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SEASONAL ABUNDANCE AND DIVERSITY OF WEB-BUILDING SPIDERS IN RELATION TO HABITAT STRUCTURE ON BARRO COLORADO ISLAND, PANAMA

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ABSTRACT

Web-building spiders were censused by a visual censusing method in tropical forest understory on Barro Colorado Island (BCI), Panama Canal Zone. An overall trend of low numbers of spiders in the late dry season and early wet season (March to May) was seen on all transects. The majority of the species on the transects had wet season distribution patterns. Some species which occurred year-round on the forest transects had wet season distributions on a clearing-edge transect. A shortage of flying insect prey or dessication may have been responsible for the observed distributions.

Species diversity and diversity of web types followed the overall seasonal pattern of spider abundance. The diversities of species and of web types were greatest on the forest transect with the highest diversity of structural supports for spider webs. Web density, however, was greatest on the transect at the edge of a small clearing.

Faunal composition, diversity of web types, and seasonal patterns of distribution of spiders on the BCI transects differed markedly from similar measures derived from censuses taken in a tropical montane habitat in New Guinea. The differences were attributed in part to differences in the habitats and in the evenness of the climate.

INTRODUCTION

Web-building spiders are conspicuous, abundant, and diverse in some tropical forest and forest-edge habitats. The spiders range in size from less than 1 mg to 2 g, construct a wide variety of web types, and may be found in microenvironments ranging from the surface of the leaf litter to forest canopy. They all have in common an insectivorous diet, and, specifically, specializations for capturing airborne insects. The ecology of this group of predators in the humid tropics is poorly known. I report here the results of a year's census of web-building spiders on Barro Colorado Island (BCI) in Panama and illustrate some of the seasonal changes in abundance and diversity of these spiders in the understory of a wet, lowland tropical forest.

The occurrence of measurable seasonal variations in population parameters of plants and animals in tropical forests is now well documented. Fruiting, flowering, and leafing of trees show one to two peaks per year on BCI, though this may vary from species to species (Foster 1973, Smythe 1974b). Peaks of insect abundance can be roughly correlated with certain flowering, fruiting, or leaf-flush peaks (Wolda in press, Fogden 1972, Smythe 1974b, Buskirk and Buskirk 1976). In at least one instance, a cocoa forest in Ghana, population peaks of primary consumer canopy insects were directly correlated with seasonality of host trees (Gibbs and Leston 1970). There is reason to expect that specialized predators, such as web-building spiders, will also show distinct seasonal fluctuations.

Robinson *et al.* (1974) showed that the abundance of web-building spiders in forest-edge and secondary-growth habitats in New Guinea did indeed vary seasonally, though the patterns of variation were different in different species. This study parallels the New Guinea census and affords a direct comparison of spider phenology and diversity in two widely separated tropical localities. Differences between patterns of abundance observed in the two localities give insight into some of the factors that may influence seasonality in the tropics..

METHODS

Visual Censusing of Web-Building Spiders—The visual censusing technique used by Robinson *et al.* (1974) was adopted in this study. The investigator walked along the edge of a line-transect and noted each web spider within the transect. Four transect lines were established, though not all were monitored throughout the entire year. The transects were 1 m wide and 2 m high, extending up from the surface of the leaf litter. Transect 1 was 50 m long, transects 2 to 4 were 100 m long; these were subdivided into units of 10 m for convenience of censusing. The censusing required about 1-2 hours per transect.

Transect 1 was censused four times each month from October 1972 to January 1973, twice in February, April, and May, and once each in March and June to September, 1973. Transect 2 was censused on the same schedule as transect 1 except in April (one census only) and in June (no census). Transect 3 was censused as above until May 1973, with only one census each in April and May. Transect 4 was censused from February to June 1973 with two censuses each in April and May and one each in February, March, and June.

Robinson *et al.* (1974) discussed the advantages and disadvantages of visual censusing for spiders. The method was used by Kajak (1967) to sample spiders in grassland, by Enders (1973) in censuses of the orb-web spider, *Argiope aurantia* Lucas, and by Elton (1973, 1975) to census cryptic insects resting on leaves and twigs in tropical wet forest. Visual censusing is an effective technique when applied to animals with conspicuous artifacts, such as most web spiders. A "search image" is rapidly acquired for webs and for silk in general, as well as for specific shapes of spiders, for retreats of spiders (e.g., curled leaves or pockets of silk on twigs), and for concealing devices of spiders (e.g., stabilimenta in webs). The advantage of visual censusing is that the spiders in the study area remain undisturbed and can be censused repeatedly. As in the New Guinea study, the same observer conducted all the censuses, thus avoiding the problem of varying individual biases.

There are a number of difficulties with the visual censusing method as applied to web spiders. Not all spiders present have intact webs during the census period. Daytime counts select for diurnal species. Some species have fragile and easily broken webs which are less likely to be seen, especially after rainfall or on windy days. Very small spiders and spiders with reduced webs (e.g., single-line webs) are less conspicuous. The same is true for spiders with small webs inside the leaf litter. Since spiders that build webs inside leaf litter prey for the most part on walking rather than flying insects, they were ignored for the purpose of the census. Low light intensities in the forest understory may reduce visibility considerably. This problem was not encountered on the second-growth transects in New Guinea, but arose on BCI particularly in the rainy season. I did not census on days of heavy rainfall; nonetheless, censusing on overcast days involved much greater searching effort than on clear days.

I evaluate the accuracy of the census figures for the various types of web-building spiders as follows: medium to large web builders (20-2000 mg), small orb-web spiders (5-20 mg), immatures of Uloboridae, *Cyclosa*, *Leucauge*, *Micrathena*, *Nephila*, and *Landana* (less than 5 mg), and the sheetweb building Linyphiidae were all censused accurately. Estimates of other immature orb weavers, all nocturnal species, and small and very small non-orb-web species (excluding linyphiids) are low.

Specimens of most species of web spiders were collected from areas outside the transect lines. Species identification was not possible in all instances. In censusing, I lumped together some species whose webs were difficult to distinguish one from another. Little information is available on the biology of tropical spiders. While censusing, I recorded details of web location, orientation, and structure, the attitude of the spider on or near its web, and its period of activity. Body weights (wet weight) were also obtained for some species. The actual census data are deposited in the library of the Smithsonian Tropical Research Institute.

The Transects—The line-transects are characterized by their location on the island, by the nature of the forest, and by the presence of "edge effects" (Fig. 1). Transect 1 skirted the edge of a small, grassy clearing in the center of the island, isolated from any other large clearings. The vegetation along the edge was dense and there was an abrupt transition from the clearing to the forest. Transects 2 and 3 were along the edge of narrow forest paths (not exceeding 2 m in width). Transect 2 was on flat terrain in 75-year-old forest near the center of the island. There were some understory shrubs and a herbaceous ground cover was generally present. Transect 3 was in old forest skirting the edge of a steep ravine (Lutz watershed). Ground cover and understory shrubs were sparse. Transect 4 was inside the forest, 20 m in from and parallel to transect 2. Understory shrubs and ground cover were present, but less than on transect 2.

In terms of the availability of web supports for spiders (i.e. the density of the vegetation) the transects may be ranked subjectively $1>2>3\geqslant4$, in order of decreasing desirability. Taking into account the variety of types of web supports (i.e., trees shrubs, lianas, herbs), I rank the transects $2\geqslant1>4>3$. These rankings are based on a simple vegetation analysis of the transects conducted in February 1973 (Table 1). For this analysis, I selected a 1 m^2 plot at the beginning of each 10-m section of transect and counted the number of stems or trunks in three size categories: (1) plants less than 50 cm high, (2) 50 to 200 cm, and (3) greater than 200 cm. The number of leaves touching a vertical, weighted thread hung 200 cm above the ground provided a "leaf index" (a mean of three measurements per plot). Low herbaceous plants were most abundant on transect 1, and least so on transect 4. Shrubs less than 2 m high were most abundant on transects 1 and 2, and trees above 2 m were least abundant on transect 3. The leaf index was highest on transect 1 and lowest on transects 3 and 4.

