
THD	Achaearanea	62	0	0	1	0	0	0	0	1	0	1
THD	Achaearanea	146	3	1	7	0	0	6	1	12	6	18
THD	Achaearanea	175	0	0	6	0	0	6	0	7	5	12
THD	Achaearanea	182	0	1	3	0	0	1	0	2	3	5
THD	Achaearanea	337	0	0	3	0	0	1	0	4	0	4
THD	Achaearanea	342	0	0	1	0	0	0	0	0	1	1
THD	Achaearanea	493	0	0	1	0	0	0	0	0	1	1
THD	Achaearanea?	123	1	0	2	0	0	1	0	1	3	4
THD	Achaearanea?	155	0	1	3	0	0	3	0	1	6	7
THD	Achaearanea?	197	0	0	1	0	0	3	0	1	3	4
THD	Achaearanea?	201	0	0	1	0	0	0	0	1	0	1
THD	Achaearanea?	309	0	0	1	0	0	0	0	1	0	1
THD	Achaearanea?	310	0	0	2	0	0	1	0	2	1	3
THD	Achaearanea?	435	0	0	0	0	0	1	0	0	1	1
THD	Anelosimus	143	0	2	2	0	6	30	0	10	30	40
THD	Anelosimus	164	0	0	5	0	2	0	0	7	0	7
THD	Argyrodes	9	1	1	34	0	7	25	3	63	8	71
THD	Argyrodes	32	0	0	1	0	0	0	0	1	0	1
THD	Argyrodes	53	0	0	1	0	0	0	0	1	0	1
THD	Argyrodes	75	1	2	24	0	2	15	0	17	27	44
THD	Argyrodes	97	0	0	0	0	0	1	0	0	1	1
THD	Argyrodes	118	0	0	0	0	0	1	0	0	1	1
THD	Argyrodes	144	0	0	8	0	3	1	1	6	7	13
THD	Argyrodes	169	0	0	1	0	1	0	0	2	0	2
THD	Argyrodes	184	0	0	0	0	2	0	0	2	0	2
THD	Argyrodes	204	1	0	2	0	0	1	0	4	0	4
THD	Argyrodes	226	1	0	0	0	1	1	0	3	0	3
THD	Argyrodes	234	0	0	0	0	1	0	0	1	0	1
THD	Argyrodes	241	0	3	21	0	2	6	0	10	22	32
THD	Argyrodes	250	0	0	1	0	0	0	0	1	0	1
THD	Argyrodes	252	1	0	14	0	0	6	0	6	15	21
THD	Argyrodes	263	0	0	1	0	0	0	0	0	1	1
THD	Argyrodes	273	0	0	1	0	0	0	0	0	1	1
THD	Argyrodes	318	0	0	0	0	0	2	0	0	2	2
THD	Argyrodes	343	0	0	1	0	1	1	0	0	3	3
THD	Argyrodes	372	2	0	4	0	0	0	0	6	0	6
THD	Argyrodes	377	0	0	0	0	0	1	0	0	1	1