There were conspicuous differences in vegetation between the clearing-edge transect 1 and the forest transects 2, 3 and 4. Transect 2 was separated from the transect 1 clearing by only 200 m of well-travelled path. As a result, transect 2 was most likely to receive invading "clearing species" and may have also provided enough of an edge habitat to maintain them. Transect 4 was probably most typical of "old forest" on flat terrain, if it is possible to speak of typical vegetation in a forest that is a mosaic of many vegetation types (Bennet 1963, Knight 1975). Transect 3 differed from transect 2 in that it was not near a clearing (separated from the laboratory clearing by at least 600 m of forest), and differed from both 2 and 4 in that it was on highly dissected and steep terrain, providing little foothold for low vegetation.

The four transects differed in their degree of exposure: the clearing-edge transect was most exposed to direct sunlight and rainfall. Changes in the appearance of understory vegetation between dry and rainy seasons were most striking on this transect.

Weather—Temperature and rainfall data for the census period are from Smythe (1974a).

Temperature. During 1973, average yearly temperatures near the forest floor on BCI were (°C): maximum 28.0 (26.1-29.4), minimum 22.1 (20.9-23.2). The difference between monthly maximum and minimum air temperatures near the forest floor did not

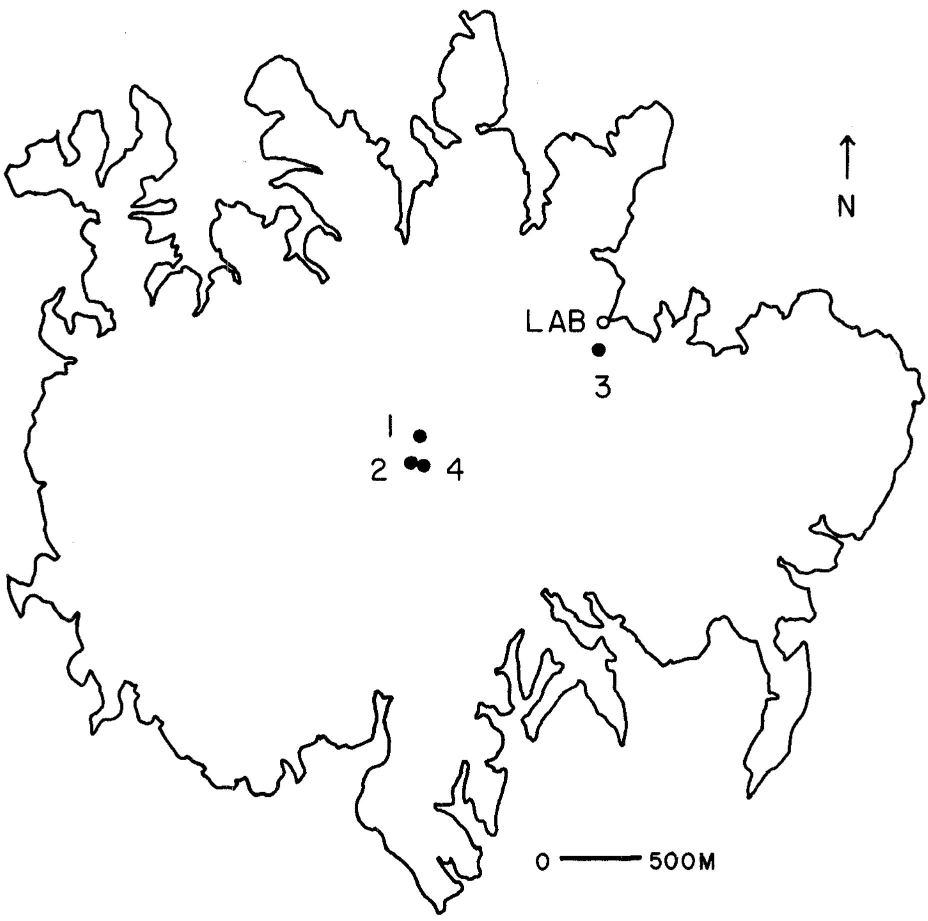

Fig. 1.—Map of Barro Colorado Island, showing the locations of the four transects.

Table 1.–Vegetation analysis of transects 1-4 on BCI, February 1973: average numbers of stems of given height per 1 m^2 and average leaf index (see text) per 1 m^2 ± 1 standard deviation.

	Transects			
	No. 1	No. 2	No. 3	No. 4
Stems < 50 cm	50.6 ± 10.7	30.1 ± 16.8	14.0 ± 5.9	10.1 ± 6.8
Stems 50-200 cm	4.2 ± 3.2	5.0 ± 3.7	0.9 ± 1.2	4.1 ± 4.9
Stems > 200 cm	1.8 ± 0.7	3.7 ± 4.2	0.6 ± 0.8	1.5 ± 1.1
Leaf Index	2.1 ± 1.5	1.0 ± 0.5	0.5 ± 0.7	0.4 ± 0.3

exceed 8°C. Air temperatures in the laboratory clearing were slightly higher than in the forest: maximum 31.4 (30.1-33.8), minimum 22.6 (21.8-23.2).

Rainfall. Two distinct seasons are distinguished based on long-term rainfall data: (1) a dry season (December to April), and (2) a rainy season (May to November). Rainfall data for the census period 1972-1973 (Table 2) show a relatively wet December, so that for the census year, the dry season is considered to be January to April. The 1973 dry season was somewhat drier than average. There was a threefold or more difference in the amount of rainfall between wet and dry seasons.

Light. Sunlight may be important for web-building spiders by influencing movements of flying insects. Observations suggest that there are more insects flying in light gaps, in patches of sunlight, and in sunflecks than in shadier areas inside the forest (Lubin, unpublished data). Data on the intensity of sunlight striking the forest understory were not available for BCI.

Table 2.–Average monthly rainfall (in mm) on BCI, Panama Canal Zone, during the census period, October 1972 to September 1973 (Dry season: January 1973-April 1973).

	Rainfall
October 1972	363.2
November	157.5
December	188.0
January 1973	53.3
February	7.6
March	5.1
April	25.4
May	299.7
June	353.1
July	241.3
August	170.2
September	304.8
Total	2,169.2

NATURAL HISTORY

Araneidae–Most spiders of this family construct orb webs. Araneids with reduced webs or no webs (e.g., *Mastophora*) were not encountered on the transects. Descriptions of the ecology and webs of some tropical orb weavers (e.g., *Cyclosa, Micrathena, Argiope*) can be found in Peters (1953, 1955).

Micrathena species: Spiders of this genus have hard and often spiny abdomens. They are diurnal and sit at the hub during the day. Males are generally very much smaller than females and were found on webs of their own or near webs of females. As it was difficult to identify the males to species, they were lumped in the census. Species found on BCI are described in Chickering (1961). The mating behavior of *Micrathena* is described by Robinson and Robinson (in press) and aspects of the predatory behavior by Lubin (in prep.).

Micrathena schreibersi (Perty) (female 160 mg, male approx. 10 mg) builds a small, usually vertical, orb web near the ground in forest or forest-edge habitats. Females are aposematically colored red, white, and black. They are easily disturbed by substrate vibrations, reacting by jumping off the web onto the ground or hiding under a leaf.

Micrathena duodecimspinosa (O.P.–Cambridge) (female 20 mg, male approx. 10 mg) constructs a small, vertical, orb web with long frame threads which enable the spider to suspend its web across paths or in gaps between trees. Females may be yellow or white; the yellow color phase is predominant on BCI.

Micrathena horrida (Taczanowski) (female 55 mg) has a small, horizontal or angled web and is most often found in tree buttresses. The brown spider sits at the hub in a cryptic position with all legs folded in toward the body, resembling a piece of leaf or twig.

Micrathena clypeata (Walckenaer) females are flattened dorsoventrally and resemble a bit of dried leaf. One individual was found on transect 1.

Pronous tuberculifer Keyserling (female approx. 10 mg) is a bright red spider which builds a tiny, vertical, orb web at ground level. The web requires very few supporting structures and may catch walking insects as well as insects flying near the ground.

Nephila clavipes L. (female 900 mg), the largest orb weaver on BCI, has been studied in some detail by Robinson and Mirick (1971). The orb web of this species is large (up to 1 m in length) and made of strong, yellowish silk. There is an irregular tangle of threads, the barrier web, on one or both sides of the orb web. Adult *N. clavipes* are often clumped in favorable locations. Kleptoparasites and inquilines are common in webs of adults and subadults. These include the theridiids, *Argyrodes* spp., which have no webs of their own, and *Uloborus* spp. which spin their orb webs within the confines of the barrier web and frame threads of the *Nephila* web (Struhsaker 1969). Adult male *N. clavipes* live as parasites in webs of subadult and adult females. Three categories of *N. clavipes* were distinguished in the census: males, subadult and adult females, and immatures less than 11 mm long.

Leucauge sp. 1 (female, male 39 mg) is a brightly colored orb weaver which builds a horizontal or angled web in forest clearings or in open spaces in forest understory. In these habitats webs were rarely more than 1 m above ground. There is often an irregular barrier web below the orb, with bits of flocculent silk at the points of attachment of the barrier web and the frame threads, making the whole web quite conspicuous. Another slightly smaller species, *Leucauge* sp. 2, was seen once on transect 2.

Cyclosa caroli (Hentz) (female, male 6 mg) constructs a fine-meshed, vertical orb web in shady areas and areas of dense undergrowth. A line of prey remains embedded in silk, the stabilimentum, bisects the orb vertically. The line does not extend across the hub and the elongated spider fits exactly in the gap between the two arms of the stabilimentum. The spider is the same color as the debris, and is virtually indistinguishable from it. The egg sacs are also concealed in the stabilimentum. The stabilimentum of immature *Cyclosa* may have an incomplete spiral or disc at the hub in addition to or instead of the vertical line.

Landana sp. (female 2 mg) is a forest species like *Cyclosa*. Its web is horizontal or angled, with bits of leaves and dirt suspended on a separate thread slightly below the plane of the web. The spider rests at the hub, at one end of the string of debris. Unlike *Cyclosa*, prey remains are not suspended in the stabilimentum.

Mangora pia (Chamberlin and Ivie) (female 20 mg) constructs a very small-meshed, vertical or angled web in forest or at forest-edge. Though primarily diurnal, intact webs were also seen at night.

Eustala spp. (female 23.5 mg). Two or three species of *Eustala* were lumped in the census. All are primarily nocturnal and construct asymmetrical webs with a retreat on a twig or on a tree trunk. The spider sits in the retreat during the day. Although webs are often intact during the day, the spider does not often respond to prey in the web. Individuals are flat dorsoventrally, cyptically colored, and difficult to see at the retreat.

Metazygia sp. (female 20 mg) is another nocturnal species whose web is sometimes left up during the day. The retreat of *Metazygia* is a silken tube on a twig and is quite conspicuous even when the web is absent. Both *Eustala* and *Metazygia* sit on the hub at night.

Eriophora nephiloides (O.P.–Cambridge) (female 400 mg) is a large and at least partly diurnal spider that sits in a curled leaf retreat during the day and on the hub at night. The large, wide-meshed webs are strong and can hold large insects (e.g., large scarab beetles and sphyngid moths). The spider attacks most prey by wrapping, and is capable of throwing silk onto large prey from a distance.

Edricus crassicaudus (Keyserling) (female approx. 30 mg) was found only on transect 2. Webs are vertical and low in the vegetation. A white, flocculent, linear stabilimentum is sometimes present below the hub. The spider is diurnal and sits at the hub facing head down. Two color phases were seen: shiny black and deep red. The spider has a large and striking anal tubercule. When disturbed, it runs off the web and sits on a leaf, folding its legs toward the body so that it resembles wet fecal material.

Araneus (*Alpaida*) *tuonabo* (Chamberlin and Ivie) (female 10 mg) builds a small vertical or angled, diurnal, orb web with long support threads. Webs are built across paths and small openings in the forest.

Araneus sp. (close to *sinuoscapus*) (female 90 mg) is mainly a forest-clearing species. It was found on one occasion each on transects 1 and 3. The spider sits in a rolled-up leaf retreat during the day and on the web at night.

Spilasma sp. This unusual araneid builds a conical silken retreat at the center of a tent-shaped, small-meshed web. The webs of two South American species were described by Simon (1896) and Quintero (1974). The retreat is covered with bits of dirt and lichen and has a hinged flap which the spider pulls in when disturbed. Egg sacs are placed in the retreat and the young remain in the retreat with the mother for several days. One individual was found on transect 2.

Argiope argentata (Fabricius) (female 500 mg) is a forest-edge and clearning species. I found it only on transect 1. Many aspects of the behavior and ecology of this spider are described in Robinson (1969), Robinson and Robinson (1970), and Robinson and Olazarri (1971).

Other Araneidae. Five species of orb-web spiders which could not be identified to genus, and were not collected, occurred rarely on the transects.

Uloboridae–Many spiders in this family construct hackled-band orb webs in which the sticky spiral of the araneid orb web is replaced by a cribellar silk spiral. The species were easily distinguished by the form of the web and the egg sac.

Uloborus sp. 1 (female 10 mg) is an elongate, stick-mimicking spider which rests on its horizontal orb web during the day in a cryptic position with legs I and II extended forward and Legs IV extended backwards. The web often has a linear stabilimentum of whitish silk.

Uloborus republicanus (Simon) (female 20 mg) is a colonial species, though solitary individuals were found occasionally. Colonies are located near the ground, in slightly open spots in the understory. They may contain several hundred individuals and persist for as long as a year (unpublished observations). Females and immatures construct their own orb webs within the framework of the colony; subadult and adult males apparently do not build webs. One large colony persisted on transect 2 from October to December.

Uloborus sp. 3 (female 9 mg). Orb webs of this species are asymmetrical and often clumped. A portion of the web is attached to a leaf or other shelter under which the spider retreats when disturbed. As in the colonial species, males are often found near or in webs of females. This species prefers open habitats.

Miagrammopes simus (Chamberlin and Ivie) constructs a single-line snare. A portion of the line is covered with hackled silk which traps the prey. The web and prey capture behavior are described by Lubin *et al.* (in press). Individuals were found rarely on transects 1 and 2.

Theridiidae

Argyrodes spp. (approx. 3 mg). Two species of *Argyrodes* kleptoparasites or inquilines were found in webs of *Nephila clavipes.* These spiders do not build webs of their own, but steal prey from the host spider.

Argyrodes sp. (close to *longissimus*) sits on a single thread which does not appear to be sticky. The manner in which this spider captures prey is not known; I have found individuals feeding on other spiders.