*Spiders of Pakitzá. Species Richness and Notes on Community Structure*

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
THD	Argyrodes	391	1	0	1	0	0	0	0	1	1	2
THD	Argyrodes	424	0	0	1	0	0	0	0	0	1	1
THD	Argyrodes	469	0	0	0	0	0	7	0	0	7	7
THD	Chrosiothes	124	0	0	2	0	0	2	0	3	1	4
THD	Chrosiothes	248	0	1	0	0	0	0	0	0	1	1
THD	Chrosiothes	266	1	0	0	0	0	1	0	0	2	2
THD	Dipoena	11	0	0	11	0	0	3	0	8	6	14
THD	Dipoena	83	0	0	2	0	0	0	0	2	0	2
THD	Dipoena	145	0	0	6	0	0	3	0	2	7	9
THD	Dipoena	174	0	0	2	0	0	0	0	1	1	2
THD	Dipoena	264	0	0	8	0	0	2	0	1	9	10
THD	Dipoena	336	1	0	0	0	0	0	0	0	1	1
THD	Dipoena	354	0	0	0	0	0	1	0	0	1	1
THD	Dipoena	360	0	0	0	0	0	1	0	0	1	1
THD	Dipoena	379	0	0	1	0	0	0	0	0	1	1
THD	Dipoena	380	0	0	0	0	1	1	0	0	2	2
THD	Dipoena	381	0	0	0	0	0	1	0	0	1	1
THD	Dipoena	450	0	0	1	0	0	2	0	2	1	3
THD	Dipoena	462	0	0	1	0	0	0	0	0	1	1
THD	Dipoena	490	0	0	1	0	0	0	0	1	0	1
THD	Echinotheridion	315	0	0	2	0	0	1	0	2	1	3
THD	Episinus	56	0	4	39	2	0	61	0	66	40	106
THD	Episinus	57	0	0	15	0	0	1	0	14	2	16
THD	Episinus	150	1	0	6	0	0	5	0	6	6	12
THD	Episinus	240	0	0	2	0	0	4	0	4	2	6
THD	Episinus	489	0	0	1	0	0	1	0	2	0	2
THD	Helvibis	10	1	0	4	0	0	1	2	6	2	8
THD	Helvibis	103	1	1	9	1	0	12	2	11	15	26
THD	Helvibis	376	0	0	1	1	2	7	0	3	8	11
THD	Phoroncidia	274	0	0	2	0	0	0	0	1	1	2
THD	Phoroncidia	486	0	0	1	0	0	0	0	1	0	1
THD	Spintharus	51	0	0	10	0	0	6	0	10	6	16
THD	Synotaxus	52	0	1	11	0	0	9	0	18	3	21
THD	Theridiid AS	40	0	0	5	0	0	0	0	5	0	5
THD	Theridiid AT	157	1	0	2	0	1	1	0	2	3	5
THD	Theridiid AU	173	0	0	1	0	0	0	0	1	0	1
THD	Theridiid AV	218	1	0	1	0	0	0	0	0	2	2
THD	Theridiid AW	222	0	2	1	0	1	0	0	2	2	4
THD	Theridiid AX	262	0	0	1	0	0	0	0	0	1	1
THD	Theridiid AY	291	0	1	0	0	0	0	0	0	1	1
THD	Theridiid AZ	317	0	0	0	0	0	3	0	1	2	3
THD	Theridiid BA	332	0	0	1	0	0	0	0	1	0	1
THD	Theridiid BB	333	1	0	0	0	0	0	0	0	1	1
THD	Theridiid BC	384	0	0	0	0	0	1	0	0	1	1
THD	Theridiid BD	387	0	0	1	0	0	0	0	1	0	1
THD	Theridiid BE	460	0	0	1	0	1	0	0	1	1	2
THD	Theridiid BF	468	0	0	0	0	0	1	0	0	1	1
THD	Theridiid BG	497	1	0	0	0	0	0	0	1	0	1
THD	Thwaitesia	76	6	1	40	0	2	17	0	23	43	66