Tidarren haemorroidale (Bertkau) (female 44 mg). This may include one or two other species of theridiid that construct irregular-mesh tent webs. The web is a "knockdown trap" for flying insects: the insects encounter the vertical threads of the barrier web and are knocked down or drop onto the tent-shaped sheet. The spider sits in a curled-leaf retreat at the apex of the tent. The web is functionally similar to that of *Achaearanea tesselata*, described by Eberhard (1972), and like that of *A. tesselata* it apparently does not contain sticky silk.

Theridiid sp. 2 (approx. 1 mg) includes perhaps several species of tiny spiders that construct irregular-mesh spherical webs. It is not known if the webs contain sticky silk. The spider sits in the center of the web, sometimes concealed under a piece of debris. Webs were generally found in tree crotches or near tree trunks.

Synotaxus ecuadorensis Exline (female 3 mg) is a theridiid which constructs a planar or 2-dimensional, wide-meshed web with an almost radial structure. Parallel, sticky silk radii extend down from a retreat under a leaf and are connected by horizontal threads which are not sticky. Eberhard (in press) has described the structure and web-building behavior of a species from Colombia.

Episinus sp. (female 3 mg) also constructs a planar, open-meshed web below a leaf. The web is smaller and less regular in structure than that of *Synotaxus.*

Other Web-Building Spiders

Theridiosoma sp. (Theridiosomatidae) (less than 1 mg) are probably quite common near the ground in the forest understory, but their tiny webs are fragile and difficult to see. Orb webs of *Theridiosoma* lack the structured hub of araneid webs. These spiders were recorded on transects 2 and 4.

Scytodid (female 7 mg). This spider constructs a rather dense, irregular-mesh, vertical web under leaves. The spider rests under a leaf or on the surface of the web. The web does not appear to be sticky, and may simply serve to alert this agile spider to the presence of an insect on its surface.

Linyphiid (female, male 4 mg). Linyphiids build small, horizontal, sheet webs with a vertical snare above the sheet. The spider rests upside down under the sheet.

Pholcid (approx. 30 mg). These long-legged spiders rest upside down under a loose-mesh sheet web, generally located near ground level. There is usually a retreat under the leaf litter, under a log, or in a crevice. Probably several species were lumped together.

Dinopis longipes Cambridge (Dinopidae), the ogre-faced spider, sits on an A-frame suspension web, facing a vertical surface and holding a square of hackled silk between its first two pairs of legs. It throws this net over insects that walk under it (Robinson and Robinson 1971) and probably specializes in walking rather than flying insects. It was seen once on transect 2.

RESULTS AND DISCUSSION

Seasonality of Web Spiders—The overall seasonal trends in abundance of web-building spiders (Fig. 2) show (1) a sharp decrease in abundance of spiders in the dry season, continuing into early wet season, and (2) two population peaks in the late wet to early dry season and in mid wet season. On transects 2, 3, and 4 there was a smaller increase in total numbers after the first rains at the end of the dry season (April), followed by a decrease at the beginning of the wet season.

Most species of web-building spiders on transect 1 occurred in low numbers or disappeared entirely during the dry season (Fig. 2, Table 3). Only *Metazygia* sp. occurred essentially year-round on transect 1. Transect 2, however, had an equal number of species with essentially year-round and wet season distributions. *Mangora pia, Cyclosa caroli, Synotaxus ecuadorensis,* and the pholcid all occurred primarily during the wet season on transect 1 and year-round on transect 2. These species must be considered primarily shade-loving, forest species for which the clearing edge is unsuitable during the dry season. Likewise, *Landana* sp. had a wet season distribution on transect 2, but occurred throughout the dry season on the forest transect number 4. It did not occur at all on the clearing-edge transect number 1.

Adults and immatures of some species had different patterns of distribution (Table 3). Immature spiders of *Leucauge* sp. 1 and of *Nephila clavipes* had broader seasonal distributions than did the adults. Immatures of both species occurred nearly year-round (absent or in low density during late dry and early wet seasons), while the adults had much more restricted distributions. Adult *Leucauge* peaked in the wet season and adult *N. clavipes* had two disjunct peaks in mid wet and early dry seasons. Immature *Leucauge* were present on transects 1 and 2 respectively on 74.1 and 86.2% of the censuses, while adults were present on only 40.7 and 24.1% respectively. On transect 1, immature *N. clavipes* occurred on 85.2% and adults on 33.3% of the censuses.

Immature Araneidae (orb-web spiders) in general were present year-round on transects 1 and 2. They comprised 30-80% of the total number of Araneidae present on any census (Figure 3). The year-round occurrence of immatures may be attributed to (1) the year-

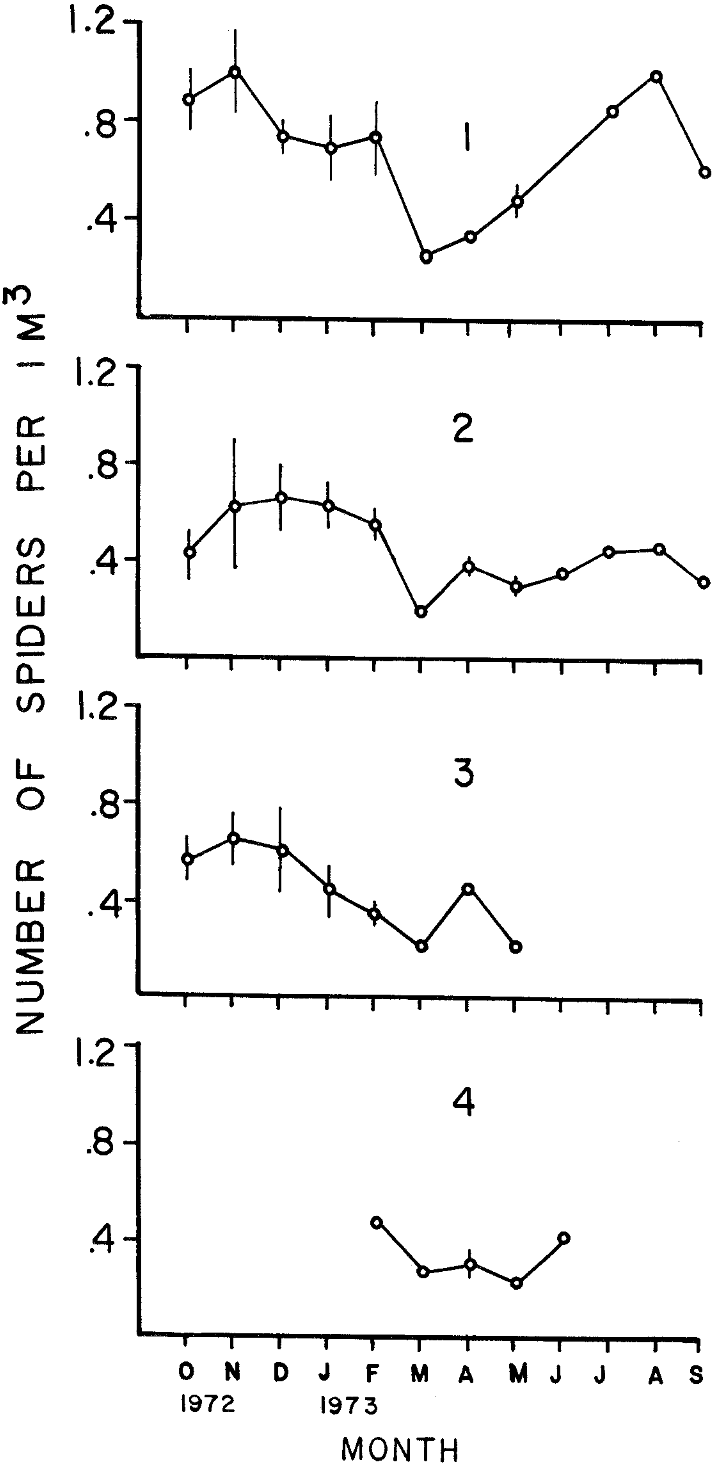

Fig. 2.–Average number of web-building spiders per month on four transects. Vertical lines are one standard deviation.

Table 3.–Occurrence of web-building spiders on transects 1-4. Shown are the transect numbers on which each species was found during the census period, and the total number of individuals recorded (all transects combined).

SPECIES	MONTHS												
	O	N	D	J	F	M	A	M	J	J	A	S	Total No.
Micrathena schreibersi	1	1	12	1					2		1	12	13
M. duodecimspinosa	1	123	123	13	2								27
M. horrida		1	123	13			2					1	19
Micrathena males	123	123	123	1		2	4	2		12		1	73
Pronous tuberculifer		3	23	123	124	2		12	2	2	12	12	35
Nephila clavipes													
adults, subadults			1	12	12	1				12	1		21
immatures	12	1	12	12	12		13	12		2		12	81
males			1	1	12					1	1		20
Leucauge sp. 1, adults		123	123	13	1			2		12	1		53
immatures	123	123	123	123	123	1	123	24		2	12		415
Cyclosa caroli	123	123	123	123	1234	24	234	1234	2	2	1	12	464
Landana sp. 1	23	23	23	23	24	24	4	4	4	2	2	2	112
Mangora pia	12	123	123	123	12	24	2	2	24	12	12	12	96
Eustala sp.	123	12	123	3	13			12		2	12	2	48
Metazygia sp.	123	12	123	123	1234	1	123	1234	2	12	1	2	167
Araneus tuonabo	123	123	123	12	23	4		2		12	12	12	105
Eriophora nephiloides			1	23	123	1	4	12		1			14
Uloborus sp. 1	123	123	123	2	234	23	24	234	2	2	2	2	352
Uloborus sp. 3	123	123	123	123	1234	124	1234	3	4	12	12	12	679
Argyrodes spp. inquilines	1			12	12	1				2	1		42
A. longissimus	3	123		12			2				2		21
Tidarren haemorroidale	123	123	123	123	123	134	1234	1234	4		2	2	244
Theridiid sp. 2	123	123	123	123	1234	1234	1234	1234	24	12	2	2	1914
Synotaxus ecuadorensis	123	123	123	23	234	3	2	12	24		2	12	70
Episinus sp.	23	123	2	23	2			23	2	2	12	2	28
Scytodid			23	23	1234	124	234	24	2	12	2		121
Linyphiid	123	23	23	23	3	23	23	13		2	1		70
Pholcid	123	123	123	123	1234	234	234	24	2	12	1	2	384

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. *Cyclosa* sp. may be typical of a spider with the first reproductive strategy. Adults and immatures were present year-round on transect 2 and it is probable that reproduction occurred throughout the year. *Nephila clavipes* may exemplify the second strategy of long development periods of immatures coupled with pronounced adult seasonality. Adult *N. clavipes* were absent from transect 1 during April-May and September-November. Immatures were present during these periods and may have been derived from egg clutches laid in February-March and July-August respectively. Another possibility is that adult *N. clavipes* are, in fact, present at very low population densities during the periods of absence from transect 1 and that offspring produced during these periods migrated into the census area. The census data suggest that immigration onto transect 1 did occur during October and November; numbers of immatures in successive weeks during this period were 8, 9, 2, 2, 1, 3, 1, and 2.

It is not immediately apparent why adults should be more restricted seasonally than immatures, as is the case in *N. clavipes* and *Leucauge* sp. 1. The negative correlation found between body size and rate of water loss in spiders (Anderson 1974) would lead one to expect that large spiders (adults) could better withstand the dry season than small spiders (immatures). Janzen and Schoener (1968) found that both small insects and very large insects seemed to drop out as one moved from wetter to drier sites in Costa Rica.

Food may be an important limiting factor at certain times of year. Data from light-traps on BCI suggest that small- and medium-size flying insects (up to 15 mm body length) are least abundant during the periods of September-November and February-April, corresponding to late rainy season and late dry season respectively (Smythe 1974b). The dry season decrease corresponds to a period of low spider populations on the transect lines. The wet season decrease corresponds roughly with the disappearance of certain species, e.g., adult female and male *N. clavipes, Pronous tuberculifer,* and the scytodid.

There were no species with strictly dry season distributions on any of the transects, although the araneid *P. tuberculifer* and *N. clavipes* adults, and the scytodid and linyphiid, had both wet and dry season population peaks. The absence of these species during the late wet season may be related to food supply as suggested above, or to other factors. *Pronous*, for example, is a small orb weaver which places its web in open spots very near the ground; such a web may be easily damaged by heavy rains.

Web Type and Seasonality—Seasonal abundance patterns correlate broadly with web type. Webs are divided here into two- and three-dimensional structures. Specialized webs form a third, nonuniform category which includes the single-line snare of *Miagrammopes*, the throwing net of *Dinopis*, and the kleptoparasites, *Argyrodes* spp. which have no web of their own but steal prey from the host web. The orb-web species include all the Araneidae, *Theridiosoma*, and the cribellate orb weavers of the genus *Uloborus*. Two-dimensional, nonorb webs (planar webs) are those of the theridiids *Synotaxus* and *Episinus*, and the scytodid. Space webs include those of the theridiids *Tidarren haemorroidale* and theridiid sp. 2; the sheetweb builders are the linyphiid and the pholcid. These groups are not uniform in size or composition: the orb weavers include many species, while the other categories have relatively few species. Furthermore, there is probably greater similarity in web structure and function among the orb weavers than among the species grouped in other categories.