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
THD	Thwaiteisia	304	0	0	5	0	0	0	0	5	0	5
THD	Thymoites	61	0	0	5	2	0	0	0	6	1	7
THD	Tidarren	232	0	0	4	0	3	6	0	5	8	13
THO	Epicadus	396	0	0	1	0	0	1	0	0	2	2
THO	Epicadus?	293	0	1	0	0	0	0	0	0	1	1
THO	Onocolus	239	0	0	1	0	0	0	0	0	1	1
THO	Synaema?	419	0	0	3	0	0	1	1	4	1	5
THO	Thomisid BH	188	0	0	0	0	0	1	0	1	0	1
THO	Thomisid BI	329	0	0	1	0	0	0	1	2	0	2
THO	Thomisid BJ	452	0	0	0	0	0	1	0	0	1	1
THO	Tmarus	405	0	0	0	0	0	1	0	0	1	1
THO	Tmarus	428	0	0	1	0	0	0	0	0	1	1
THO	Tmarus	432	0	0	1	0	0	0	1	1	1	2
THO	Tmarus	474	0	0	0	0	0	1	0	1	0	1
THO	Tmarus	495	1	0	2	0	0	0	1	3	1	4
THS	Baalzebub	39	0	0	1	0	0	0	0	1	0	1
THS	Baalzebub	44	0	0	4	0	0	0	0	4	0	4
THS	Chthonos	98	0	0	0	0	0	1	0	0	1	1
THS	Chthonos	99	0	0	0	0	0	2	0	1	1	2
THS	Epeirotypus	12	20	0	20	0	0	0	10	49	1	50
THS	Naatlo	77	2	0	3	0	0	3	0	6	2	8
THS	Naatlo	485	0	0	5	0	0	0	0	5	0	5
THS	Ogulnius	13	1	0	0	0	0	0	0	1	0	1
THS	Ogulnius	46	1	0	2	0	0	0	0	3	0	3
THS	Ogulnius	281	3	0	6	0	0	0	0	7	2	9
THS	Plato	482	0	0	0	0	0	0	1	1	0	1
THS	Theridiosoma	34	2	0	29	0	0	0	0	31	0	31
THS	Theridiosoma	35	0	0	10	0	0	0	0	10	0	10
THS	Theridiosoma	36	0	0	1	0	0	0	0	1	0	1
THS	Theridiosoma	136	0	0	1	1	0	0	0	2	0	2
THS	Theridiosoma	137	0	0	4	1	0	0	0	5	0	5
THS	Theridiosoma	305	0	0	1	0	0	0	0	1	0	1
THS	Theridiosoma	416	0	0	0	0	1	0	0	1	0	1
THS	Theridiosoma	476	0	0	0	0	0	1	0	1	0	1
TRE	Hesydrus	89	0	0	0	0	0	3	0	2	1	3
TRE	Hesydrus	200	0	0	0	0	0	2	0	0	2	2
TRE	Rhoiciniae A	429	0	0	1	0	0	0	0	0	1	1
TRE	Syntrechalea?	446	0	0	1	0	0	0	0	0	1	1
ULO	Miagrammopes	59	0	1	8	0	0	6	0	7	8	15
ULO	Miagrammopes	117	1	0	0	0	0	0	0	0	1	1
ULO	Miagrammopes	202	0	0	1	1	0	1	0	1	2	3
ULO	Miagrammopes	214	3	2	5	0	0	4	0	1	13	14
ULO	Miagrammopes	244	0	0	3	0	0	0	0	2	1	3
ULO	Miagrammopes	414	0	0	3	0	0	1	0	1	3	4
ULO	Philoponella	14	10	5	14	0	1	10	1	25	16	41
ULO	Philoponella	225	0	0	0	0	1	0	0	0	1	1
ULO	Philoponella	328	0	2	0	0	4	0	0	0	6	6
ULO	Uloborus	120	0	1	1	0	0	0	0	1	1	2
ULO	Uloborid BK	229	1	0	0	0	0	0	0	1	0	1

*Spiders of Pakitzá. Species Richness and Notes on Community Structure*

FAM	GENUS	SP	DAT	LFF	OAT	RVF	TGH	UFF	USF	Early	Late	TOTAL
ULO	Uloborus	15	2	1	30	0	1	16	0	22	28	50
ULO	Uloborus	60	1	0	3	0	1	2	0	2	5	7
ULO	Uloborus	121	0	0	1	1	1	1	0	2	2	4
ULO	Uloborus	215	3	0	1	0	0	0	0	0	4	4
ULO	Uloborus	238	0	0	1	0	0	0	0	0	1	1
ULO	Uloborus	257	0	1	0	0	0	0	0	0	1	1
ULO	Uloborus	284	0	0	0	0	0	2	0	2	0	2
ULO	Uloborus	307	0	0	4	0	0	4	0	2	6	8
ULO	Uloborus	327	0	0	0	0	0	2	0	2	0	2
ULO	Uloborus	367	0	1	1	0	2	5	0	4	5	9
ULO	Uloborus	390	1	0	0	0	0	0	0	0	1	1
ULO	Uloborus	447	0	0	1	0	0	0	0	0	1	1
ULO	Zosis	172	0	1	1	0	1	1	0	2	2	4

# MANU

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Edited by

Don E. Wilson  
Abelardo Sandoval



NATIONAL MUSEUM of  
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