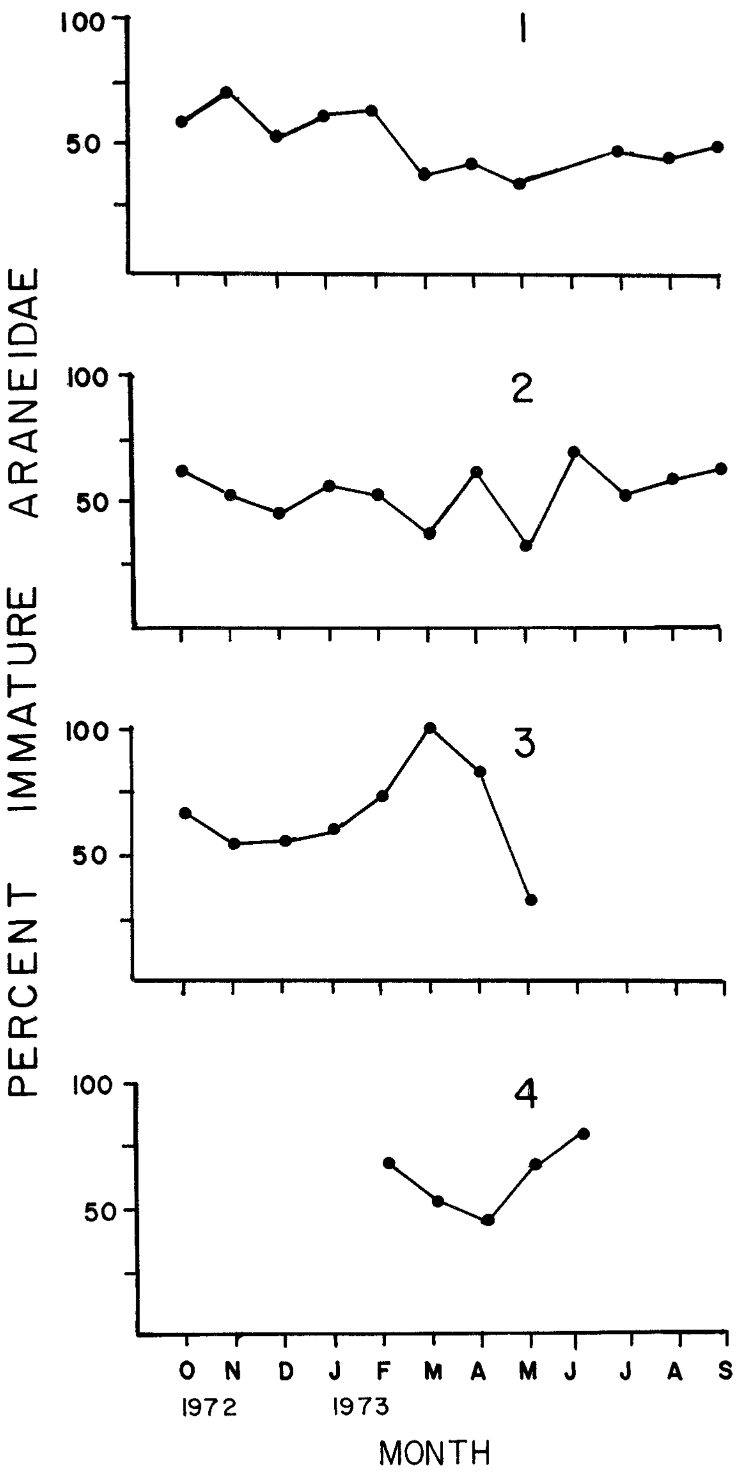

Fig. 3.–Percent of immature Araneidae occurring on four transects, expressed as percent of the total number of Araneidae.

In Fig. 4, I compare the relative abundance of the different web types on transects 1 and 2 in November and April, during late wet and late dry seasons respectively. Orb-web species decreased in relative abundance in April on both transects and, concomitently, space webs increased in importance. Planar webs and sheet webs disappeared from transect 1 in the late dry season, and increased in relative abundance on transect 2.

Most orb-web spiders rest at the hub of the orb during the day and are susceptible to heating and desiccation. Larger orb weavers, such as *N. clavipes*, exhibit behavioral thermoregulation when exposed to direct sunlight (Robinson and Robinson 1974b). Small orb weavers, however, would be more prone to desiccation due to a greater surface/volume ratio. Webs of orb weavers are generally fragile (with the exception of those of *Nephila*) and may be easily damaged or destroyed by falling leaves and branches.

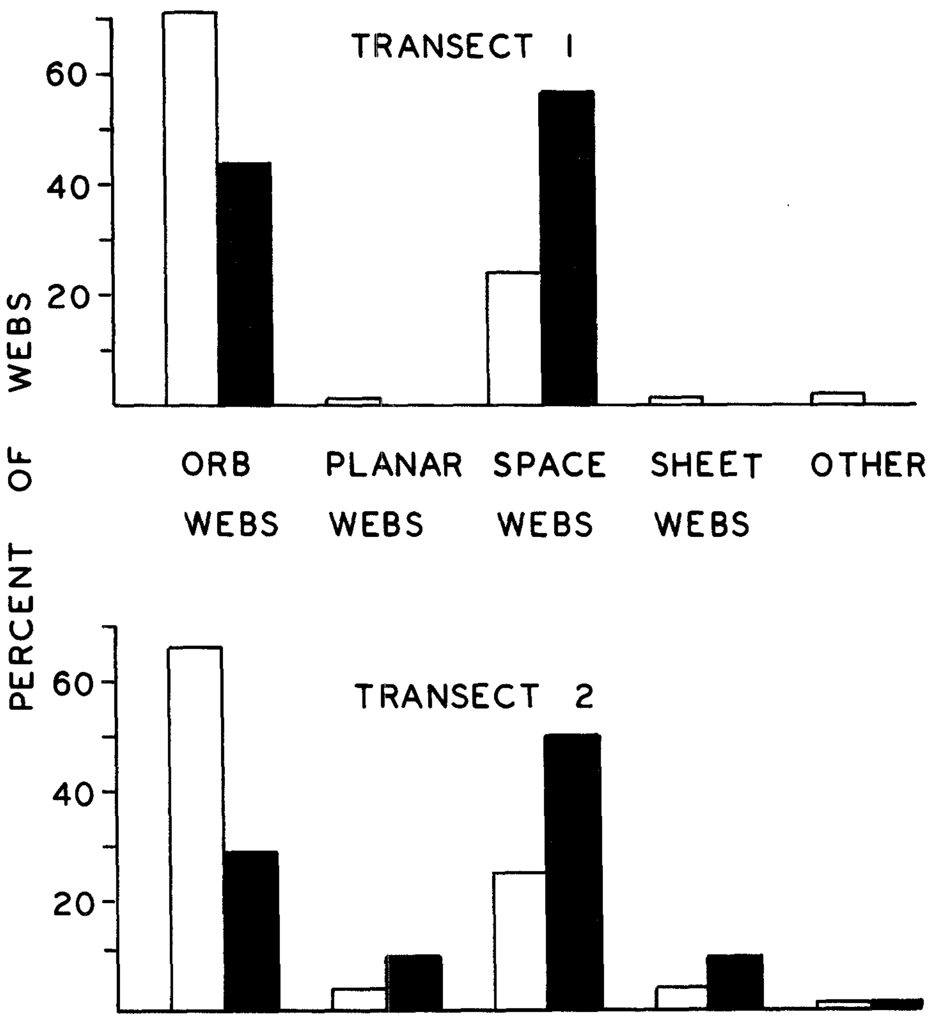

Fig. 4.–Percent of occurrence of different web types on transects 1 and 2 in November and April, expressed as percentages of the total number of webs found on the transects during these months. In November there were 350 webs on transect 1 and 413 on transect 2. In April there were 23 webs on transect 1 and 121 on transect 2.

Dust and pollen may coat the viscid spiral of araneid webs and reduce their effectiveness. These factors may be partly responsible for the decrease in abundance of orb webs during the late dry season. In fact, the decrease in total abundance of web-building spiders during the late dry season was due almost entirely to the drop in numbers of orb-web species.

The argument presented above does not apply to planar, nonorb species or to nocturnal orb weavers. *Synotaxus* and *Episinus* both rest under leaves during the day and are most active at night; the scytodid web is durable and nonsticky and the spider sits in a silk retreat under a leaf. Nocturnal araneids, as well as the diurnal *Spilasma*, sit in retreats during the day. All of these species are less exposed to the dry seasons' adverse conditions.

If flying insects are in short supply during the late dry season, as suggested earlier, then seasonal changes in the distribution of web types may be related to food supply. Most orb weavers renew their webs daily. The actual cost of web construction is relatively small, perhaps as little as 1% of the total energy intake, assuming a cost of 1.1 cal per 0.1 mg web (Peakall and Witt 1976, Prestwich 1977) and approximately 80 cal of food per day assimilated by a 1-g spider (Robinson and Robinson 1970). Nonetheless, in order to renew the web daily, orb weavers need a constant and predictable food supply which may not be available during the late dry season. The cost of web building for an orb weaver may remain constant even during periods of food shortage. *Araneus diadematus*, for example, builds webs of more-or-less constant size even after a week of food deprivation (Witt *et al.* 1968). Space-web and sheet-web spiders, by comparison, renew their webs infrequently and therefore do not have the daily energy demand of the orb weaver. *Filistata hibernalis*, a spider with a durable, nonrenewed, sheet web, reduced its metabolic rate by about 40% during starvation and survived for extended periods (Anderson, 1974). Comparable tests with orb weavers would be worth doing.

Species Diversity, Seasonality, and Habitat Structure—On the basis of the total numbers of species found throughout the census, the transects are ranked in order of descending numbers 2>1>3>4 (Table 4). This ranking is consistent with earlier impressions of vegetation structure and availability of web supports (Methods, p. 32). Transect 2 had the largest number of web-supporting structures, and both transects 1 and 2

Table 4.—Number of species of web-building spiders encountered on transects 1-4: yearly totals, average numbers per census, and range. Averages ± 1 standard deviation are shown for three periods of high and low spider densities (transects 1 and 2 only): High 1 = October-February, Low = March-June, High 2 = July-September.

	Transects			
	No. 1	No. 2	No. 3	No. 4
Total	31	36	25	17
Average per census	11.3 ± 2.6	14.7 ± 3.1	11.05 ± 2.8	9.0 ± 1.7
Range	5-16	9-20	6-15	6-11
High 1	11.8 ± 2.4	14.8 ± 3.3		
Low	8.25 ± 2.6	13.0 ± 1.9		
High 2	11.75 ± 2.4	18.3 ± 0.6		

Transect 1: High 1 vs. Low, t = 5.3115, $p < 0.001$
High 2 vs. Low, t = 2.6205, $0.02<p<0.05$
Transect 2: High 1 vs. Low, t = 2.4340, $0.02<p<0.05$
High 2 vs. Low, t = 8.0643, $p<0.001$

showed a more pronounced "forest-edge effect," with increased structural diversity at the ecotone, than did transects 3 and 4.

The numbers of species present on the transects were high during periods of high spider density and low during periods of low spider density (Table 4). During the latter period (March through June) transects 1 and 2 had significantly fewer species than during the two high-density periods. The high- and low-density periods, and therefore high- and low-diversity periods, correspond only roughly to wet and dry seasons based on rainfall data. In fact, after dividing the census period into wet and dry seasons (October-December, January-April, and May-September), I found no significant differences in species diversity between these seasons. Since the interactions between climate and the life histories of spiders are undoubtedly complex, one would not expect either abundance or diversity to correlate directly with season as defined solely by climatic data. This was also the case in temperate-zone wandering spiders (Uetz 1975) and in tropical montane rain-forest insects (Buskirk and Buskirk 1976).

Shannon-Weaver diversity indices (Pielou 1966) were calculated using the yearly totals of all species (Table 5). The index of diversity ($\bar{H}$) is greatest on transect 2, and considerably higher on both 1 and 2 by comparison with transect 3. This is apparently a function of both more species and a more equitable distribution of abundances (E) among the species. This supports the view that species diversity of web spiders is influenced to a large extent by structural diversity of the habitat.

The Shannon-Weaver index of diversity is valid only when sample sizes are large, and the total number of species is known (Pielou 1966). The species discovery curves for the four transects (Figure 5) show that this is approximately true for transects 2-4, but not the case on transect 1, where the curve shows no sign of leveling. These curves also suggest that in order to sample rare species of web-building spiders in a tropical wet forest habitat, one needs a very large area indeed. The shape of these curves is typical of species discovery curves of many groups of tropical organisms (Janzen 1973).

The number of species encountered often varied considerably from one census to the next; for example, transect 1 had 9, 15, 10, and 10 species on four successive censuses in January 1973. Such differences are to be expected if many species occur in low densities and/or for short durations. Although it is not possible with these data to separate these two factors, they undoubtedly both contribute to species rareness.

Table 5.—Species diversity of spiders on three transects: Shannon-Weaver index ($\bar{H}$), maximum diversity ($\bar{H}_{max}$), and equitability (E) indices (Pielou 1966) based on yearly totals of species on transe transects 1-3. s 1-3.

	Transects		
Diversity Index	No. 1	No. 2	No. 3
$\bar{H}$	3.568	3.717	2.518
$\bar{H}_{max}$	4.954	5.170	4.644
E	0.72	0.72	0.54

The majority of the species of web-building spiders were recorded at least once on all transects. Over the entire census year, transects 1 and 2 shared 93% of the species, transects 2 and 3 shared 83% and transects 1 and 3 shared 65%. During a period of high spider abundance (November) the transects had more species in common than during a period of low abundance (February-March) (Table 6). During the latter period, many species disappeared selectively from one transect, but not from another.

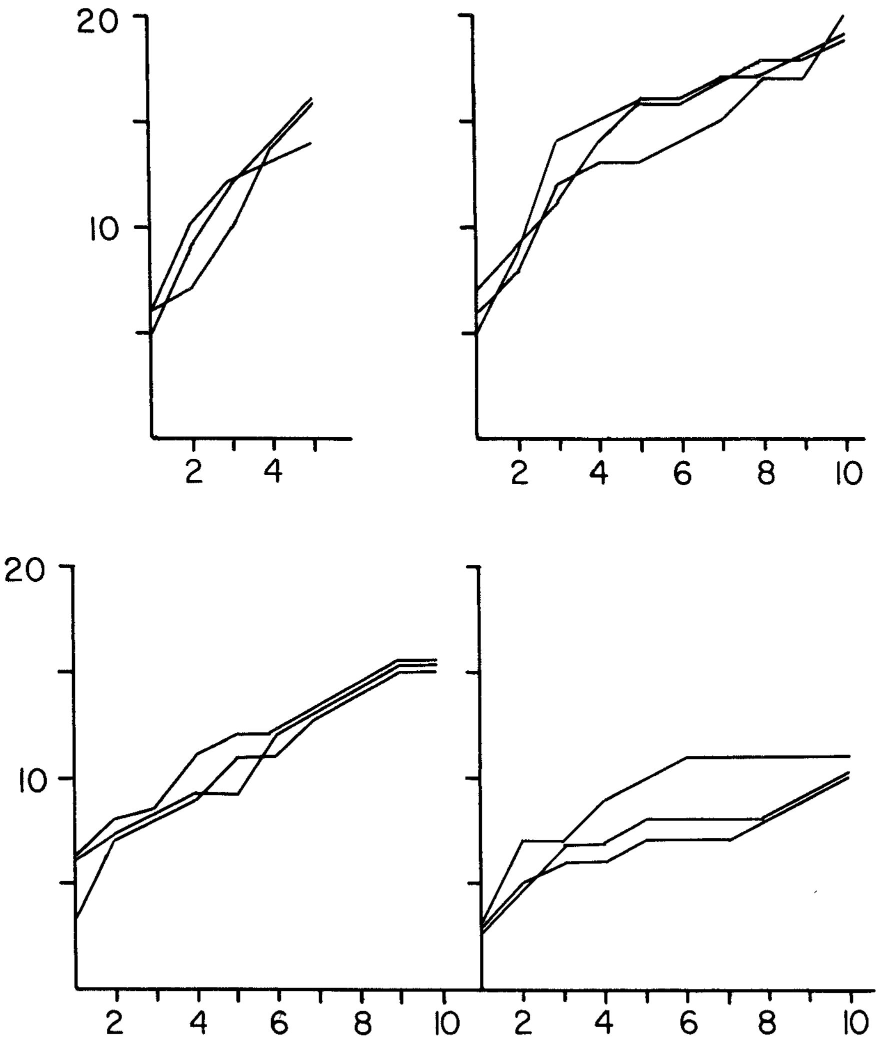

Fig. 5.–Species discovery curves: cumulative numbers of species encountered on successive 10 m sections along transects 1-4. Curves are shown for three dates with the highest numbers of species: transect 1–20 Nov., 25 Dec., 15 Jan.; transect 2–27 Nov., 12 Dec., 25 Dec.; transect 3–13 Nov., 4 Dec., 12 Dec.; transect 4–27 Feb., 23 Mar., 8 Apr.

Coefficients of similarity between the transects were lower in February-March than in November (Table 6). These differences were not statistically significant, with the exception of transects 1 and 2 ($t=3.29$, $0.01<p<0.02$). The coefficient of similarity takes into account the abundances of species in common, and thus gives greater weight to the numerically dominant species (Kershaw 1964). Most similar were transects 1 and 2 during November, and the two forest transects, 2 and 3, in both November and February-March. The similarity between the wet season faunas of transects 1 and 2 may be related to (1) the high overall abundance of spiders and greater possibility of movement of spiders

Table 6.–Percent of species overlap on transects 1, 2, and 3 (Number of species in common x 100/Total number of species), and coefficients of similarity, C=2w/a+b, where *a* and *b* are the numbers of individuals of all species found on the two transects, and *w* is the sum of the lesser values of the species common to the two transects (Kershaw 1964:165). Shown are percent species overlap for four censuses combined in November and four in February and March; coefficients of similarity are means of the four censuses in each period ± 1 standard deviation.

Transects	November		February-March	
	% overlap	C	$ overlap	C
1 and 2	69.6	0.51 ± 0.06	58.3	0.34 ± 0.11
1 and 3	62.5	0.39 ± 0.01	55.0	0.25 ± 0.004
2 and 3	68.2	0.47 ± 0.07	54.2	0.47 ± 0.01

between the two transects, and (2) a greater similarity in habitat structure during the wet season, namely the presence of a well-developed herbaceous layer on both transects.

BCI and New Guinea: A Comparison–Populations of web-building spiders at Wau, New Guinea, and on BCI reflect the favorable climatic conditions of moist tropical habitats in that there is no season that is entirely unsuitable for spiders (Robinson *et al.* 1974). Fluctuations in total population size were of the same order of magnitude and did not exceed threefold at either locality. Adults and immatures occurred year-round and even the most seasonal species (e.g., *Nephila clavipes* on BCI) had overlapping generations. The implications of year-round occurrence and overlapping generations are discussed by Robinson *et al.* (1974) in terms of allowing a large number of biotic interactions or links between a given species and other species in its environment, and thereby contributing to greater species diversity.

Both census localities have distinct wet and dry seasons, but the dry season is very much more pronounced on BCI. Although total rainfall over the census period was similar at the two localities, rainfall was distributed more evenly over the year at Wau than on BCI. The driest month at Wau (August) had 28 mm of rain, while on BCI the driest month (March) had only 5 mm. Total rainfall during the four driest months at Wau was 279 mm (June-July, August-September) and only 91 mm on BCI. Furthermore, the driest month at Wau was preceded by a relatively wet month with over 100 mm of rain.

Daily temperature fluctuations were greater at Wau (10-12°C) at about 1150 m altitude than at BCI (7-10°C in the clearing and 4-8°C in the forest) at an altitude of 50-100 m. The differences between daily minimum and maximum temperatures were greatest in both places at the end of the dry season or early wet season.

On all of the Wau transects there was a preponderance of species with abundance peaks during the drier months, whereas on the BCI transects there were virtually no web-building species that peaked in abundance during the dry season. Most species on the BCI transects had essentially wet season distributions, and some had population peaks corresponding to mid wet season and late wet or early dry seasons. I suggest that the dry season is a critical period on BCI, and that population sizes are limited during this period due to food shortage and/or desiccation. At Wau, there is probably sufficient moisture throughout the dry season to permit continued activity and reproduction in web spiders. Insect-trap data suggest that insect prey are available year-round (Robinson and Robinson 1973, Lubin unpubl.).

A major difference between the two censuses is in the nature of the transects. The Wau transects were all in open, second-growth habitats along forest edge or along the edge of overgrown coffee plantation. Unlike the BCI clearing transect (no. 1), which was quite isolated, they were connected with extensive areas of roadside and second-growth habitat. This difference is reflected in the distribution of web types at the two localities. Thirteen species of non-orb-web builders were found on all BCI transects combined, or 37% of all species, while only 22% of all species on the Wau transects were non-orb-web builders. There were 35 species on all of the BCI transects over the period of the census and only 27 on the Wau transects. In general, there was a greater diversity of web types and more three-dimensional webs on the BCI transects than at Wau. I attribute this difference to the more structured habitat on the BCI transects which provides supports for different web types.

Differences between the physical nature of the Wau and BCI transect lines are also reflected in the actual species composition. *Gasteracantha, Argiope, Leucauge,* and *Tetraganatha* are all early second-growth, forest-edge genera; on the Wau transects there were four species of *Argiope*, and two of *Gasteracantha. Leucauge* and *Tetragnatha* were abundant. On the BCI census lines only *Leucauge* sp. 1, *Nephila clavipes*, and *Argiope argentata* can be considered true clearing species. *Argiope* was rare and occurred only on transect 1 (the clearing transect), and *Nephila* was found in low densities on transects 1 and 2, but more commonly on transect 1. *Leucauge* seems to be a truly versatile spider and invaded the forest paths with great success, but nonetheless was most abundant along the clearing edge. A substantial number of species found on the BCI transects are entirely or primarily forest-dwelling species. These are *Micrathena schreibersi, M. clypeata, Pronous tuberculifer, Landana* sp., *Eriophora nephiloides, Spilasma* sp., *Miagrammopes simus,* and *Synotaxus ecuadorensis.*

Although clearings and forest-edge habitats may be less favorable for some species, these habitats tend to support higher densities of spiders than do inside-forest habitats. On BCI the highest densities of web-building spiders were recorded on transect 1, with a maximum of 1.1 spiders per 1 m^3 in November. Maximum spider densities on the forest transects on BCI were slightly lower: 0.6 spiders per 1 m^3 on transects 2 and 3, and 0.4 on transect 4. Maximum population densities on the Wau transects were of similar magnitude to that of BCI transect 1, approximately 0.75, 1.2, and 1.3 spiders per 1 m^3 on the three transects (assuming each transect is $2 \times 2 \times 100 = 400$ m^3). Robinson and Robinson (1974a) estimated a higher density yet (2.9 spiders per 1 m^3) of diurnal web builders inside a coffee plantation in Wau in July 1974.

There is evidence suggesting that insect abundance and diversity are higher in mid-elevation, tropical montane rain forest than in comparable lowland forest (Janzen 1973, Buskirk and Buskirk 1976). The difficulty is in finding comparable habitats at different altitudes. The Wau and BCI censuses indicate less fluctuating and perhaps more evenly distributed populations of web-building spiders in the montane habitat, but not necessarily larger or more diverse. The differences are complicated by the fact that the Wau census was in second-growth habitat and the BCI census in forest understory. The July, 1974, daytime census (Robinson and Robinson 1974a) in a coffee plantation, which is closer in vegetation structure to a forest understory, yielded approximately 18 species of web spiders, a figure comparable to the highest species counts on the BCI transect 2. It also yielded higher population estimates than any of the BCI transects. From this, one can only conclude that generalizations about arthropod abundance and diversity in montane versus lowland tropical habitats may be premature.

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